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Landscape connectivity: a key to effective habitat restoration in lowland agricultural landscapes

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Abstract

Landscape scale habitat restoration has the potential to reconnect habitats in fragmented landscapes. This study investigates landscape connectivity as a key to effective habitat restoration in lowland agricultural landscapes and applies these findings to transferable management recommendations.

The study area is the Stonehenge World Heritage Site, UK, where landscape scale chalk grassland restoration has been implemented. Here, the ecological benefits of landscape restoration and the species, habitat and landscape characteristics that facilitate or impede the enhancement of biodiversity and landscape connectivity were investigated.

Lepidoptera were used as indictors of restoration success and results showed restoration grasslands approaching the ecological conditions of the target chalk grassland habitat and increasing in biodiversity values within a decade. Restoration success is apparent for four species with a broad range of grass larval host plants (e.g. *Melanargia galathea, Maniola jurtina*) or with intermediate mobility (*Polyommatus icarus*). However, two species with specialist larval host plants and low mobility (*Lysandra bellargus*), are restricted to chalk grassland fragments.

Studies of restoration grassland of different ages show that recent grassland restoration (1 or 2 years old) may reduce the functional isolation of chalk grassland fragments. A management experiment showed that mowing increases boundary following behaviour in two species of grassland Lepidoptera; *Maniola jurtina* and *Zygaena filipendulae*.

Analysis of the landscape scale implications of the grassland restoration illustrates an increase in grassland habitat network size and in landscape connectivity, which is likely to benefit the majority of grassland associated Lepidoptera.

Landscape and habitat variables can be managed to increase the success of restoration projects including the spatial targeting of receptor sites, vegetation structure and selection of seed source and management recommendations are provided that are transferrable to other species-rich grassland landscape scale restoration projects.

Overall results show restoration success for some habitats and species within a decade. However, additional management is required to assist the re-colonisation of specialist species. Despite this, habitat restoration at the landscape scale can be an effective, long term approach to enhance butterfly biodiversity and landscape connectivity.

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Declaration

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Grace Twiston-Davies, September 2014

Contents

Chapter 1 Introduction

1.1 Ecological networks and landscape connectivity

1.1.1 Why we need ecological networks; habitat fragmentation and climate change

Habitat loss and fragmentation can reduce insect biodiversity (Davies *et al.* 2000; Larsen *et al.* 2005), is a driver of current global pollinator declines (Potts *et al.* 2010) and changes community compositions (Barbosa & Marquet 2002; Davies *et al.* 2000; Ewers *et al.* 2007; Major *et al.* 2003). Changes in community compositions are due to the decline of fragmentation-sensitive species (Davies *et al.* 2000; Larsen *et al.* 2005), in the reduced population and increased probability of extinction (Driscoll & Weir 2005) which reduces biodiversity (Larsen *et al.* 2005) and changes trophic interactions (Tscharntke & Brandl 2004; Valladares *et al.* 2006). However, some of these negative effects can be reversed through conservation actions and there is evidence to show that species richness declines have been reversed for bees in Great Britain and the Netherlands (Carvalheiro *et al.* 2013). Additionally, some insect species may benefit from or are unaffected by fragmentation, specifically those that are more mobile and less specialised in host-plant and habitat requirements (Driscoll & Weir 2005; Woodcock *et al.* 2012b).

Future climate change could increase the negative effects of habitat fragmentation on invertebrate species biodiversity (Gonzalez-Varo *et al.* 2013), although some species may benefit from an expanding range margin (Lawson *et al.* 2012). For example, half of the butterfly species that are mobile and habitat generalists at the Northern limit of their range in the UK, have increased their distribution in 30 years in response to climate change (Warren *et al.* 2001). Some species, populations and individuals will face extinction, adaptation or migration in response to climate change and these ecological and evolutionary responses are already apparent (Thomas *et al.* 2001a). Adaptation and migration in response to climate change can be at the cost of important host-plant associations (Parmesan 2007; Schweiger *et al.* 2008) and reproductive potential (Gibbs *et al.* 2010; Gibbs & Van Dyck 2009; Hughes *et al.* 2003). To illustrate this, butterfly larval emergence is adapting more quickly to climate change than plants with earlier emergence times and this could disrupt trophic interactions (Parmesan 2007). For example, the monophagous Purple Bog Fritillary butterfly (*Boloria titania*) could lose as much as 88% of its range as its larval host-plant is unable to expand its range in response to climate change (Schweiger *et al.* 2008). Adaptations relating to increased dispersal ability have enabled some butterfly species (for example, Speckled Wood, *Pararge aegeria*) to respond to the movement of their suitable habitat due to climate change, but at the expense of reproductive success (Gibbs *et al.* 2010; Gibbs & Van Dyck 2009). Many populations have shifted distributions where a shift to high latitudes and altitudes is evident for butterflies and their communities in under 50 years (Chen *et al.* 2009; Hickling *et al.* 2006; Hill *et al.* 2002; Van Swaay *et al.* 2010; Wilson *et al.* 2007). Climate change and habitat fragmentation are likely to act synergistically, worsening these effects, for example, the Silver-spotted Skipper (*Hesperia comma*) is predicted to occupy just a small fraction of suitable habitat patches in the United Kingdom (UK) in 100 years time with as little as 11% of tetrads (2 km by 2 km squares) predicted to be occupied due to the effects of climate change, habitat fragmentation and landscape barriers (Wilson *et al.* 2010) and habitat specialists will be at most risk from this effect (Warren *et al.* 2001).

1.1.2 What are ecological networks

Ecological networks which connect habitat fragments are advocated widely and as a management practice supported by policy for mitigating habitat fragmentation and facilitating spatial adaptation to climate change (Baguette *et al.* 2013; Lawton *et al.* 2010; Lindenmayer *et al.* 2008; McIntyre & Hobbs 1999). These are being implemented at European and National scales through the Pan-European Ecological network and the Joint Nature Conservation Committee (ECNC 2010; JNCC 2010). An example of a projects is the Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales (SCALES 2014) which includes recent research on species distributions, effects of climate change and pollinator networks across large spatial scales and community assembly (de Bello *et al.* 2012; Guisan *et al.* 2013; Marini *et al.* 2013; Travis *et al.* 2013).

There are differences between structural and functional networks in ecology; structural networks refer to a network of similar habitat type patches or vegetation structure whereas, functional networks take into account the dispersal distances of the target species or group and the landscape including the intervening matrix between habitat patches. Landscape connectivity is another concept used to describe functional network which includes the behaviour of the target organisms and the degree to which landscape they occur in facilitates or impedes movement between habitat patches (Taylor *et al.* 1993; Tischendorf & Fahrig 2000). Ecological networks aim to functionally link isolated populations in order to conserve biodiversity and stabilise ecosystem services providing some degree of conservation management insurance in the face of future uncertainty. There is a powerful argument for a landscape restoration approach to expand and buffer existing habitat fragments, create new habitat, increase the permeability of the intervening matrix and act as stepping stones and corridors through the landscape (Lawton *et al.* 2010; Pfadenhauer 2001).

The wider landscape priority is important as it combines many aspects including conservation, culture and heritage and is important for the long term persistence of semi-natural grasslands for example (Lindborg *et al.* 2008). The restoration and enhancement of a functionally connected ecological network will require landscape scale restoration involving a combination of habitat restoration and re-creation as well as matrix enhancement.

1.2 Landscape restoration theory

1.2.1 Landscape scale restoration methods

Landscape scale restoration has the potential to mitigate the negative impacts of habitat loss, degradation and fragmentation. However, the main issues are the temporal and financial commitment needed, conflicts arising from the need for collaboration and cooperation of many land owners and stake-holders, the constraints and objectives of the coordination method e.g. Agri-environment schemes and New Environmental Land Management Scheme as well as what type of habitat and for what target species (Andersson *et al.* 2013; Fuentes-Montemayor *et al.* 2011; Menz *et al.* 2013; Pocock *et al.* 2012; Pywell *et al.* 2012; Young 2000). Agri-environment schemes can be an effective mechanism to increase landscape connectivity (Donald & Evans 2006) and habitat creation specifically, has been shown to increase plant, bee and bird species diversity and abundance when it is targeted to the ecological requirements of the target taxa (Pywell *et al.* 2012). However, not all insect groups will respond in the same way to farm management and not all Agri-environment methods will increase the diversity and abundance of the target insect group (Andersson *et al.* 2013; Fuentes-Montemayor *et al.* 2011; Pocock *et al.* 2012). There are many methods for landscape scale restoration involving increasing the quality of current habitat patches, protecting them, expanding them, and linking them as well as creating new habitats and managing the matrix land cover that separates them.

1.2.2 How to re-create species-rich temperate grasslands?

There are three commonly used methods to create species-rich grasslands: natural regeneration; seed mixtures (either commercial or sourced from a local area) and hay strewing where hay is collected from a local area and transferred to the field, area of landscape under restoration.

Natural regeneration of grassland creation is the most cost-effective method for habitat restoration, but can be inefficient due to the lack of adequate soil seed banks or adjacent seed sources required to restore plant communities (Poschlod *et al.* 1998; Pywell *et al.* 2002; Pywell *et al.* 2003). The lack of soil seed banks limits much of the chalk grassland restoration in the UK (Fagan *et al.* 2010) and is especially problematic in fragmented patches where adjacent seed sources are not available (Plue & Cousins 2013).

The creation of species-rich grasslands on ex-arable lands is successful when seeds or seed containing plant materials (for example, hay) are transferred to bare soil (Kiehl *et al.* 2010). Habitat restoration using locally sourced seed mixtures has been especially successful when used to restore species-rich grasslands (Pywell *et al.* 2002; Walker *et al.* 2004), a technique which overcomes some of the problems associated with habitat fragmentation and reduces the establishment of weedy plant species from seed rain (Mortimer *et al.* 2002). Hay strewing can overcome some of the limitations of species-rich grassland restoration due to the isolation of restoration habitat patches from reference habitat patches and the low dispersal abilities of some target species, and has been effective in restoring not only plant communities, but also their associated invertebrates (Woodcock *et al.* 2008; Woodcock *et al.* 2010).

Species-rich grassland plant communities that share similar species to the reference community can be apparent in about 10 years from the start of re-creation (Conrad & Tischew 2011; Kiehl & Pfadenhauer 2007; Mitchley *et al.* 2012) and invertebrate species characteristic of the target habitat can colonise in as little as two years (Deri *et al.* 2011). However, these restored or re-created grasslands lack many of the plant species characteristic of the reference habitat patches (Conrad & Tischew 2011; Kiehl & Pfadenhauer 2007; Mitchley *et al.* 2012) and it may be decades before the precise target botanical conditions are reached (Fagan *et al.* 2008). This means that restoration grasslands may not be suitable habitat for some specialist insect species for many years.

The management of species-rich grasslands is vital as this type of habitat is a mid-succession stage requiring management to conserve and enhance species diversity and to halt encroachment from scrub. Sheep or cattle grazing is highly advocated (Poschlod *et al.* 1998) as well as frequent mowing and topping in early years to restrict the fast growing weedy plant species. But the precise restoration and management methods advocated for successful species-rich grassland restoration are case specific and depend on the budget of the project, the target species (plants and/or animals) and the objectives of the stakeholders (Kiehl *et al.* 2010).

1.2.3 What to restore?

1.2.3.1 Habitat quality

Conservation actions and management for invertebrates have been mainly implemented based on traditional island biogeography and metapopulation theory (Hanski 1998; MacArthur & Wilson 1967) whereby increasing the size of habitat patches and reducing their distance from one another are prioritised. There is still much support for the area and extent of habitat patches as the focus of conservation efforts (Hodgson *et al.* 2011; Hodgson *et al.* 2009; Prevedello & Vieira 2010). However, the amount of habitat present within a dispersal radius of a target species or group may be the most important aspect to consider rather than the size of patches and their isolation (Fahrig 2013).

Increasing the quality of a habitat patch is also vital as this can increase the carrying capacity of a patch, allowing it to support larger and more stable butterfly populations (Fleishman *et al.* 2002) and increasing immigration (Baguette *et al.* 2011), and this may be more important than increasing patch area or connectivity (Fleishman *et al.* 2002). The quality of habitat patches determines butterfly distributions in fragmented landscapes and can contribute more to species persistence than area or isolation (Thomas *et al.* 2001b; WallisDeVries & Ens 2010). In the UK, habitat patch occupancy is better explained by habitat quality than patch isolation for the butterflies, Glanville Fritillary (*Melitaea cinxia*), Adonis Blue (*Lysandra bellargus*) and Lulworth Skipper (*Thymelicus acteon*) (Thomas *et al.* 2001b) and was the main limiting factor for the colonisation of Lepidoptera to heath land restoration patches, mainly due to the lack of host-plants (WallisDeVries & Ens 2010).

Habitat quality and the characteristics of the surrounding landscape can interact, whereby the effect of the landscape context on species-richness of invertebrates can depend on the quality of habitat patches (Kleijn & van Langevelde 2006). For example, habitat quality as measured by flower abundance only had a positive effect on hoverfly richness when there were lots of habitat patches in the landscape but was more important for bee species-richness in landscape with few habitat patches (Kleijn & van Langevelde 2006).

Landscape factors, including the characteristics of the matrix, may be more important than patch characteristics for mobile insects (Haynes *et al.* 2007b). Additionally, restoration actions that focus on the habitat patch may not be appropriate if some resources are located in the matrix. For example, butterflies use complementary and supplementary resources such as larval host plants, nectar plants, shelter, protection and microclimate, that may not all be located within the boundaries of the habitat patch (Dennis *et al.* 2003; Ouin *et al.* 2004). Additionally, resources such as bare ground, leaf litter and varied or particular vegetation height provide important resources and microclimate for courtship, oviposition, thermoregulation and camouflage for butterflies (Beyer & Schultz 2010; Lawson *et al.* 2014; NCC 1986; Thomas *et al.* 2009). This means that consideration of the densities of specific resources rather than land-cover type is more appropriate for butterfly conservation (Dennis *et al.* 2003). Therefore, restoration and conservation cannot just focus on habitat patches alone: resources may occur in both the habitat patch and the matrix and therefore a landscape scale approach is required.

1.2.3.2 Habitat heterogeneity

Managing habitats for heterogeneity can provide more resources and micro-habitats in a patch which can increase niche space thereby supporting more populations within a given area. It may therefore be a vital consideration for insect conservation (Benton *et al.* 2003; Davies *et al.* 2007; Shreeve & Dennis 2011). It is especially crucial because response to fragmentation is species-specific and therefore habitat heterogeneity can provide a range of resources to accommodate different requirements as well as insurance against future environmental uncertainty.

Examples of habitat management for habitat heterogeneity include that for the vulnerable butterfly Scotch Argus (*Erebia aethiops*) which prefers highly heterogeneous habitat as there are sex-specific habitat preferences: males preferred sparse woodlots and females preferred grassland patches (Slamova *et al.* 2013). The Dryad butterfly (*Minois dryas*) uses two different habitat types for resources; wet meadows and xerothermic grasslands and therefore requires conservation actions which manage each habitat differently and enhance a landscape mosaic of both habitat types (Kalarus *et al.* 2013).

Habitat heterogeneity at a landscape scale strongly affects butterfly and bee species-richness (Kumar *et al.* 2009; Steffan-Dewenter *et al.* 2002) and helps maintain stable populations in response to climate change at a landscape level (Oliver *et al.* 2010). Management for habitat heterogeneity does need to be implemented at a range of scales from patch to landscape for example, different pollinator guilds will response to heterogeneity at different spatial scales (Steffan-Dewenter *et al.* 2002) and habitat specialists will respond at a smaller landscape scale than generalists (Oliver *et al.* 2010).

Habitat heterogeneity with the patch, around the patch and at the landscape scale are important to encompass the ecological requirements of a range of species and to cover the scales at which ecological processes occur at. Structural heterogeneity, for example is especially vital for the conservation of specie in calcareous grasslands (Diacon-Bolli *et al.* 2012). At and within the habitat patch scale, structural heterogeneity provides a variety of host plant oviposition and thermoregulation sites (e.g. Beyer & Schultz 2010; Lawson *et al.* 2014; Tropek *et al.* 2013), at the landscape scale, structural and habitat type heterogeneity increases available resources which is especially important for butterflies that use more than one habitat type, for dispersal and to increase the stability of populations (Kalarus *et al.* 2013; Oliver *et al.* 2010; Slamova *et al.* 2013). A key challenge in biodiversity conservation is to match the scale that conservation actions are implemented at with the scale that the ecological processes that they aim to conserve operate at. There is often a mismatch between these ecological processes and policy and management scales specially as governance and administrative boundaries are often smaller than large scale ecological processes such as metapopulation dynamics and ecosystem services (Guerrero *et al.* 2013; Henle *et al.* 2010; Young *et al.* 2005).

1.2.4 Restore and enhance connectivity

1.2.4.1 Corridors and stepping stones

Connectivity can be enhanced using 'corridors' and 'stepping stones', as well as managing the matrix land cover that separates habitat patches. The importance of linear features such as field margins, hedgerows and road verges in fragmented and agriculturally-intensified landscapes has been extensively highlighted in the literature as vital features for colonisation, population dispersal, growth, survival and species-richness (Berggren *et al.* 2002; Driscoll & Weir 2005; Duelli & Obrist 2003; Ockinger & Smith 2007a). These provide important areas for invertebrates. For example, 63% of arthropod species were dependent upon natural and semi-natural remnants for vital resources, including 83% of bee species (Duelli & Obrist 2003). These remnants are also considered as a source for some butterfly species (for example, Small Heath, *Coenonympha pamphilus* and Meadow Brown, *Maniola jurtina*), which act as important pollinators in a highly fragmented intensified agricultural landscape where bee densities and species richness may be restricted due to low availability of appropriate nest sites (Ockinger & Smith 2007b). However, focussing on the enhancement and creation of linear features may have a limited conservation value for mobile insects as they are essentially edge habitat and may not be adequate habitat for some species that required interior habitat conditions . The artificial creation of corridors is a controversial matter especially as a conduit for some species may act as a barrier for others and they are not always utilised by the target insect species (Collinge 2000). For example, corridors were shown to only be marginally effective for less mobile species (June beetle, *Phyllophaga lanceolata*), and were not used by mobile or rare species (Collinge 2000). Also, many experimental studies have assessed corridors on small spatial scales and are restricted to uniform rather than a range of matrix types, limiting the transferability of research findings to real landscapes. Another key issue is that although increased connectivity may increase biodiversity and link populations of threatened or key-stone species, it can also increase connectivity for fire or pest or invasive vertebrate and plant species (Bartuszevige *et al.* 2006; Brudvig *et al.* 2012; Gurnell *et al.* 2006; Wilkerson 2013).

1.2.4.2 Enhancing the matrix

In contrast to traditional island biogeography and metapopulation theory (Hanski 1998; MacArthur & Wilson 1967) which has been the basis of much of habitat fragmentation research, the characteristics of the surrounding matrix are potentially more important than area or isolation for diversity and population persistence in fragmented patches for vertebrates, invertebrates and plants (Prugh *et al.* 2008; Roland *et al.* 2000). Enhancing the quality of the matrix so that it is more 'permeable' is highly advocated. Enhancing matrix permeability can increase the amount of resources that are available to populations in fragments as well as reduce isolation by facilitating movement between fragments.

Landscape scale restoration may provide a more flexible solution than habitat patch focused restoration for biodiversity because enhancing the quality of the matrix can facilitate the movement of species between fragments, consequently increasing the functional connectivity of isolated patches (Reeve *et al.* 2008; Ricketts 2001; Roland *et al.* 2000). Functional connectivity takes into account the dispersal distances of the target species or group and the landscape including the intervening matrix between habitat patches (Tischendorf & Fahrig 2000). This is because individuals are more likely to cross matrix edges that are in less different to the target habitat (Haynes & Cronin 2006) and therefore this will increase immigration and emigration rates (Haynes & Cronin 2003; Haynes *et al.* 2007a). Due to this effect, a more permeable matrix can increase species richness, buffer against the negative effects of isolation (Jauker *et al.* 2009) and support higher species population densities (Haynes *et al.* 2007a). Therefore, the quality of the matrix may be more important than distance or isolation for the conservation of mobile species in fragmented landscapes (Prugh *et al.* 2008), although for plants, and other sessile organisms, isolation can be more important. For example, Wood Cranesbill (*Geranium sylvaticum*) a perennial species with no specialism for dispersal, the impact of the local environment is more important (Pacha & Petit 2008).

The characteristics of the matrix affects the species richness of habitat fragments and can buffer against the negative effects of isolation (Jauker *et al.* 2009) and the composition of the matrix affects the movement of species between fragments subsequently increasing or decreasing the functional connectivity between isolated patches (Reeve *et al.* 2008; Ricketts 2001; Roland *et al.* 2000). A more 'permeable' matrix with a lower contrast to the fragmented habitat will increase immigration and emigration rates (Haynes & Cronin 2003; Haynes *et al.* 2007b) and higher population densities have been shown in plots surrounded by a less hostile matrix and a lower contrast to the habitat (Haynes & Cronin 2006). However, individual movement in the matrix is taxon specific, for example, in a matrix of high contrast to target habitat, movement has been shown to increase (Goodwin & Fahrig 2002) decrease (Frampton *et al.* 1995), become less directed (Goodwin & Fahrig 2002), more directed (Reeve *et al.* 2008), have greater step length and more linear movements (Haynes & Cronin 2006) depending on the taxa studied.

A limitation of matrix permeability studies arises from the categorical classification of the matrix land cover, for example, woodland habitat with a clear-cut matrix or native grass habitat with invasive grass or bare ground matrix for insect studies (Haddad 1999; Haddad & Tewksbury 2005; Haynes & Cronin 2006; Haynes *et al.* 2007b). This traditional binary or categorical definition of the matrix is unlikely to occur in real landscapes where the matrix would be heterogeneous and provide some resources to the insect species within habitat patches (Dennis *et al.* 2003; Ouin *et al.* 2004). This means that assessing the permeability of the matrix on an ordinal scale would be beneficial to assess thresholds of connectivity and matrix quality.

1.3 Landscape restoration in practice

1.3.1 In Europe

The restoration of grasslands has been implemented in Europe and offers a method to restore and enhance a species-rich grassland ecological network within a decade (Conrad & Tischew 2011; Fagan *et al.* 2008; Kiehl *et al.* 2006; Lengyel *et al.* 2012; Piqueray *et al.* 2011; Prach & Walker 2011). Examples of landscape scale grassland restoration projects are from Germany and the Czech Republic where areas of ex-arable fields of 230 ha and 500 ha respectively, have been re-seeded with chalk grassland seed. These aim to establish species-rich grasslands of local plant community types and to enhance biodiversity (Prach & Walker 2011). Additionally in Hungary, 760ha have been sown with a low diversity seed mixture (Lengyel *et al.* 2012).

Experiments conducted in German grassland creation patches to determine the best method for the restoration of species-rich calcareous grasslands, concluded that only a few target species occurred after nine years, even when restoration habitat patches were adjacent to seed sources, unless hay transfer methods were used (Kiehl & Pfadenhauer 2007). For example, target grassland forb species of Horseshoe Vetch (*Hippocrepis comosa)* and Common Rock-rose (*Helianthemum nummularium*) only established with hay transfer and top-soil removal methods. Although these methods were successful overall in establishing species-rich grasslands, the botanical community still differed in community assemblages from ancient target grasslands (Kiehl & Pfadenhauer 2007). Similarly Conrad and Tischew (2011) describe how after nine years, restoration plots differed from reference grasslands with lower number, abundance and dominance of target species (Conrad & Tischew 2011).

In the Czech Republic, 500 ha of grassland were put into a grassland restoration project: 34 grasslands were restored with regional seed mixtures, 30 with commercial seed mixtures and 16 from natural colonisation (Prach & Walker 2011). Authors concluded that the regional seed mixture was a successful method to restore Bromion grasslands (chalk grassland community type) but all the grassland communities generally converged towards a similar species community composition; the regional seed mixtures had the highest number of target species in a shorter time span compared with the other two methods (Prach & Walker 2011).

In Hungary, 760 ha of arable land has been re-seeded with low-diversity seed mix (Lengyel *et al.* 2012). In this study weedy species decreased in the first three years, and the diversity and cover of target species increased from the first to the fourth year, but the distance from target habitat did not affect the success of the grassland restoration project. The authors concluded that although applying low-diversity seed mixtures was successful, more management was needed for target species colonisation (Lengyel *et al.* 2012).

These European studies illustrate some appropriate methods to restore species-rich grasslands or to restore a grassland network. These also highlight that restoration and grassland creation may not always result in the same community type as the reference grasslands and that additional management may be needed to assist the colonisation of specialist species with low dispersal abilities.

1.3.2 In the UK

Habitat creation using locally sourced seed mixtures has been especially successful when used to restore species-rich grasslands in the UK (Pywell *et al.* 2002; Walker *et al.* 2004). A review of UK species-rich grassland restoration has concluded that although restoration habitat patches can share some of the same plant species as reference habitat patches, enhancement of restoration patches is limited as species more associated with increased nutrient richness are abundant and therefore reference and restoration habitat patches do not have the same community assemblages (Fagan *et al.* 2010). The enhancement of grassland restoration and creation has been apparent when focussing on vegetation communities (Fagan *et al.* 2008; Poschlod *et al.* 1998; Pywell *et al.* 2002; Pywell *et al.* 2003; Walker *et al.* 2004) and to some extent when investigating the subsequent invertebrate colonisation (Woodcock *et al.* 2012a; Woodcock *et al.* 2012b). However, the contribution of these grassland restoration and creation projects to the ecological grassland network has not been investigated, nor has the behaviour of mobile invertebrates at habitat boundaries in response to grassland creation. The time lag of invertebrate species to colonise newly created grasslands has been studied but the results may be habitat patch or landscape-specific and therefore more investigation is required.

1.4 Lepidoptera as indicators of restoration success

Butterflies are UK Biodiversity indicators as they are widespread an relatively easy to identify compared to other invertebrates (DEFRA 2009) and have been used in many matrix permeability and edge behaviour studies (Merckx & Van Dyck 2007; Ricketts 2001; Ries & Debinski 2001; Roland *et al.* 2000). Butterflies have been used as indicator taxa as they often may respond quickly to environmental and land use changes (Hill *et al.* 2002; Warren *et al.* 2001), and can reflect trends in other taxa such as birds, plants and other insects (Thomas 2005; Thomas *et al.* 2004). They are used as indicators for chalk grassland management and restoration (Rakosy & Schmitt 2011). However, Lepidoptera trends do not always represent trends in bees for example, and UK trends are not always representative of other EU countries (Biesmeijer *et al.* 2006; Carvalheiro *et al.* 2013)

The impacts of climate change are already evident for Lepidoptera (Hill *et al.* 2002; Warren *et al.* 2001), and these are likely to reinforce any negative impacts of existing habitat fragmentation on biodiversity (Hill *et al.* 2002). Although some mobile, habitat generalist species at the Northern limit of their range may benefit from a warmer climate (Warren *et al.* 2001). This is because habitat fragmentation can impede the rate and ability of some Lepidoptera species to track moving climate envelopes as they are unable to cross the matrix that separates habitat fragments (Hill *et al.* 2002) and therefore may be 'committed to extinction' (Thomas & Clarke 2004).

1.5 Landscape scale restoration evaluation

Botanically, landscape scale restoration of species-rich grasslands have been extensively evaluated based on botanical community composition and reference species in habitat patches but there is a lack of studies that consider the colonisation of more mobile taxa as a result of habitat restoration and creation or the restoration of biological interactions. Habitat patch or individual field-based evaluation is commonplace, but the biodiversity enhancement as a result the restoration project and the potential ecological network need to be measured at a range of scales from the behaviour of mobile species at habitat edges, to their distribution and resource use in the landscape through to landscape connectivity measures.

Landscape scale restoration consists of the habitat patches and intervening land cover in a landscape. A habitat patch in this context refers to a habitat type that a target species is associated with and includes the resources it needs for all parts of its life cycle, although individuals will utilise resources that are in the intervening land cover that is described as the matrix (Dennis *et al.* 2003; Ouin *et al.* 2004). In the context of the restoration of grasslands from ex-arable land, the new grassland habitat patch is often a field confined within hedges or fencing and in this study is referred to as grassland re-creation field or grassland re-creation habitat patch for simplification. The landscape refers to the wider habitat network as well as the different habitat and land cover types and in the context of this study refers to the Stonehenge World Heritage Site Study area and within 1 km of its boundary unless otherwise defined.

1.5.1 Are landscape scale restoration studies transferable to management recommendations?

Landscape restoration science is a relatively new discipline with a lack of studies that translate evidence-based research into policy and explicit management recommendations for landscape scale projects (Brudvig 2011; Menz *et al.* 2013; Young *et al.* 2005). This means that studies that evaluate landscape scale restoration and translate these results and conclusions into management recommendations are required whilst recognising that some management recommendations will be case specific.

1.5.2 Focus on restoring and evaluating botanical conditions?

There is much evidence for the enhancement of botanical communities and species-richness of restoration projects, and this focus on restoring plant communities is where the strength of restoration science lies (Young 2000; Young *et al.* 2005). However, the restoration of animals is not necessarily guaranteed (Cristescu *et al.* 2013) and colonisation will lag behind especially for characteristic species of Orthoptera (Racz *et al.* 2013), Lepidoptera (Woodcock *et al.* 2012a) and Coleoptera (Woodcock *et al.* 2012b). Lag times in animal colonisation are not often studied alongside the development of plant communities. Research that considers both the botanical characteristics and the colonisation of target taxa is required to understand what is required for a functional ecological network.

1.5.3 Focus on species-specific responses?

Rare, specialised species with low dispersal ability in a high trophic level are most sensitive to fragmentation and these effects can combine and reinforce each other to increase the negative impact of habitat fragmentation (reviews see Henle *et al.* 2004; Tscharntke *et al.* 2002). Measuring the effect of habitat restoration on invertebrate biodiversity is complex as a wide range of their life history traits can determine their response to restoration habitats and the landscape (Batary *et al.* 2012; Dover & Settele 2009; Tscharntke & Brandl 2004; Woodcock *et al.* 2012b) and therefore a single indicator species, taxon or guild is not adequate to measure biodiversity or assign conservation actions (Gossner *et al.* 2013).

The effects of habitat fragmentation on insect/plant interactions are dependent on species and landscape characteristics (for a review, see Tscharntke & Brandl 2004), therefore it is important to consider landscape connectivity for individuals of different taxa and functional groups, with varying species traits and different habitat associations. This means that the strength and direction of the response to landscape features and conservation measures can be dependent on these traits, characteristics and associations and vary between and within species (Keller *et al.* 2013; Prevedello & Vieira 2010; Ricketts 2001; Ries & Debinski 2001). The occurrence of species-specific responses suggests that observation of individuals is required to assess the effect of restoration habitat on the dispersal of individuals in the habitat patches and their use of resources in the matrix.

1.5.4 Focus on habitat patch or the landscape?

A landscape scale perspective is required as habitat mosaics are important for ecological management of many species (Lindenmayer *et al.* 2008) and heterogeneity of habitat types and vegetation structures at different scales is important for the enhancement of biodiversity (Gossner *et al.* 2013). This landscape approach can be used to prioritise areas most suitable for restoration and habitat creation and enhance conservation of species sensitive to fragmentation. Planning at a large scale can also be used to reconcile multiple objectives (Thomson *et al.* 2009). Consideration of landscape connectivity is important, as reduced connectivity can have a negative effect on ecosystem service provision, with evidence from research on both pollination and pest regulation (review by Mitchell *et al.* 2013). This means that considering both habitat patch characteristics and the landscape perspective is important to fully evaluate landscape scale restoration and the potential ecological network.

There is some scientific debate about the relative importance in conservation management strategies of habitat patch conditions versus landscape context. Although habitat conditions are important, they are difficult to classify and should not be prioritised without consideration of landscape context (as discussed previously in sections 1.2.3 and 1.2.4). Although the connectivity of an ecological network will include the aspects of patch size, proximity and the dispersal ability of the target group or species, connectivity is a classification with many different interpretations and measures. Overall there should be more landscape focussed studies of the effects on insect communities in calcareous grassland fragmentation (Steffan-Dewenter & Tscharntke 2002).

1.5.5 Focus on behaviour of mobile individuals?

The behaviour of individuals at habitat boundaries often determines immigration and emigration rates and the effect of fragmentation has been studied with species specific differences shown in butterflies and damselflies (Pither & Taylor 1998; Ries & Debinski 2001). This is especially important as boundary behaviour can be predicted (Ries & Sisk 2008) and Individual Based Models are being used to evaluate functional connectivity for example (Severns *et al.* 2013). Connectivity measures would benefit from consideration of individual dispersal, as individuals can leave high quality habitat and stay in poor quality habitat depending on the costs and benefits associated with dispersal (Baguette *et al.* 2013). Species populations and individuals don't all react similarly and because dispersal and fitness are related, they would be under selection pressure, meaning that there could be rapid adaptation (Baguette *et al.* 2013).

1.5.6 Objectives of habitat and landscape-scale re-creation and restoration

There are a wide range of objectives for habitat and landscape restoration and re-creation such as focussing on the conservation of rare species, for wider biodiversity enhancement and for enhancing ecosystem services as examples (Ruiz-Jaen & Aide 2005). Measurable criteria exists to evaluate the progression of restoration projects for plants, for example, Natural England in the UK has set criteria for the favourable condition of restored grasslands (Natural England 2012), but for animal communities there is no explicit criteria available. Most studies on the colonisation of restored habitats measure and describe improvements and the enhancement of biodiversity (e.g. Woodcock *et al.* 2012a; Woodcock *et al.* 2012b), however, even if community assemblages are similar between target and restoration habitats, ecological interactions may not be restored (Forup *et al.* 2008;

Henson *et al.* 2009). This illustrates that there is a clear gap for research, practice and policy to set quantitative criteria to measure to progression and the success of restoration projects and these criteria need to be set prior to restoration. A risk of not having set criteria is that not all aspects of restoration will be considered, such as ecological interactions or resilience to disturbances and these are important for the long term effect restoration of animal communities and therefore functioning ecosystems (Ruiz-Jaen & Aide 2005).

1.6 Objectives of this thesis

This study explores the use of landscape connectivity for the conservation of species in fragmented landscapes and the overall goal is to investigate landscape connectivity as a key to effective habitat restoration in lowland agricultural landscapes for butterflies. There have been many case studies and experiments looking at species-rich grassland habitat restoration and landscape scale restoration. However, the Stonehenge Landscape case-study in the UK provides over 500ha of species-rich grassland restoration and creation with a chronosequence of age and fragments of ancient chalk grassland proving a study landscape suitable for a variety of research questions. The responses of Lepidoptera have been used as indicators to evaluate the restoration project and to represent the restoration of plant/insect ecological interactions (for example, phytophagous interactions). The restoration project is assessed at a range of scales from individual behaviour at chalk grassland fragment boundaries to their distributions and resource use through to the landscape scale connectivity using a range of evaluation measures not covered in other studies.

This study investigates the application and ecological benefits of restoration techniques at a landscape scale. The behaviour, distribution, community compositions and landscape scale implications of grassland restoration using Lepidoptera were investigated as indictors of enhancement as a result of landscape restoration (Chapters 3-6). This study aims to apply these findings to management recommendations that are transferable to other and future landscape scale restoration projects (Chapter 7). Although there is no set quantitative criteria or thresholds that are used in this study to measure the effects of restoration on Lepidoptera biodiversity and landscape connectivity, this observational study can provide an evidence base for what sorts of changes may be expected when long-term, large-scale habitat restoration is implemented through Agri-environment Schemes.

The following chapters of this thesis are outlined below:

In Chapter 2, the materials and methods used for this study are described and includes a description of the Stonehenge World Heritage Site and the grassland restoration techniques used to re-create species-rich grasslands at a landscape scale. Here the methods used to investigate Lepidoptera as indicators of grassland restoration and landscape connectivity are outlined.

In Chapter 3, the effect of the landscape scale grassland restoration project on Lepidoptera richness, distribution and community compositions at the Stonehenge World Heritage Site are investigated and aims to:

- evaluate the biodiversity enhancement of grassland restoration and re-creation at the habitat patch and landscapes scale using Lepidoptera as biodiversity indicators,
- distinguish which landscape and species characteristics facilitate or impede the colonisation of restored habitats by target insect species, determine the role of species traits in the colonisation of new habitats and the movement of species from isolated chalk grassland fragments.

Hypotheses;

i. Re-creation grassland habitats with vegetation structure and nectar resources similar to the reference habitat will have higher Lepidoptera species richness and abundance than those that do not
ii. Re-creation grassland habitats that are more structurally connected as measured by the amount of surrounding linear features will have higher Lepidoptera species richness and abundance tan those that do not.
iii. Older grassland re-creation habitat patches will have higher species richness and abundance and be more similar to reference grasslands in community assemblage than newer habitat patches.
iv. Lepidoptera associated with grassland habitats will be an effective indicator of the effect of restoration measures on biodiversity.
v. Species traits will be significant in determining the colonisation of new habitats and the movement of species from isolated chalk grassland fragments.
vi. Species that use grasses as larval-host plants will colonise re-creation grasslands faster than those with specialist herb larval host-plants.
vii. More mobile species will colonise re-creation grasslands faster compared to those with low mobility.

In Chapter 4, the impacts of habitat creation on the boundary crossing of Lepidoptera from chalk grassland fragments are investigated and aims to:

- distinguish what habitat and species characteristics determine boundary crossing behaviour,

- compare boundary behaviour for Lepidoptera in habitat fragments to the adjacent land cover,
- determine the utility of new grassland re-creation in increasing the functional connectivity of the landscape.

Hypotheses;

1. New grassland re-creation will increase with functional connectivity for Lepidoptera species associate with grasslands.
2. There will be more crossing behaviour by species that are less specialist in larval host-plants compared to those species with specialist larval host-plants.
3. There will be more crossing behaviour by species with higher mobility compared to those species with lower mobility.
4. There will be more crossing behaviour and a higher permeability value with an adjacent land cover more similar in vegetation structure and nectar resources to the chalk grassland fragment.

In Chapter 5, the effect of mowing on the boundary behaviour of two grassland associated Lepidoptera species are studied and aims to:

- investigate Lepidoptera behavioural response to small scale alterations in habitat structure at experimental boundaries,
- determine whether Lepidoptera response to the physical attributes of the mown boundary itself or the lack of resources in the mown area,
- determine if there are differences in boundary behaviour between Lepidoptera species.
- inform the spatial targeting of grassland re-creation.

Hypotheses;

1. Mowing will reduce boundary crossing behaviour and increase boundary following and avoiding behaviour.
2. Behaviour at mown boundaries will be species specific due to differences in larval host-plant specialism and mobility.
3. Differences in behaviour at mown boundaries will be due to difference in structure rather than lack of resources.

In Chapter 6, effects of the grassland re-creation scheme on landscape connectivity at the Stonehenge World Heritage Site are evaluated and aims to:

- evaluate landscape connectivity by comparing the grassland networks before and after the implementation of the grassland restoration project,
- evaluate landscape connectivity by including the effect of matrix land cover types and the different dispersal abilities of butterflies,
- measure habitat patch characteristics and landscape connectivity at two landscape scales- within the Stonehenge World Heritage Site and across the wider landscape.

Hypotheses;

i. Landscape scale habitat restoration will increase the area, mean patch size and structural connectivity of the grassland network.
ii. The permeability of the matrix land cover will be important in measuring connectivity.
iii. Lepidoptera species with higher mobility will potentially be able to utilise more of the grassland network compared to those with lower mobility.
iv. Effects of grassland re-creation will be higher at the landscape scale compared to the wider landscape scale but wider landscape scale effects will be evident.
v. Grassland re-creation will increase the habitat heterogeneity of the landscape.

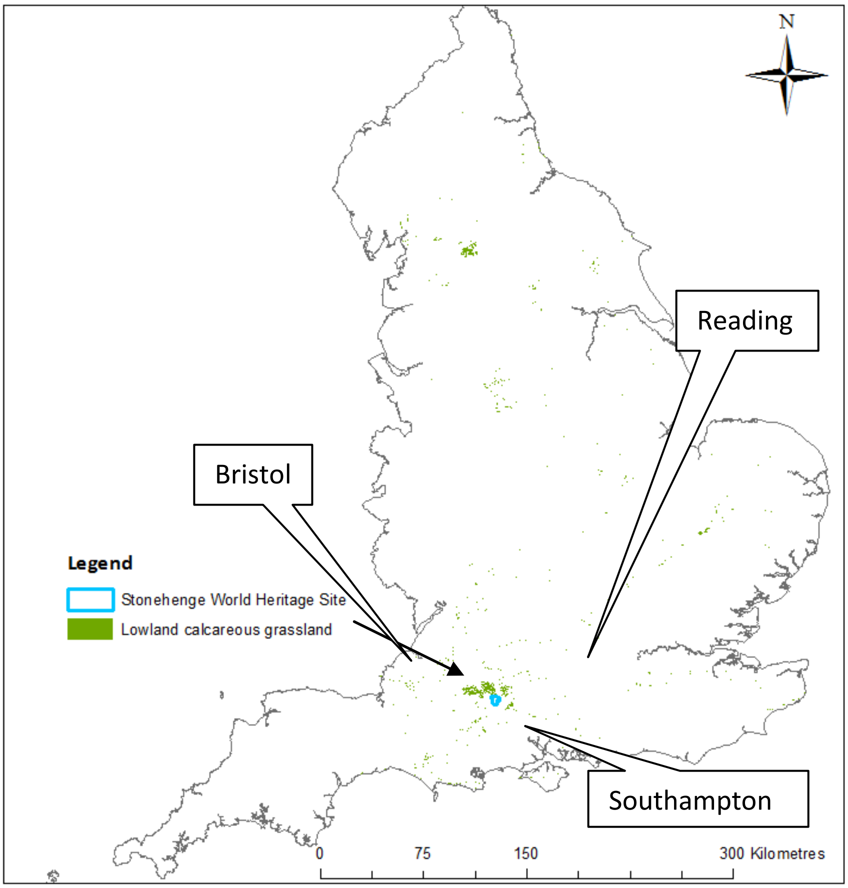
In Chapter 7, the results of Chapters 3-6 are discussed and management recommendations are made for the Stonehenge World Heritage Site grassland restoration that are transferrable to other landscape scale restoration projects. These involve management at the habitat boundary, field or habitat patch and landscape scales. The limitation of this study and avenues for future research are also discussed.

Chapter 2 Study site and methods

2.1 Description of the study site

2.1.1 Overview

The area selected for the study is the Stonehenge World Heritage Site (WHS) in Wiltshire, south-west England, United Kingdom (UK) (Figure 2-1). The Stonehenge WHS is surrounded by three large expanses of lowland calcareous (chalk) grasslands with over 6,729 ha of this within an eight kilometre radius of the WHS boundary. These areas of calcareous grassland occur on Sites of Special Scientific Interest (SSSI) across Salisbury Plain, Porton Down and Parsonage Down which cover a total of 19,700ha, 1,560ha and 188ha, respectively (Figure 2-2).



Map produced by Grace Twiston-Davies 2014 © Natural England copyright (2014). Contains Ordnance Survey data © Crown copyright and database right 2014. World heritage Site boundary from English Heritage National Monuments Record.

Figure 2-1. Map of England, UK showing areas of lowland chalk (calcareous) grasslands and the location of the Stonehenge World Heritage Site. Cities and towns of Bristol, Reading and Southampton are located on the map.

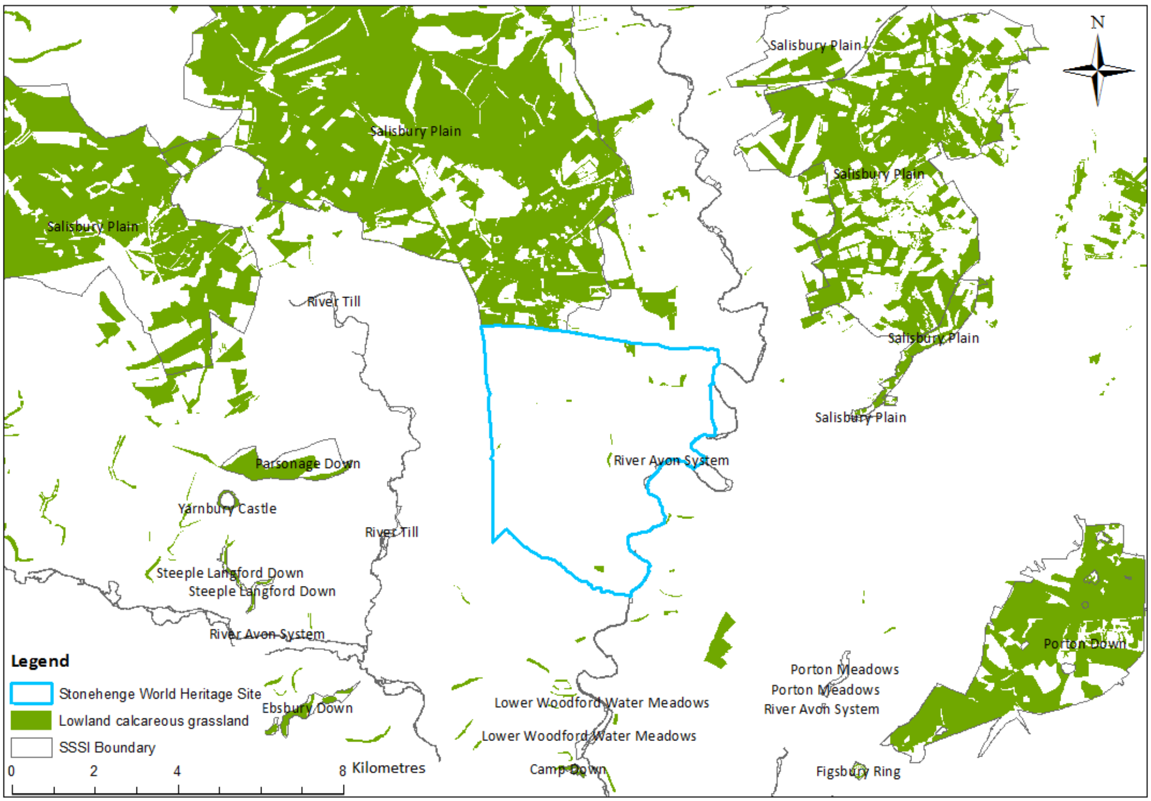


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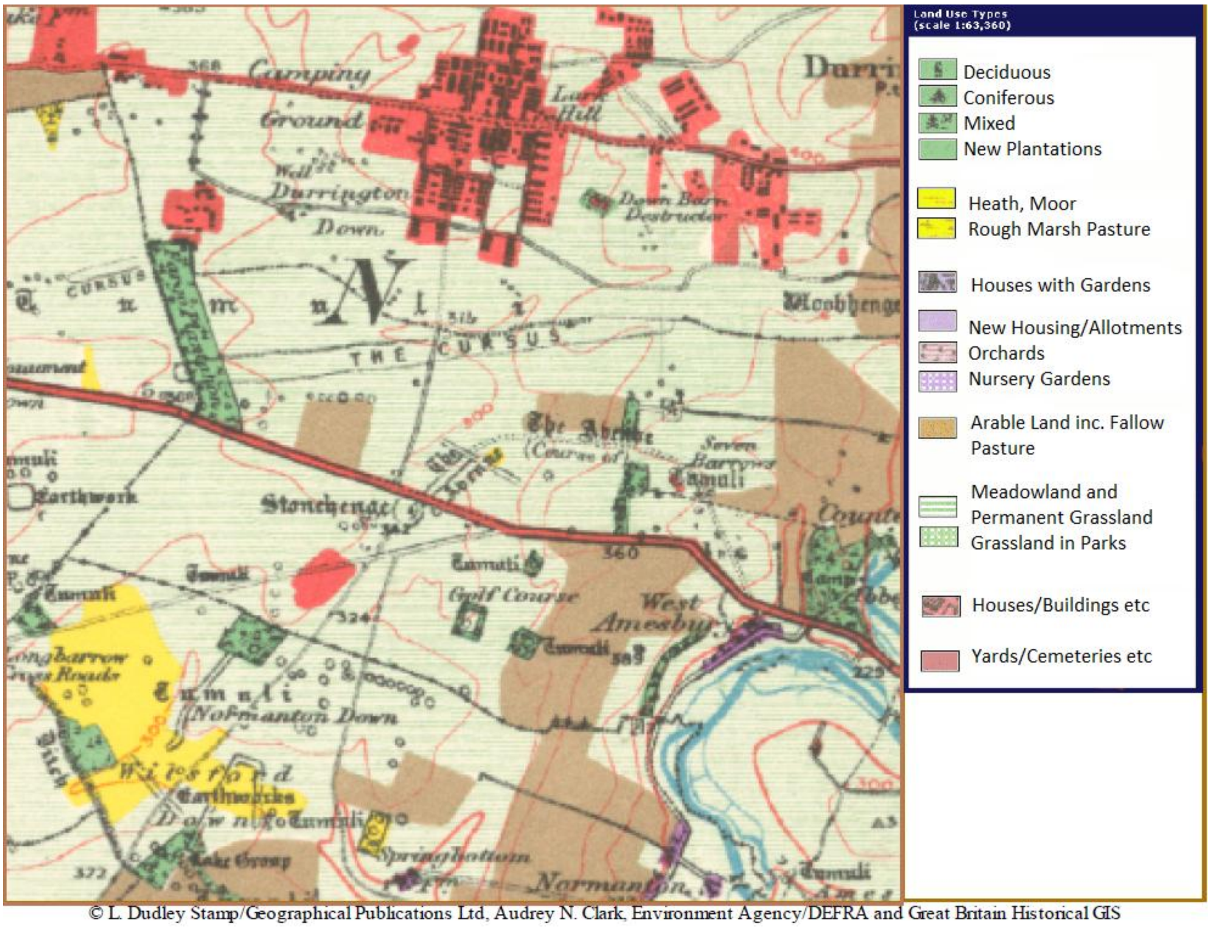
Figure 2-2. The Stonehenge World Heritage Site and surrounding Sites of Special Scientific Interest (SSSI) of Salisbury Plain, Parsonage Down and Porton Down all large expanses of lowland chalk (calcareous) grasslands.

The Stonehenge WHS extends over 26,000 ha south of Salisbury Plain; there are 784 known archaeological features including 180 Scheduled Ancient Monuments within the WHS boundary (Young *et al.* 2009). The Stonehenge landscape was an important site in the Neolithic and Bronze ages with burial mounds (barrows), other henges and earthworks scattered across the landscape providing evidence of the impact of humans on the landscape for over 10,000 years (Darvill 2007). The Stonehenge stone-circle is situated in the centre of the WHS and has been referred to in literature from as far back as the 12th century (Henry Huntington (1080-1160) in Historia Anglorum) and most famously painted by English Romantic artists Joseph Mallord William Turner and John Constable within the grassland landscape in the 19th century (Chippindale 1983). The archaeological and cultural importance of the landscape is therefore, extremely high and in 1986 the landscape was designated a WHS by the United Nations Educational, Scientific and Cultural Organization (UNESCO). The landscape currently attracts approximately 1 million visitors each year (Young *et al.* 2009).

Over 800 ha of the landscape surrounding the stone-circle was given to the National Trust in 1928, consisting of predominantly improved pasture, classified as meadow land and permanent pasture in the Dudley Stamp land use map which would be categorised as pasture or natural grassland in

Corine Land Cover (European Commission 2014), with small areas of arable land and fragments of woodland (Figure 2-3). Since the beginning of the Second World War the Stonehenge landscape, as well as the majority of the UK's permanent lowland semi-natural grassland, has been converted to arable land or improved pasture and the little that remains is fragmented and mostly of low conservation value (Fuller 1987; Hodgson *et al.* 2005). Semi-natural grasslands are defined as those that have been modified by fertiliser or grazing for example, and where a high proportion of the vegetation is a mixture of native grasses and herbs but woody shrubs are mostly absent. Improved pasture is dominated by grasses with a low diversity of forb species and more than 50% *Lolium perenne*, *Trifolium repens* or other agricultural species (Crofts & Jefferson 1999; JNCC 1990). By the year 2000 the Stonehenge landscape was dominated by arable land and semi-improved pasture which is defined as having a high diversity of forb species with less than 50% agricultural species and not dominated by grasses and there were also (JNCC 1990) small fragments of chalk grassland and woodland.



© L. Dudley Stamp/Geographical Publications Ltd, Audrey N. Clark, Environment Agency/DEFRA and Great Britain Historical GIS

Figure 2-3. Land use map of the Stonehenge Landscape in the 1930's depicting the large expanse of permanent grassland with small areas of arable land.

2.1.2 Plant and Lepidoptera nomenclature

Plant nomenclature for this study follows Stace (2010), New Flora of the British Isles Third edition and Lepidoptera nomenclature follows Langmaid *et al.* (1989) The Butterflies of Great Britain and Ireland: Hesperiidae to Nymphalidae and Heath & Emmet (1985) The Moths and Butterflies of Great Britain and Ireland: Cossidae to Heliodinidae. In the field Lepidoptera were identified using Field Studies Council Guide to the Butterflies of Britain and Guide to the day-flying moths of Britain .

2.1.3 Chalk grasslands

In the UK, calcareous grasslands are defined as existing on free-draining chalk or limestone soils. In the UK National Vegetation Classification (NVC) the vegetation communities are referred to as calcicolous or chalk grasslands and different types are dominated by Meadow Oat-grass (*Avenula pratensis*), Downy Oat-grass (*Avenula pubescens*), Tor grass *(Brachypodium pinnatum*), Upright Brome (*Bromopsis erecta*) and Sheep's Fescue (*Festuca ovina*) (Rodwell 1992). These types of grassland are classified as semi-natural grasslands as they require management to maintain their species diversity and to halt ecological succession. The most widespread and extensive chalk grasslands in lowland southern UK are classified as either CG2, *Festuca ovina-Avenula pratensis* dominated or CG3, *Bromopsis erecta* community (Rodwell 1992). There are currently up to 41,000 ha of lowland calcareous grassland in the UK which are distributed as large expanses and small fragments, with large expanses across the South Downs in Hampshire and East Sussex and Salisbury Plain in Wiltshire (Anon 1998). Across Salisbury Plain, Parsonage Down and Porton Down in Wiltshire (Figure 2-4), there is approximately 15,000 ha accounting for around 30% of the UKs lowland calcareous grassland (Natural England 2008).

Chalk grasslands were present in Europe in pre-Neolithic times as small isolated patches of natural grasslands and have expanded, with the maximum spread apparent in Europe in the 14th-18th centuries from large sheep flock-grazing (Poschlod & WallisDeVries 2002). In the last century, chalk grasslands have declined in Europe from abandonment, conversion to arable land and afforestation and are now threatened (Poschlod & WallisDeVries 2002). In the UK these types of semi-natural lowland grasslands have declined by as much as 97% since World War II where intensive farming and subsequent fragmentation has occurred (Fuller 1987; Hodgson *et al.* 2005). The majority of the remaining lowland chalk grasslands have shifted to more mesotrophic conditions attributed to the invasion of more competitive plant species and the local extinction of rarer calcicolous species as a result of fragmentation and nitrogen enrichment (Bennie *et al.* 2006).

Chalk grasslands are Special Areas of Conservation (SACs), Sites of Special Scientific Interest (SSSI), are included in the European Union legislation and the Habitats Directive as Biodiversity Action Plan (BAP) priority habitat in the UK.

2.1.4 The Stonehenge World Heritage Site Management Plan

The Stonehenge WHS Management Plan was drafted in 2000 with the aims of extending the area of permanent grassland to protect the archaeological features of the landscape from ploughing, to restore the ecological and aesthetic value of the landscape and to provide open access areas for visitors (Young *et al.* 2009). This landscape restoration project involved creating new species-rich grasslands on ex-arable land which adjoined fragments of chalk grassland and increased the overall area of permanent grassland and is henceforth referred to as grassland re-creation when referring to individual fields (also grassland re-creation habitat patch) and restoration when referring to the landscape scale project.

The Management Plan outlined aims for the restoration project and these were for the new grasslands to be species-rich, based on local grassland community types and for natural regeneration and development to be possible (Table 2-1). Guiding principles for management were provided to achieve these aims and to enhance the nature conservation value of the grasslands and included:

- sheep and cattle grazing regimes designed to encourage varied and selective grazing,
- grazing and mowing to enhance the structural heterogeneity of grasslands to allow for natural regeneration and colonisation,
- seed dispersal enhanced from grazing and mowing regimes which allow time for seeds to mature and disperse.

Table 2-1. Management aims or 'policies' relating to grassland and its impact on nature conservation from the Stonehenge World Heritage Site Management Plan (Young *et al.* 2009).

Policy 3b	Appropriate Agri-environment schemes should be maintained and developed to maximise the protection of archaeological sites and their settings.
Policy 3f	In the management of land in the future, permanent grasslands should be maintained, enhanced and extended where appropriate.
Policy 3g	The overall nature conservation value of the WHS should be maintained and enhanced, in particular maintaining and improving the biodiversity of permanent grassland including the existing limited areas of floristically rich chalk down-land turf, leading to greater diversity not just of plants but also of birds and insects.

The grassland re-creation project required the collaboration and cooperation of a range of stakeholders including the National Trust, English Heritage, the Royal Society for the Protection of Birds (RSPB) and private landowners, with the tenant farmers committing to 10 years of the project funded through Agri-environment schemes. From 2000-2005 tenant farmers entered into the Avebury and Stonehenge Special Project Grant designed for the conservation and enhancement of ancient monuments and received £120 per hectare of arable land that was changed to permanent grassland. From 2005 onwards, tenant farmers entered in to a Higher Level Stewardship agreement and were given £420 per hectare of arable land that was changed to permanent grassland (Craythorne 2007). In 2000, seed was sourced from local species-rich chalk grassland on Salisbury Plain Site of Special Scientific Interest (SSSI), approximately 5 km north-west of the Stonehenge Landscape and sown in the first grassland re-creation field. From 2000 to 2012 a series of ex-arable fields have been sown resulting in approximately 524 hectares of re-created grassland.

At the beginning of this study (2010), the landscape was a mosaic of chalk grassland fragments on ancient burial mounds (barrows) and slopes, grassland re-creation fields of different ages since sowing, semi-improved pasture, arable farmland and woodland (Figure 2-4). Fragments of chalk grassland on slopes at Full-moon Bank and Luxenborough Bank (Figure 2-2) were considered as target or reference habitat patches as they most resembled the donor habitat patch on Salisbury Plain in terms of botanical characteristics with a chalk grassland community of (*Bromopsis erecta*, CG3 community, Rodwell 1992, (Table 2-3).

These fragments contained a range of species characteristics of chalk grassland including grasses *Bromopsis erecta*, Quaking Grass (*Briza media*) and herbs Small Scabious (*Scabiosa columbaria*), Common Rock-rose (*Helianthemum nummularium*), Horseshoe Vetch (*Hippocrepis comosa*) and Devil’s-bit Scabious (*Succisa pratensis*) (Allen & Brash 2008; Pemberton 2011). Smaller chalk grassland fragments are also found at Cursus Barrows (*Bromopsis erecta* grassland community type) and the small tussocky areas with ant hills at the Wintebourne Stoke Group of barrows and Fargo Barrow, which were rabbit grazed and had Red Fescue (*Festuca rubra*), *Hippocrepis comosa*, *Helianthemum nummularium* and Wild Thyme (*Thymus polytrichus*) (*Avenula pubescens* and *Brachypodium pinnatum* grassland community types, CG6 and CG4, respectively (Pemberton 2011; Twiston-Davies, *Unpublished data*). Groups of burial mounds at King Barrows and the Winterbourne Stoke Group consisted of a mixture of chalk grassland species as listed above, as well as rough grassland and shade tolerant species such as False Brome (*Brachypodium sylvaticum*), False Oat Grass (*Arrhenatherum elatius*), *Festuca ovina*, Ground Ivy (*Glechoma hederacea*), Bird's-foot Trefoil (*Lotus corniculatus*), Pyramidal Orchid (*Anacamptis pyramidalis*) and Greater Knapweed (*Centaurea scabiosa*) (Allen & Brash 2008; Pemberton 2011; Twiston-Davies, *Unpublished data*). These were both classified as a mosaic of *Arrhenatherum elatius* mesotrophic grassland, MG1 and *Avenula pubescens* chalk grassland CG6 community types (Allen & Brash 2008; Rodwell 1992).

These chalk grassland fragments and barrow groups were managed by sheep or cattle grazing depending on what livestock were in the adjacent field for a few weeks in the summer to control scrub (Twiston-Davies, *Unpublished data*).

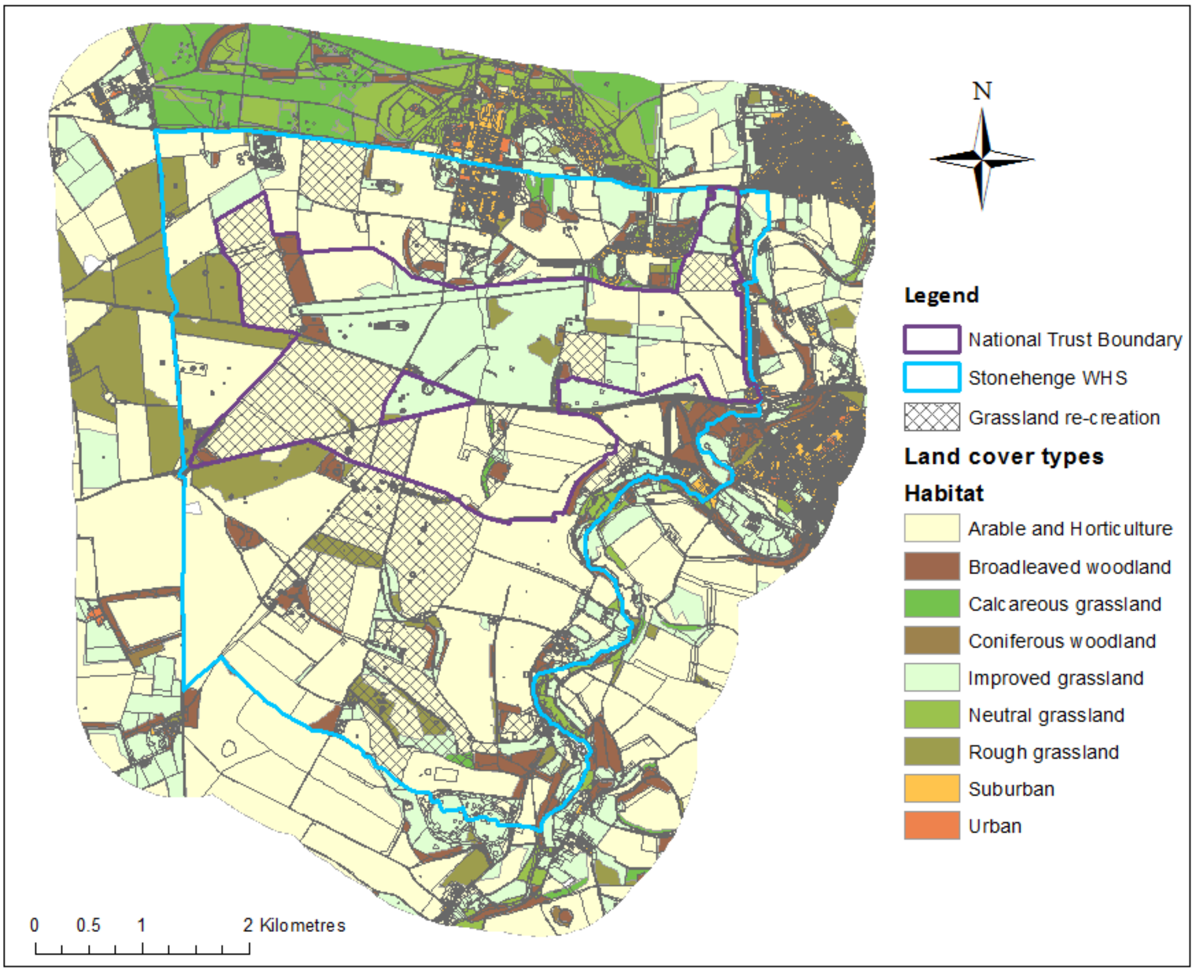


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Figure 2-4. Map of the Stonehenge World Heritage Site (WHS), boundary of the National Trust owned lands and land cover types in the year 2010 and the areas for grassland re-creation from 2000-2012.

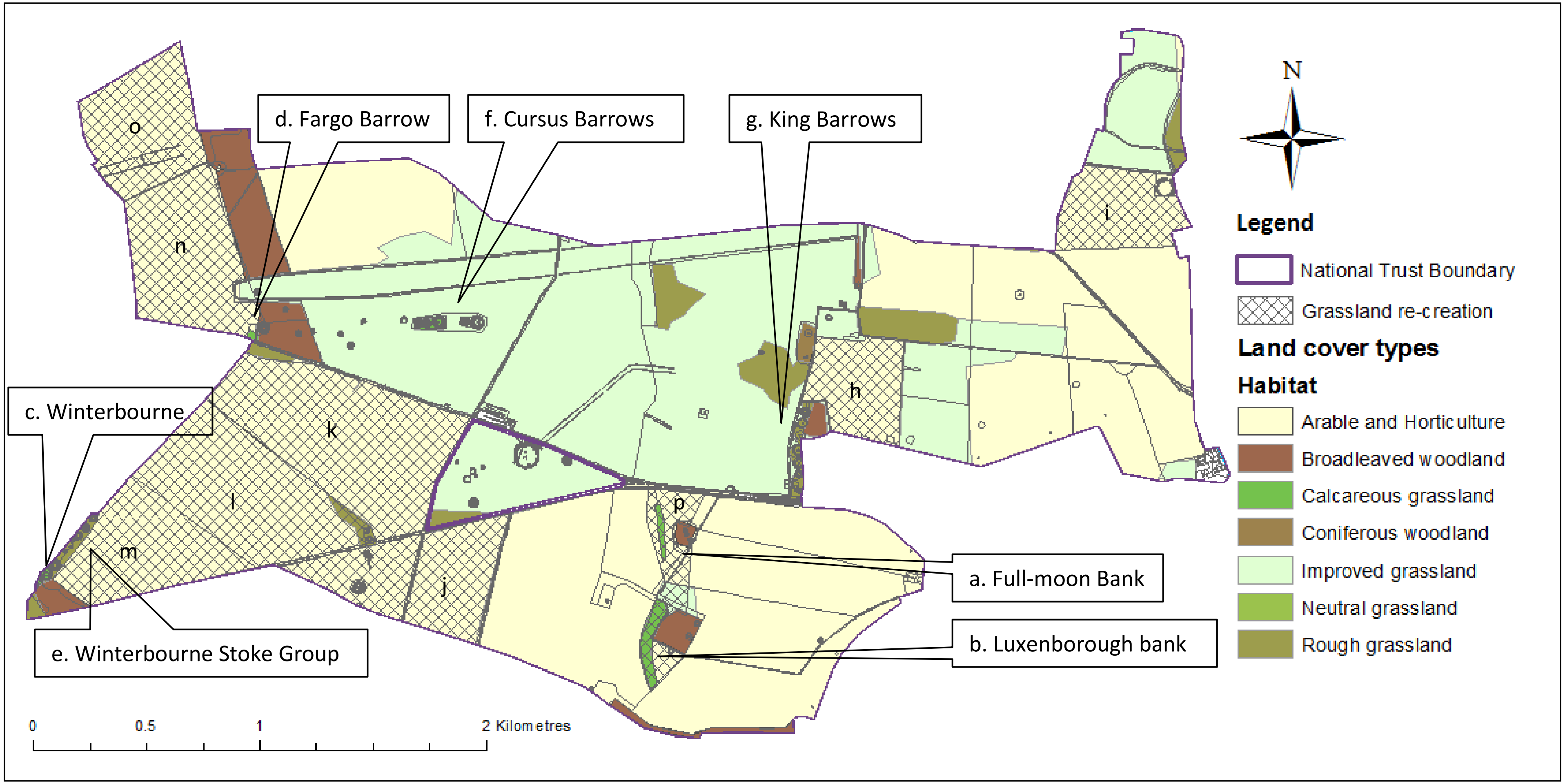

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Figure 2-5. The Stonehenge landscape in 2010 area owned and managed by the National Trust and fragments of chalk (calcareous) grassland on slopes, a) Full-moon Bank, b) Luxenborough Bank, c) Winterbourne and on burial mounds, d) Fargo Barrow, e) Winterbourne Stoke Group, f) Cursus Barrows, g) King Barrows. Fields for grassland re-creation of different ages since sowing, h) Seven Barrows, i) Cuckoo Stone, j) Noice's Piece, k) Stonehenge 05, l) Stonehenge 07 and m) Stonehenge 09. Grassland re-creation fields sown, o) in the year 2010, n) in the year 2011 and p) in the year 2012. Stonehenge stone-circle in the centre of the map.

2.1.5 Grassland re-creation technique

Seed was collected from the donor habitat patch using a brush harvester which is a specially designed machine that harvests seed directly from wild meadows and grasslands and allows for the seed to be processed and stored until it is sown at the receptor site (Edwards *et al.* 2007). Seed was brush harvested in early August 2000 from Ministry of Defence (MOD) owned land on Salisbury Plain SSSI (not within the area shown in Figure 2-4) classified as *Bromopsis erecta* grassland (in 1998, CG3 in the UK National Vegetation Classification; Rodwell 1992). In late August 2000, the seed was applied (at a rate of 20 $kg.ha^{-1}$) to Seven Barrows, the first grassland re-creation field. The seed was mixed with fertiliser (at a rate of 222 $kg.ha^{-1}$), using a phosphate fertiliser brand (Fibrophos 2014) in order to aid the broadcasting of the seed. Although it is unusual to include fertiliser in the restoration of low nutrient grassland, this low level of fertiliser was not considered likely to have much impact on growth of vigorous species which would also be controlled by cutting (topping) during the early years.

Seed sourced from the target or reference habitat patch is considered the best restoration technique to establish similar plant communities (Prach *et al.* 2013; Pywell *et al.* 2002; Walker *et al.* 2004), but is also the most expensive technique (Toeroek *et al.* 2011). To increase cost effectiveness, seed from this first re-creation field, Seven Barrows, was brush harvested in July 2002 and sown in further grassland re-creation fields at the end of the summer in 2002, 2003, 2005 and 2007 and all excess seed was stored for future re-creation. For the 2010, 2011 and 2012 re-creation fields, seed was brush-harvested from the 2003 Normanton Gorse and Noice's Piece fields.

The difference in seed source, either from Salisbury Plain, Seven Barrows field or the 2003 restoration fields will have an impact on the subsequent plant community that will establish due to different original community types (Table2-3, Figure 2-6) and the seed dilution effect. For example, as much as 30% of seed transferred from a donor to the receptor habitat patch will not be viable (Kiehl *et al.* 2006). Additionally the available seed bank and soil nutrient conditions of the receptor patch and its proximity to other sources of seed will also affect the subsequent plant community type (Fagan *et al.* 2008; Fagan *et al.* 2010). Results of plant surveys across the landscape over a four year period to investigate the progression of the restoration project and disseminate some of these differences are described in section 2.1.6.

The management of the grassland re-creation fields after sowing included mechanical topping two or three times a year in the first two years to control weeds followed by a late summer hay cut and autumn grazing with cattle or sheep. The precise management regimes that were applied differed between fields depending on the tenant farmers' preferences and are summarised below Table 2-2).

Table 2-2. Grassland re-creation field management (Twiston-Davies *Unpublished data;* Campbell 2009; Craythorne 2007; Pemberton 2011). Grazing intensity is no. of livestock units per hectare per year (LU/ha/Yr).

Fields	**Year sown**	**Mowing**	**Grazing**
Seven Barrows	2000	Topping to control weeds in the first 2 years. Brush harvesting in years 2, 3, 5, 7 and 9 in July or August.	No grazing in the first 2 years. Autumn sheep grazing from years 3-5. Summer grazing year 6, no grazing in year 7. Sheep grazing from year 8 onwards (approx 130 ewes and lambs a year).
Cuckoo Stone	2002	Topping to control weeds in the first 2 years and in subsequent years if weedy species became dominant or grasses were too large and unpalatable. Hay cut year 5 early August and in year 6.	High density cattle grazing April-June in years 2-4, No grazing in year 5 or 6. Sheep grazing 6 weeks in July and 2-3 weeks in Sept year 9 and onwards (Grazing density unknown).
Noice's Piece	2003	Topping to control weeds in the first 2 years. Hay cut late September in year 4 and brush harvested in year 6 and 7.	Grazed after 2 years. Cattle grazing from years 2-6. No grazing 2010 onwards (0.6-0.75 LU/ha/yr).
Stonehenge 05	2005	Topping to control weeds in the first 2 years and subsequently if weedy species became dominant or grasses too large and unpalatable. Topped early July and September year 2. Hay cut June/July year 4 and onwards.	Cattle grazed from year 2 onwards (0.6-0.75 LU/ha/yr).
Stonehenge 07	2007	Topping to control weeds in the first 2 years.	Cattle grazed from year 2 onwards (0.6-0.75 LU/ha/yr).
Stonehenge 09	2009	Topping to control weeds in the first 2 years in June/ July.	Cattle grazed from year 2 onwards (0.6-0.75 LU/ha/yr).

2.1.6 Botanical characteristics of the re-creation grasslands

Botanical surveys of the grassland re-creation fields were conducted in 2007, 2009 and 2011 (Campbell 2009; Craythorne 2007; Pemberton 2011). The most recent survey showed that for most of the re-creation grassland fields the highest similarity was with mesotrophic grassland communities of the NVC (Pemberton 2011; Twiston-Davies *et al. in press*) determined by comparing the species and abundance using floristic tables (Rodwell 1992) and using MAVIS Plot analyzer 1.0 to calculate Czekanowski coefficient (Smart 2001). The first grassland re-creation field, Seven Barrows (sown in 2000 with seed brush harvested from a nearby donor habitat patch) was more similar to the chalk grassland reference community *Bromopsis erecta* grassland; *Knautia arvensis-Bellis perennis* sub community (Rodwell 1992). Other re-creation fields sown in 2003, 2004 and 2005 with seed brush harvested from Seven Barrows showed transitional mesotrophic/calcicolous grassland vegetation characteristics of *Cynosurus cristatus-Centaurea nigra*/*Bromopsis erecta* communities (Pemberton 2011; Twiston-Davies *et al. in press*). Seven Barrows restoration field had reached similar botanical conditions to the target habitat within seven years with the plant community type most associated with chalk CG3 (NVC, Rodwell 1992) although with a much lower similarity than the target habitat patch. However, the 20003 restoration fields after seven years had transitional chalk/mesotrophic community types (Table 2-3, Figure 2-6). This suggests that seed sourced from the Seven Barrows restoration field may result in transitional chalk/mesotrophic grassland characteristics and not fully reach the botanical conditions of the original donor habitat patch, although this hypothesis can only be tested given more time for the younger fields to mature. Younger grassland re-creation fields sown since 2007 showed similarities with mesotrophic grassland communities of *Arrhenatherum elatius, Lolium perenne-Cynosurus cristatus* or open vegetation *Matricaria perforata-Stellaria media*.

Many of the grassland re-creation fields had characteristic chalk grassland species but not all in the abundances required for it to be classified as chalk grassland community types for example, grasses *Bromopsis erecta* and *Briza media* were present in all grassland re-creation fields and herbs *Hippocrepiss comosa* in Cuckoo Stone and Stonehenge 05 (Craythorne 2007) and *Helianthemum nummularium* in Seven Barrows (Campbell 2009). The lack of these species in the 2011 surveys may have been due to just ten 2m by 2m quadrats being used to survey each field, which was much lower than the one quadrat per hectare in 2009 (minimum 12) and 1.5 per hectare in 2007 (minimum 18) (Campbell 2009; Craythorne 2007; Pemberton 2011).

Figure 2-6 shows the similarity of grassland re-creation habitat patches (fields) with chalk grassland from botanical surveys in 2007, 2009 and 2011 (Campbell 2009; Craythorne 2007; Pemberton 2011). As the grassland matures the similarity with chalk grassland increases. The similarity of the species-rich grassland donor habitat patch to a NVC chalk grassland vegetation community was 68% (in

1998) and the reference fragment at the Stonehenge landscape at was 66% (in 2011) in the Seven Barrows grassland re-creation field sown in the year 2000 and recorded in 2011 was 57%. This indicates that within a decade the grassland re-creation fields are reaching similar botanical conditions to the target habitat but they have lower percentage similarity to chalk grassland community type (CG3 in NVC) than the target habitats.

Seed harvested from a target habitat patch is one of the best methods for achieving plant communities similar to the target habitat patch. However, these results suggest that seed harvested from young restoration which is only three years old can provide species-rich grassland with some target species characteristic of the target habitat patch even if it doesn't have the same community classification of the target habitat patch (Twiston-Davies *et al. in press*). This is a lower cost option for a large landscape scale projects and can provide incentives to farmers to manage restoration land in order to sell the seed for other projects. Differences between the established communities depending on their seed source is difficult to evaluate within the short time period of the Stonehenge restoration landscape, but would be possible for example, after the 2009 field sown with seed sourced from 2003 fields had reached a decade in age.

Table 2-3. Results from the botanical surveys (Craythorne 2007; Campbell 2009; Pemberton 2011) showing area of field (Ha), year of re-creation (Year), seed source (from a) ancient chalk grassland, b) Seven Barrows re-creation field and c) Noice's Piece and Normanton Gorse re-creation fields). Grassland type is based on the UK National Vegetation Classification (NVC) and floristic table similarity and constant species (Rodwell 1992) and MAVIS Plot analyser version 1.00 (Smart 2001), classified as chalk- CG2 *Festuca ovina-Avenula pratensis,* CG3 *Bromopsis erecta,* CG6 *Avenula pubescens,* Mesotrophic- MG1 *Arrhenatherum elatius,* MG5 *Cynosurus cristatus-Centaurea nigra,* MG6 *Lolium perenne-Cynosurus cristatus,* and Open Vegetation OV9 *Matricaria perforata-Stellaria media.* Chalk grassland communities in bold.

Field Name	**Ha**	**Year**	**Seed**	**Grassland type (NVC)**		
				2007	**2009**	**2011**
Target habitat patch						
MOD	N/A	N/A	N/A	**CG3** (1998)		
Full-Moon Bank	0.5	N/A	N/A			**CG3**
Luxenborough Bank	2	N/A	N/A	**CG2/CG3**		**CG3**
Winterbourne Stoke	2	N/A	N/A			**CG6**
Re-creation fields						
Seven Barrows	16	2000	a	**CG3c**	**CG2 /CG3**	MG5 /**CG3**
Cuckoo stone	17	2002	b	MG6	MG6	MG6
Noice's Piece	17	2003	b	MG5/MG6	**CG2/CG3**/MG5	MG5/**CG3**
Normanton Gorse	12	2003	b	MG5/MG6	MG6	MG5/**CG3**
Stonehenge 05	50	2005	b	MG1	**CG2/CG3**	MG5/**CG3**
Stonehenge 07	38	2007	b		MG6	MG6
Stonehenge 09	23	2009	a			MG1
Stonehenge 10	26	2010	c			OV9

Figure 2-6. Similarity of grassland re-creation fields sown with species-rich grassland seed from the year 2000 to 2009 (Campbell 2009; Craythorne 2007; Pemberton 2011) to a chalk grassland NVC CG3 community (as described in Rodwell 1992). Percentage similarity calculated in MAVIS Plot Analyser version 1.00 (Smart 2001). Calcicolous community types of CG3 *Bromopsis erecta* except for the field sown in the year 2002 surveyed in 2007 which had similarity with CG2 *Festuca ovina-Avenula pratensis* and mesotophic community types of MG5 *Cynosurus cristatus-Centaurea nigra* (sown in 2000, 2003, and 2005), MG6 *Lolium perenne-Cynosurus cristatus* (sown in 2002 and 2007) and MG1 *Arrhenatherum elatius* sown in 2010. Similarity of chalk grassland target habitat patch to CG3 NVC community where seed was brush harvested was 68% and for target chalk grassland fragments at the Stonehenge landscape was 66%.

2.2 Lepidoptera Survey

Butterflies are used widely as indicator species as they can represent trends in other taxa and show response to climate change, land use change and conservation actions (Hill *et al.* 2002; Thomas 2005; Thomas *et al.* 2004; Warren *et al.* 2001). Trends in British butterfly abundance are representative of some other insect taxa, plants and birds and are a potential warning indicator for birds and plants as they have showed more rapid declines (Thomas 2005; Thomas *et al.* 2004). However, butterfly trends do not necessarily represent bee or hoverfly trends and therefore assumptions made from butterfly data need to be carefully interpreted (Biesmeijer *et al.* 2006; Carvalheiro *et al.* 2013). Additionally, some conservation actions to increase the abundance and distribution of Lepidoptera species have shown positive results over a short time span of a decade. For example, Agri-environment schemes have slowed and even reversed the declines in some Biodiversity Action Plan priority species such as Silver spotted skipper (*Hesperia comma*) and Adonis Blue (*Lysandra bellargus*) and the High Brown Fritillary (*Argynnis adippe*) (Fox *et al.* 2007).

All Lepidoptera transect (Chapter 3) and behaviour surveys (Chapters 4 and 5) were conducted in suitable conditions and methods adapted from the Butterfly Monitoring Scheme (Pollard & Yates 1993) between 10am-5pm on dry days with a wind speed less than Beaufort scale 5, a temperature of more than 13 °C on days with 60% sunshine or more than 17 °C when overcast.

Lepidoptera were identified using Field Studies Council guides for butterflies and day flying moths of Britain (1998 and 2006, respectively, nomenclature follows Heath & Emmet 1985; Langmaid *et al.* 1989) and close-focus binoculars when required. If Lepidoptera were feeding on nectar, the species of plant was identified (nomenclature follows Stace Third edition, 2010).

For the distributions of Lepidoptera distributions in the wider landscape used in Chapter 3, data were provided from the Butterflies for the New Millennium recording scheme, courtesy of Butterfly Conservation and the Wiltshire and Swindon Biological Records Centre.

2.2.1 Species ecological groups and mobility group

The butterflies surveyed were grouped using ecological classifications of species associated with: a) ruderal vegetation, b) short-grass herb-rich vegetation, c) open grassland with medium to tall sward or warm open grassland with short-sward and, c) woodland (Shreeve *et al.* 2001). The difference between the two grassland ecological groups was that those associated with short-grass herb-rich vegetation were not dependant on grasses for any part of their life-cycle, whereas, those associated with short, medium or tall warm open grassland were (Shreeve *et al.* 2001). The larval host plants of the herb-rich grasslands associated group were Legumes and they were likely to have a symbiotic relationship with ants. The ruderal-vegetation group is not associated with a particular family of larval host plants, but is likely to be associated with tall and/or mature herbs and to overwinter as pupae. These categories are based on a Principal Component Analysis based on the ecological attributes at all stages of the Lepidoptera life cycle, with the defined groups differing mostly in range, distribution, biotope range, dispersal ability and recent declines in abundance between groups (Shreeve *et al.* 2001).

Day flying moths were categorised based on their association with different habitat types: the Six-spot Burnet (*Zygaena filipendulae*) was more associated with herb-rich grassland as its larval host plant is legume species *Lotus corniculatus*, (although this species will use tall grass stems and pupation sites), the Forester moth (*Adscita statices*) as it is associated with herb-rich chalk grassland where its larval host plant Common Rock-rose (*Helianthemum nummularium*) is abundant (Heath & Emmet 1985). Both of these moth species were also categorised as sedentary in mobility (Naumann *et al.* 1999). The Hummingbird Hawk moth (*Macroglossum stellatarum*) was categorised as associated with ruderal vegetation as it is a widespread immigrant species associated with a variety of habitat types (Heath & Emmet 1985; Langmaid *et al.* 1989).

Mobility groups were of widespread, intermediate and sedentary groups which are estimated using a mark and recapture study and represent emigration rates and colonisation distances as described in Pollard & Yates (1993), this is a widely used but relatively coarse classification whereby mobility categories are an assumption and likely to be an underestimate mobility. Species categorised as sedentary are unlikely to move outside the habitat patch and are considered to have a closed population structure, whereas, species categorised as widespread are wide-ranging and frequently move between habitat patches and have an open population structure. species categorised as intermediate are somewhere in-between sedentary and widespread. Other mobility categories are availably such as Bink (1992) which has nine mobility categories as well as Cowley *et al.* (2001) and Komonen *et al.* (2004) which are continuous index value based on questionnaires to experts. However, all of these measures were significantly strongly positively correlated (Komonen *et al.* 2004) and therefore the most simple measure of three categories by Pollard and Yates (1993) is used for this study.

2.3 Habitat quality

Habitat quality was recorded using the number and species of nectar flowers and vegetation characteristics in the habitat fragments and the wider landscape to include both the habitat and matrix resource measures as not all resources occur in the defined 'habitat' of an individual (Dennis *et al.* 2003; Ouin *et al.* 2004).

Habitat quality, in terms of the number of nectar resources (flowering units)and vegetation characteristics was measured for transect surveys in Chapter 3 and boundary behaviour surveys in Chapters 4 and 5 using quadrats measuring 0.5 m by 0.5 m. Nectar resources were measured by the total number, family and individual species densities of flowering units that Lepidoptera use for nectar sources (Hardy *et al.* 2007). The availability of nectar plants was measured as this resource is used by both male and female Lepidoptera. Other habitat characteristics measured included the vegetation height and density (using the drop disc method, Stewart *et al.* 2001), percentage coverage of bare ground and dead vegetation and the heterogeneity of these variables (calculated as the Coefficient of Variation).

Variables relating to vegetation height and density and the coverage of bare ground and leaf litter are important for butterflies, as they effect the microclimate and can be used as a resource for oviposition, pupation, courtship and thermoregulation (Beyer & Schultz 2010; Lawson *et al.* 2014; NCC 1986; Thomas *et al.* 2009). Different butterfly species are associated with different vegetation heights (NCC 1986) for example, the recovery of a threatened Butterfly species, the Large Blue (*Maculinea arion*) can be determined by the vegetation height as this effects the microclimate and the subsequent establishment of a successful symbiotic relationship with the *Myrmica sabuleti* ant species which prefers warmer microclimate when there is a shorter (Thomas *et al.* 2009). The cover and height of grasses and depth of leaf litter can determine the selection of oviposition sites for Skipper species (*Pokes mardon*) (Beyer & Schultz 2010) and in cooler sites, bare ground may provide a warmer microclimate for oviposition site for *Heperia comma* (Lawson *et al.* 2014).

Vegetation surveys that were conducted prior to Lepidoptera surveys (Campbell 2009; Craythorne 2007; Pemberton 2011) provided detailed species lists to determine the presence of larval host plants in grassland re-creation fields and chalk grassland fragments (Table 2-4).

Table 2-4. List of host plants for Lepidoptera species associated with grasslands or ruderal vegetation (Hardy *et al.* 2007; Shreeve *et al.* 2001).

Larval host plant	**Lepidoptera species**
<u>Grasses</u>	
Common Bent *(Agrostis capillaris)*	Meadow Brown (*Maniola jurtina*), Gatekeeper (*Pyronia tithonus*), Small Heath (*Coenonympha pamphilus*)
Creeping Bent *(Agrostis stolonifera)*	Ringlet (*Aphantopus hyperantus*), Meadow Brown (*Maniola jurtina*), Gatekeeper (*Pyronia tithonus*), Small Heath (*Coenonympha pamphilus*)
Cock's Foot *(Dactylis glomerata)*	Essex Skipper (*Thymelicus lineola*), Marbled White (*Melanargia galathea*), Ringlet (*Aphantopus hyperantus*), Gatekeeper (*Pyronia tithonus*)
Sheep's Fescue *(Festuca ovina)*	Marbled White (*Melanargia galathea)*, Meadow Brown (*Maniola jurtina*), Gatekeeper (*Pyronia tithonus*), Small Heath (*Coenonympha pamphilus*)
Meadow Fescue *(Festuca pratensis)*	Gatekeeper (*Pyronia tithonus*)
Red Fescue *(Festuca rubra)*	Marbled White (*Melanargia galathea*), Gatekeeper (*Pyronia tithonus*)
Yorkshire Fog *(Holcus lanatus)*	Small Skipper (*Thymelicus sylvestris*), Meadow Brown (*Maniola jurtina*)
Perennial Ryegrass *(Lolium perenne)*	Meadow Brown (M*aniola jurtina*)
	Essex Skipper (*Thymelicus lineola*), Small Skipper(*Thymelicus*

Timothy Grass *(Phleum pratense)*	*sylvestris*), Marbled White (*Melanargia galathea*)
Smooth Meadow Grass *(Poa pratensis)*	Ringlet (Aphantopus *hyperantus*) , Meadow Brown (*Maniola jurtina*), Gatekeeper (*Pyronia tithonus*), Small Heath (*Coenonympha pamphilus*)
Rough Meadow Grass *(Poa trivialis)*	Meadow Brown (*Maniola jurtina*), Gatekeeper (*Pyronia tithonus*), Small Heath (*Coenonympha pamphilus*)
<u>Herbs</u>	
Cuckoo Flower *(Cardamine pratensis)*	Green-veined White (*Pieris napi*)
Common Rock-rose *(Helianthemum nummularium)*	Brown Argus (*Arica agestis*)
Horseshoe Vetch *(Hippocrepis comosa)*	Adonis Blue (*Lysandra bellargus*)
Bird's-foot Trefoil *(Lotus corniculatus)*	Chalkhill Blue (*Lysandra coridon*), Clouded Yellow (*Colias croceus*), Six-spot Burnet (*Zygaena filipendulae*)
Lesser Hop Trefoil *(Trifolium dubium)*	Chalkhill Blue (*Lysandra coridon*), Clouded Yellow (*Colias croceus*)
Red Clover *(Trifolium pratense)*	Chalkhill Blue (*Lysandra coridon*), Clouded Yellow (*Colias croceus*)
White Clover *(Trifolium repens)*	Chalkhill Blue (*Lysandra coridon*), Clouded Yellow (*Colias croceus*),
Common Nettle *(Urtica dioica)*	Small Tortoiseshell (*Aglais urticae*), Red Admiral (*Vanessa atalanta*)

The average weather conditions to the nearest hour of survey time were also recorded from the closest Meteorological station at Boscombe Down, Amesbury, Wiltshire (approximately 6.5 km WSW from the stone-circle, British National Grid reference SU 17763 39246). For the boundary behaviour experiment detailed in Chapter 5, the average microclimate conditions of humidity, wind speed and air temperature were recorded using a digital hand held recorder held one metre from the ground for three minutes at the start of the survey.

2.4 Mapping the Stonehenge WHS and the wider landscape

An Ordnance Survey Mastermap Topology layer of the Stonehenge World Heritage Site and a buffer of 1 km of its boundary was obtained from EDINA (Ordnance Survey Mastermap 2010, EDINA Digimap 1: 1250 scale) in polygon format and edited in ArcMap (version 10.1 ESRI©) to include the small fragments of chalk grassland, the classification of linear features (road verges, track verges and field margins) and other un-classified polygons using personal knowledge, Google Earth©, Land Cover Map 2007 and the Stonehenge World Heritage Site Management Plan (Morton *et al.* 2011; Young *et al.* 2009). For this map the minimum mapable unit was 0.25 ha. This map was used in Chapter 3 to calculate different land cover types and features in buffers around Lepidoptera transect using ArcMap (version 10.1 ESRI©).

Land Cover MAP 2007 data was sourced from the Centre for Ecology and Hydrology, consisting of broad habitat types at 25 m by 25 m raster grid square resolution (Land Cover Map 2007, Table 2-5, Morton *et al.* 2011). These were edited to represent the land cover types in the landscape prior to grassland re-creation in 2000, and in 2012 after the last grassland re-creation fields had been sown with an additional category of grassland re-creation, based on Stonehenge World Heritage Site Management Plans (Young *et al.* 2009) and personal observations (Figure 2-7). Grassland re-creation areas that were sown with species-rich seed mixtures prior to 2007 were classed as either improved grassland or neutral grassland in Land Cover Map 20007 and so were edited to be classed as arable and horticulture in 2000 and to be classed as re-creation grasslands in 2012. Grassland re-creation areas sown in and after 2007 were classed as arable and horticulture in Land Cover Map 2007 and so were edited to be classed as re-creation grassland in 2012.

Table 2-5. Land Cover Map 2007 habitat types and description. Ex arable fields that were sown with species-rich grassland seed mixtures between 2000-2012 were classed as re-creation grassland.

Land Cover Map	Description
Broadleaved Woodland	Broadleaved, mixed and yew woodland with stands >5m high and tree cover >20%.
Coniferous Woodland	Semi-natural stands and plantations with cover >20%.
Arable and Horticulture	Includes annual crops, perennial crops (e.g. orchards) and freshly ploughed land
Improved Grassland	Higher productivity distinguished improved grasslands from the other categories as well as the lack of winter senescence
Neutral Grassland	Determined by botanical composition
Calcareous Grassland	As above but often mis-classified as improved grassland
Rough Grassland	Mix of areas managed, low productivity grassland and some semi-natural which could not be assigned acid, neutral or calcareous
Freshwater	Standing open water, canals, rivers and streams
Urban	Dense urban, town and city centres with little vegetation also docks, car parks and industrial estates
Suburban	Includes urban area with vegetation

GIS layers of the Lowland Calcareous Grasslands were obtained from Natural England (MAGIC, Natural England 2010) in polygon format (data from 1998-2001) and edited to include the additional fragments at the Stonehenge Landscape on slopes and burial mounds (Winterbourne Stoke Group, Fargo Barrow, Full-moon Bank and Luxenborough Bank). These fragments were too small to be categorised by the Lowland Calcareous Grassland survey (less than 25m by 25m n area). The new Lowland Calcareous Grassland layer was combined with the edited Land Cover Maps 2007 layer as the Lowland Calcareous Grassland Survey was more accurate at identifying chalk grassland than the Land Cover Map 2007. The Sites of Special Scientific Interest and World Heritage Site boundaries were obtained from Natural England (MAGIC, Natural England and English Heritage 2010) and the National Trust Boundary was digitised by hand from maps in Young *et al.* (2009).

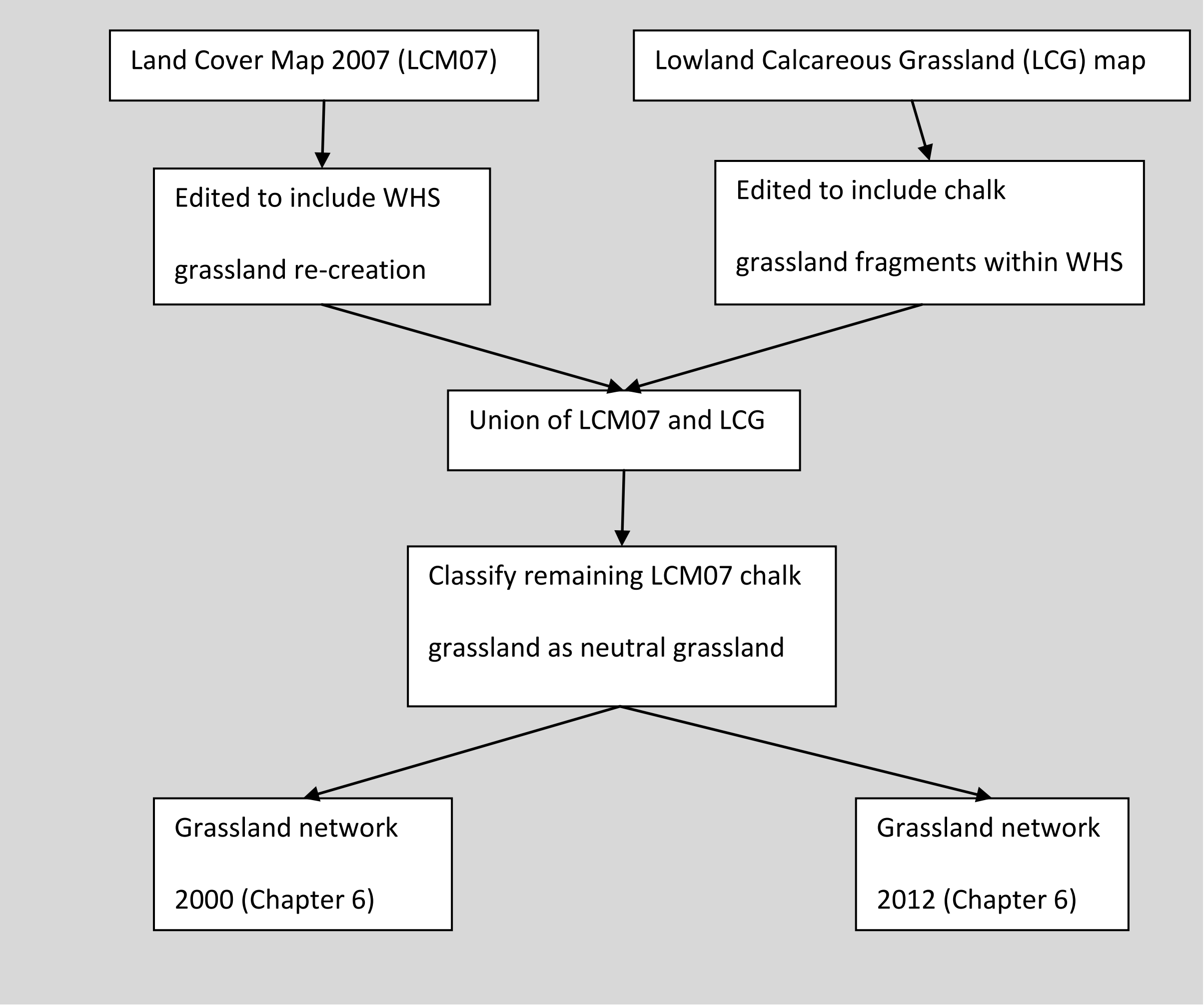

Figure 2-7. Outline of method for creating grassland habitat network maps using Land Cover Map 2007 (Morton *et al.* 2011) and Lowland Calcareous Grassland map (1998-2001), edited to represent the Stonehenge World Heritage Site in 2000, 2010 and 2012.

All maps in this thesis are produced using ArcGIS© software by ESRI and contain the copyright information from the data sources. All diagrams are created using Microsoft Word©. All graphs are created using Microsoft Excel © and all ordination diagrams using CanoDraw© for CANOCO 5 ©.

Chapter 3 Landscape scale grassland restoration at the Stonehenge World Heritage Site, UK: Lepidoptera biodiversity enhancement?

3.1 Introduction

Habitat restoration at the landscape scale has the potential to create new habitats, expand and buffer existing habitat fragments, increase the permeability of the intervening matrix and act as stepping stones and corridors through the landscape (Pfadenhauer 2001). Landscape restoration science is however, a relatively new discipline with a lack of studies that translate evidence-based research into policy and explicit management recommendations for landscape scale projects (Brudvig 2011; Menz *et al.* 2013; Young *et al.* 2005).

Habitat restoration using regional seed mixtures has been utilised to restore botanically species-rich grasslands (Mitchley *et al.* 2012; Prach *et al.* 2013; Pywell *et al.* 2002; Walker *et al.* 2004) and the strength of restoration science lies in this focus on restoring flora communities (Young 2000; Young *et al.* 2005). The restoration of fauna is not necessarily guaranteed (Cristescu *et al.* 2013), and yet it is vital to restore biodiversity and ecological interactions. This is especially crucial in species-rich grassland such as calcareous grasslands, which have high biodiversity value in Europe (van Swaay 2002; WallisDeVries *et al.* 2002) and a third of semi-natural dry grassland in the Atlantic Europe region of the Natura 2000 network in are in the UK (Calaclura & Spinell 2008).

Measuring the biodiversity enhancement as a result of habitat restoration for invertebrates is complex as their different functional, ecological and mobility groups can determine their response to habitats under restoration and the landscape (Batary *et al.* 2012; Dover & Settele 2009; Tscharntke & Brandl 2004; Woodcock *et al.* 2012b). Therefore, it is crucial to understand, interpret and predict these differences and complex interactions of invertebrates to habitat and landscape modification (Dennis *et al.* 2004; Diamond *et al.* 2011; Hardy *et al.* 2007).

The relative importance of landscape characteristics and configuration compared with habitat patch characteristics are much debated. Habitat patch connectivity is considered by some, as crucial as habitat extent and quality (Doerr *et al.* 2011; Prugh *et al.* 2008) and in agricultural landscapes non-habitat features such as the intervening matrix and linear features (for example, field margins and hedges) provide resources and enhance landscape connectivity (Delattre *et al.* 2010b; Ouin *et al.* 2004). Additionally, landscape complexity and heterogeneity (diversity of habitat types and structure) can be as important as habitat patch characteristics for conservation especially for the majority of species for example, butterflies and other pollinators (Batary *et al.* 2011; Shreeve & Dennis 2011).

The influence of the surrounding landscape and intervening matrix is arguably less important than the effects of the area, extent or isolation of habitat patches (Hodgson *et al.* 2011; Hodgson *et al.* 2009; Prevedello & Vieira 2010). This means that investigating the relative contribution of both the habitat and landscape characteristics is necessary to assign appropriate restoration site targeting and for the subsequent management of these sites.

As part of the Stonehenge World Heritage Site (WHS) Management Plan, over 500 hectares of species-rich grassland are currently being restored and re-created on ex-arable fields in Wiltshire, UK, using species-rich, locally sourced seed mixtures from a donor habitat patch. Fields that were sown with this seed mix are henceforth referred to as grassland re-creation fields. The aim of this restoration project is to re-connect the isolated fragments of ancient chalk grassland to the wider landscape. The project also provides an opportunity to investigate the ecological benefits of landscape restoration and the landscape factors and identify species traits that may facilitate or impede the re-colonisation of newly created habitats.

Previous surveys of the botanical characteristics of this restoration project have shown that the grassland re-creation fields have reached similar ecological conditions of the donor habitat patch within 7-10 years (Campbell 2009; Pemberton 2011), a time-span that is supported by other studies (Piqueray *et al.* 2011; Prach *et al.* 2013). However, for some species-rich grassland restoration projects it can take decades to reach the precise botanical conditions of the donor habitat patch (Fagan *et al.* 2008).

Butterflies are used as an indicator group to evaluate the biodiversity enhancement of the restoration project as they respond quickly to environmental and land use changes (Hill *et al.* 2002; Warren *et al.* 2001), can reflect trends in other taxa (Thomas *et al.* 2004), and are especially suited for short term restoration measures in calcareous grasslands (Rakosy & Schmitt 2011). However, trends in UK Lepidoptera do not always represent those in other taxa, for example they do not necessarily reflect trends in bees and may not be representative of other EU countries (Biesmeijer *et al.* 2006; Carvalheiro *et al.* 2013).

3.2 Aims and Hypotheses

Aims;

- To evaluate the biodiversity enhancement of grassland restoration and re-creation at the habitat patch and landscape scales using Lepidoptera density, diversity and community compositions as biodiversity indicators in re-created fields and reference habitat patches.
- To investigate the habitat and landscape characteristics that encourage the colonisation of new habitats and the movement of taxa from isolated chalk grassland fragments.
- To determine the role of species traits in the colonisation of new habitats and the movement of species from isolated chalk grassland fragments.

Hypotheses;

i. Re-creation grassland habitat patches with vegetation structure and nectar resources similar to the reference habitat will have higher Lepidoptera species richness and abundance than those that do not
ii. Re-creation grassland habitat patches that are more structurally connected as measured by the amount of surrounding linear features will have higher Lepidoptera species richness and abundance tan those that do not.
iii. Older grassland re-creation patches will have higher species richness and abundance and be more similar to reference grasslands in community assemblage than newer habitat patches.
iv. Lepidoptera associated with grassland habitats will be an effective indicator of the effect of restoration measures on biodiversity.
v. Species traits will be significant in determining the colonisation of new habitats and the movement of species from isolated chalk grassland fragments.
vi. Species that use grasses as larval-host plants will colonise re-creation grasslands faster than those with specialist herb larval host-plants.
vii. More mobile species will colonise re-creation grasslands faster compared to those with low mobility.

3.3 Materials and Methods

3.3.1 Study site

The study site was the National Trusts' Stonehenge landscape within the Stonehenge WHS in Wiltshire, South-West UK, where a long term landscape scale grassland restoration and re-creation project has been underway. In the year 2000, seed was brush harvested from a nearby calcareous grassland donor habitat patches on Salisbury Plain, (NW of the Stonehenge Landscape) and used to establish new grassland on ex-arable fields until 2012 (Chapter 2). The aim of this was to protect the archaeological features across the landscape and to restore the aesthetic and ecological value of the landscape (Young *et al.* 2009).

During this study (2010-2011) the landscape consisted of a mosaic of chalk grassland fragments on ancient burial mounds (barrows) and slopes, grassland re-creation fields of different ages since sowing, semi-improved pasture, arable farmland and woodland (Figure 3-1).

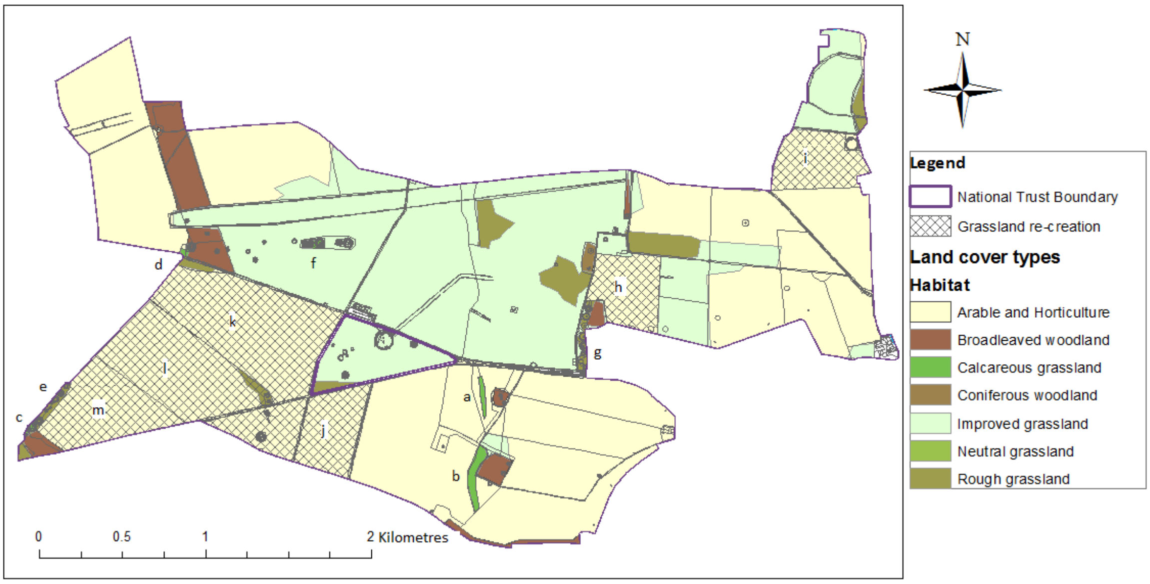

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Figure 3-1. Land cover types and sites for surveys in The National Trusts' Stonehenge Landscape boundary. Fragments of chalk (calcareous) grassland on slopes: a) Full-moon Bank, b) Luxenborough Bank, c) Winterbourne and d) Fargo Barrow) and barrow groups, e) Winterbourne Stoke Group, f) Cursus Barrows and g) King Barrows. Grassland re-creation of different ages since sowing from 2000-2009, h) Seven Barrows, i) Cuckoo Stone, j) Noice's Piece, k) Stonehenge 05, l) Stonehenge 07 and m) Stonehenge 09. Stonehenge stone-circle situated in the centre of the map.

3.3.2 Lepidoptera surveys

All survey were carried out on the National Trust owned land of the Stonehenge World Heritage Site using transect survey methods adapted from the Butterfly Monitoring Scheme (Pollard & Yates 1993, Chapter 2). During the survey, the researcher walked along the transect at a slow, steady pace allowing five minutes for each 20 m section of transect and recorded the number and species of

Lepidoptera present 5 m either side and ahead. If Lepidoptera were observed feeding, then the nectar plant species was also recorded.

Habitat transect surveys were carried out from June to September 2010 using 17, 200 m long transects located in the centre of different grassland re-creation fields of different ages since sowing and broad habitat types; re-created grassland sown in the years 2000, 2002 and 2003 (older re-creation collectively), re-created grassland sown in the years 2005, 2007 and 2009 (newer re-creation collectively), arable land (bare ground at the time), chalk grassland fragments on slopes (reference habitat) and on ancient burial mounds (barrows) and semi-improved pasture (adjacent to chalk grassland fragments on barrows) (Figure 3-1, Table 3-1). Transects were surveyed on three occasions spread across the field season, and throughout the day and were selected ad-hoc for survey in order to minimise the effect that the time of year and day would have on results.

Table 3-1. Lepidoptera transect survey sites across the Stonehenge landscape described with the name of the habitat patch (Patch), location of survey site relating to (ID) in Figure 3-1 (n,o,p,q and r not on map), Broad habitat type (Broad habitat), particular habitat type including year of grassland re-creation (Habitat) and the number of transects at each site for surveys of habitat transects (Habitat transect) or survey of matrix transects (Matrix transect).

Patch	**ID**	**Broad habitat**	**Habitat**	**Habitat transect**	**Matrix transect**
Chalk grassland fragments					
Full-moon Bank	a	Chalk fragment	Chalk slope	1	4
Luxenborough Bank	b	Chalk fragment	Chalk slope	1	4
Winterbourne	c	Chalk fragment	Chalk slope	1	2
Fargo Barrow	d	Chalk fragment	Barrow		2
Barrow groups					
Winterbourne Stoke Group	e	Chalk fragment	Barrow	1	
Cursus Barrows	f	Chalk fragment	Barrow	1	
King Barrows	g	Chalk fragment	Barrow	1	
Seven Barrows	h	Re-creation field	Older re-creation (2000)	1	
Cuckoo Stone	i	Re-creation field	Older re-creation (2002)	1	
Noice's Piece	j	Re-creation field	Older re-creation (2003)	1	
Stonehenge 05	k	Re-creation field	Newer re-creation (2005)	1	
Stonehenge 07	l	Re-creation field	Newer re-creation (2007)	1	
Stonehenge 09	m	Re-creation field	Newer re-creation (2009)	1	
Semi-improved east of Winterbourne Stoke Group	n	Semi-improved pasture	Semi-improved pasture	1	
Semi-improved north of Cursus Barrows	o	Semi-improved pasture	Semi-improved pasture	1	
Semi-improved west of King Barrows	p	Semi-improved pasture	Semi-improved pasture	1	
Arable west of Full-moon Bank	q	Bare ground	Bare ground	1	
Arable west of Luxenborough Bank	r	Bare ground	Bare ground	1	

3.3.3 Habitat quality and landscape variables

Habitat quality, defined in terms of vegetation characteristics and nectar resources were quantified throughout each transect by sampling a), five (habitat transects, survey and b), four (matrix transects survey quadrats measuring 0.5 m by 0.5 m in each 20 m segment of transect. To enable analysis and comparison between habitat and transect surveys one of the five quadrat samples from the habitat transects were taken out randomly prior to analysis to compare these results to the four quadrats of the matrix transects and to represent a 1m by 1m quadrat survey area for both transects. Vegetation characteristics were measured in terms of the mean and variation (coefficient of variation) of vegetation height and density (drop-disc method of Stewart *et al.* 2001) , henceforth referred to as vegetation density) and the percentage cover of bare ground and dead vegetation. Nectar resources were measured in terms of the density and species richness of flowering units (sensu Carvell 2002) and the density of relevant families (Dipsacaceae, Fabaceae and Asteraceae).

The average weather conditions to the nearest hour of survey were recorded from the closest meteorological station at Boscombe Down, Amesbury, Wiltshire, approximately 6.5 Kilometres WSW from the Stonehenge stone-circle. All Lepidoptera, habitat and matrix quality surveys were repeated three times during the field season (except for one chalk grassland fragment at Winterbourne labelled c and the arable transects).

The percentage cover of linear features (for example, tracks and road verges) were calculated using buffers of 50, 100, 250, 500 and 1,000 m (ArcMap Version 10.1 ESRI©) at each habitat transect to accommodate a range of scales and Lepidoptera dispersal abilities (Baguette 2003; Menendez *et al.* 2002; Merckx *et al.* 2009; Nieminen *et al.* 1999). Maps were obtained from Ordnance Survey in polygon format and any inaccurately classified land cover was edited to reflect the landscape during the surveys using personal site knowledge and Young *et al.* (2009)(Section 2.4).

3.3.4 Ecological and mobility group

Ecological groups of Lepidoptera were recorded using the classifications of Shreeve *et al.* (2001) into groups of species associated with, a) generalist ruderal-vegetation, b) short-turf herb-rich grassland, c) short-tall sward open mesotropic grassland and, d) woodland. The ruderal-vegetation group is not associated with a particular family of larval host plants, but is likely to be associated with tall and/or mature herbs and to overwinter as pupae. The larval host plants of the herb-rich grasslands associated group were Legumes and they were likely to have a symbiotic relationship with ants. The difference between the two grassland ecological groups was that those associated with short-grass herb-rich vegetation were not dependant on grasses for any part of their life-cycle, whereas, those associated with short, medium or tall warm open grassland were (Shreeve *et al.* 2001). The woodland associated group were defined as using trees or shrubs for larval host plant and adult feeding. These are referred to as ruderal-veg, herb-rich, open-grass and woodland associated species respectively (Shreeve *et al.* 2001). Mobility groups were recorded using the classifications of widespread, intermediate and sedentary mobility group which reflect emigration rates and colonisation distances (Pollard & Yates 1993). Species categorised as sedentary are unlikely to move outside the habitat patch and are considered to have a closed population structure, whereas, species categorised as widespread are wide-ranging and frequently move between habitat patches and have an open population structure. species categorised as intermediate are somewhere in-between sedentary and widespread. Day flying moths were categorised based on their association with different habitat types: the Six-spot Burnet (*Zygaena filipendulae*) was more associated with herb-rich grassland as its larval host plant is legume species *Lotus corniculatus*, (although this species will use tall grass stems and pupation sites) (Heath & Emmet 1985) and categorised as sedentary in mobility (Naumann *et al.* 1999).

3.3.5 Data analysis

3.3.5.1 Comparing variables from habitat transect and matrix transects

For habitat transects, the mean Lepidoptera density, species richness and density of ecological and mobility group categories were calculated as response variables for each habitat type per 100 m (to account for differences in sampling effort). Bray-Curtis dissimilarity index was calculated in R (version 2.11, R Core Team 2010) to compare the mean dissimilarity in community compositions between chalk grassland fragments on slopes (reference habitat) with the other habitat types. This index is less likely to over or under estimate community dissimilarity (Bloom 1981). Two habitat patches with exactly the same community compositions would have a Bray-Curtis dissimilarity value of zero whereas two habitat patches sharing no similar species would have a value of 1.

Wilcoxon sum rank and linear mixed-effects models (Poisson distribution) were calculated in R (version 3.0, R Core Team 2013) to compare the mean Lepidoptera response variables between broad habitat types of chalk grassland on slopes and barrows to grassland re-creation of all ages.

For matrix transects, the mean Lepidoptera density, species richness and density of ecological and mobility group categories were calculated as response variables for each matrix type as mean per transect. Linear mixed-effects models were created to compare the mean Lepidoptera response variables between newer grassland re-creation (1-2 years since sowing) and arable land (wheat or oil-seed rape).

All habitat transect and matrix transect mixed-effects models included explanatory variables of broad habitat/matrix type, time replicate and the interaction between these as fixed effects and the transect identity as the random effect. These used fixed and random effects; a fixed effect influences only the mean of the response variable and a random effect influences only the variance of the response variable (Crawley 2007). So random effects are variables that may affect the variation in the data but that we are not interested in testing their effects on the response variable specifically.

Habitat quality was calculated per transect for both habitat and matrix transects in terms of the total density, richness and density of those in the Asteraceae, Dipsacaceae and Fabaceae families (nectar resources), the mean and the variation in the percentage of bare ground coverage and vegetation density (vegetation characteristics) as described in Section 3.3.3 (Figure 3-2). Two levels of vegetation characteristic variation were calculated; the Coefficient of Variation of vegetation characteristics within each transect and as the Coefficient of Variation of mean vegetation characteristics within the 20 m segments in the transect. The habitat quality variables were statistically compared using Wilcoxon sum rank in R (Version 3.0, R Core Team 2013) between broad habitat types and between the matrix types as described above for Lepidoptera response variables.

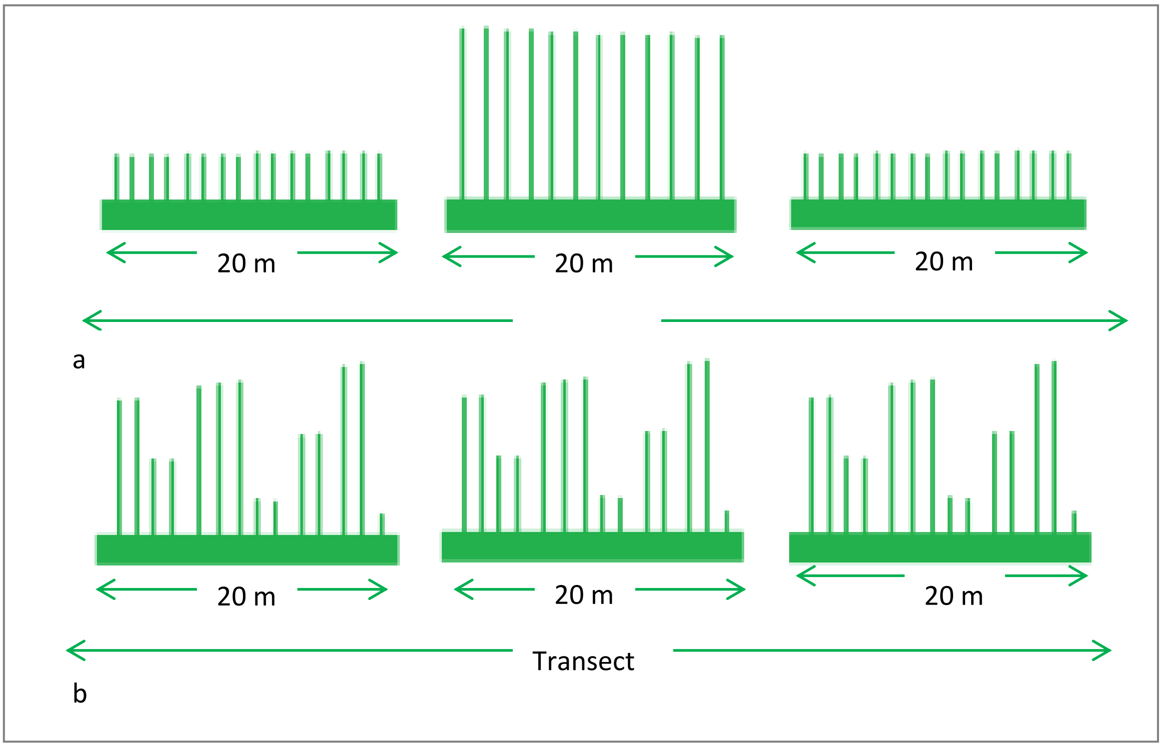


Figure 3-2. Example of vegetation characteristics variation measured as the Coefficient of Variation (CV) showing the difference between a) and b) which both have the same mean height but different CV. values . In this example transects consist of three, 20 m segments.

The nectar feeding preferences of Lepidoptera were calculated by dividing the number observed feeding on a nectar plant with the density of the nectar plant in the transect. The Lepidoptera/nectar plant network parameters for different habitats were then calculated in R (version 3.0, R Core Team 2013) using the Bipartite package.

3.3.5.2 Comparing Lepidoptera communities

Lepidoptera community compositions were analysed using multivariate techniques of unconstrained Principal Component Analysis (PCA, analysis based on just the response variable) and constrained Redundancy Analysis (RDA, analysis based on the response variable and the potential explanatory variables) conducted in CANOCO 5 (ter Braak & Smilauer 2012). These linear methods were appropriate for response data with a gradient length of less than four standard deviation units. This is a measure of how unimodal the curves of response variables are along the ordination axes and is expressed in standard deviation units. If the gradient length is below 4 then linear methods are recommended and if over 4 the unimodal methods are recommended (for example, Canonical Correspondence Analysis, CCA). Lepidoptera counts were Log(x+1) transformed prior to ordination.

In order to avoid over-fitting of the models and reduce the probability of Type 1 error (rejecting the null hypothesis when it is true), Lepidoptera communities were analysed in response to three different models in each transect type (habitat and matrix). This was due to the relatively low numbers of samples and species compared to potential explanatory values. These investigated habitat quality, nectar resources and habitat characteristics;

a) measures of habitat quality and percentage coverage of natural linear features at,
    i) habitat transects and,
    ii) matrix transects;
b) measures only of nectar resources at,
    i) habitat transects and,
    ii) matrix transects and,
c) measures of habitat characteristics at,
    i) habitat transects and
    ii) matrix transects.

Constrained ordination (PCA) tested the significance of environmental explanatory variables in explaining the variation in Lepidoptera community compositions and gave a percentage of variation explained by the model, an adjusted percentage (a more conservative percentage based on the sample size) and the contribution of each of the ordination axes. Significance of the model was based on 999 unrestricted Monte-Carlo permutations and interactive forward selection was used to choose the subset of explanatory variables that had significant conditional effects. Conditional effects are the variation that is explained by the variable once the shared variation that is explained by the other selected variables has been removed (Figure 3-3).

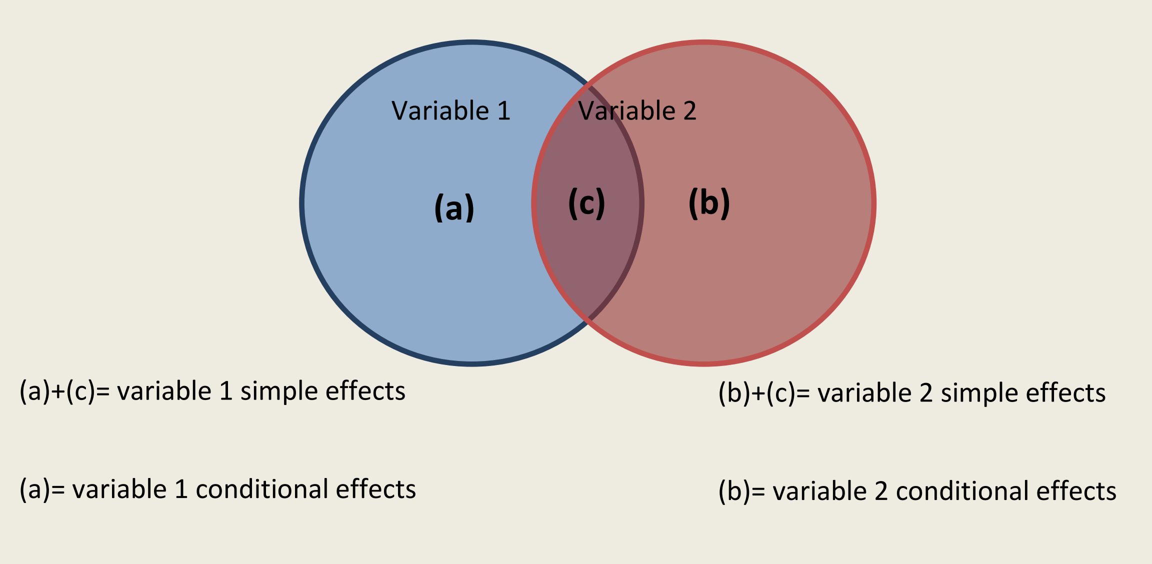


Figure 3-3. Diagram explaining simple and conditional effects and variation partitioning. The simple effects of Variable 1 (a + c), the conditional effects of Variable 1 (a), the simple effects of Variable 2 (b+c), the conditional effects of variable 2 (b) and the shared variation explained by both variables 1 and 2 (c). In variation partitioning, the variation explained by the conditional effects of variable 1 (a once c has been removed) is tested and the variation explained the conditional effects of Variable 2 (b once c has been removed) is tested. For example, if variable 1 explained 20% of the variation (simple effect), variable 2 explained 10% of the variation (simple effect) then when the explained variation that they shared of 5% was removed, then variable 1 would explain 15% of the variation (conditional effect) and variable 2 would explain 5% (conditional effect).

Variation partitioning was used to test the conditional effects of the variables in the model. This calculates the proportion of explained variation that remains once the shared variation that is explained by the other variables has been removed and tests their significance. This enables the unique contribution of each variable and their significance in the model to be tested (Figure 3-3).

Principal Coordinates of Neighbour Matrices analysis (PCNM, 1 nearest neighbour) was used to remove the variation that could be explained by spatial auto-correlation of the survey site, e.g. similarities between transects closer together could be due to their proximity rather than other explanatory variables.. This analysis partitioned the variation in Lepidoptera species composition that was explained by the spatial arrangement of the transects (using X, Y coordinates) from the variation that was explained by the environmental variables in the model. This variation explained by the spatial arrangement was then removed from the model which contains the environmental variables and the significance of the new model was tested. This works similarly to Variation Partitioning as illustrated in Figure 3-3 but in this case variable 1 is the set of environmental variables and variable 2 is the spatial variable. This was done for each model but was not significant in explaining the variation in Lepidoptera communities and so is not reported in the following results.

Lepidoptera total density, species richness and individual species response to environmental variables were analysed using Generalized Linear Models (Linear response, Poisson distribution) and used to select ecologically relevant variables for inclusion in the ordination models (see Appendix B for all GLM and RDA results). The age of the habitat type was assigned for grassland re-creation fields as the number of years since sown with species rich grassland seed. Chalk grassland was assigned an age of 60 years as this is the number of years estimated for some re-creation grasslands to reach the same botanical conditions as chalk grassland (Fagan *et al.* 2008) and semi-improved pasture was assigned an age of three years for. All species and samples were given equal weighting.

Co-variables were also included if they explained a high proportion of the variation but were not of interest. A co-variable is an explanatory variable that is either a noise or nuisance variable where the variation that it explains needs to be factored out or a variable that is important but not of interest to the study questions. Potential co-variables were measures of mean and variation (Coefficient of Variation) in cloud coverage and wind speed as well as temperature and sampling day. For habitat transects, no co-variables were used as Lepidoptera community assemblages were not significantly affected by weather conditions or sampling day (Appendix B). For matrix transects the mean percentage of cloud cover was used as a co-variable as it had the highest significance and lowest AIC when explaining Lepidoptera density in GLM and explained 24.1% of variation in community assemblages (Appendix B).

3.4 Results

3.4.1 Lepidoptera density, species richness and distributions in habitat and matrix transects

For habitat transects, 1,121 individual Lepidoptera were recorded of 18 different butterfly species and one day-flying moth species (*Zygaena filipendulae*). Species composition results indicated that Lepidoptera communities were approaching that of the target habitat. In older grassland re-creation (7-10 years since sowing) there was a lower Bray-Curtis dissimilarity compared with newer re-creation (1-5 years since sowing) but this was not significant. This was attributed to the colonisation of grassland associated butterflies such as the Marbled White (*Melanargia galathea*), Common Blue *(Polyommatus icarus*) and Meadow Brown (*Maniola jurtina*) (Table 3-2,Table 3-3).

Lepidoptera species more associated with short-grass and herb-rich habitats (Shreeve *et al.* 2001) which are characteristic of calcareous grassland such as Adonis Blue (*Lysandra bellargus*) and Brown Argus (*Arica agestis* see Appendix B), were restricted to chalk grassland fragments and absent from the grassland re-creation. Species associated with ruderal-vegetation and of widespread mobility such as the Small Tortoiseshell (*Aglais urticae*) and Large White (*Pieris brassicae*) were surveyed in chalk grassland fragments, grassland re-creation fields and arable land (see Appendix B for Lepidoptera distribution in semi-improved pasture and arable land).

Table 3-2. The eight focal species recorded at surveys at the Stonehenge landscape including code used for figures and graphs in this chapter. Ecological group of species associated with Ruderal vegetation (ruderal-veg), short-turf herb rich grassland (herb-rich) and short-tall sward open grassland (open-grass) (Shreeve *et al.* 2001) and mobility groups of sedentary, intermediate and widespread (Pollard & Yates 1993).

Common name	**Latin name**	**Code**	**Ecological group**	**Mobility group**
Adonis Blue	*Lysandra bellargus*	*Lys.bel*	Herb-rich	Sedentary
Small Heath	*Coenonympha pamphilus*	*Coe.pam*	Open-grass	Sedentary
Marbled White	*Melanargia galathea*	*Mel.gal*	Open-grass	Sedentary
6-spot Burnet	*Zygaena filipendulae*	*Zyg.fil*	Herb-rich	Sedentary
Common Blue	*Polyommatus icarus*	*Pol.ica*	Herb-rich	Intermediate
Meadow Brown	*Maniola jurtina*	*Man.jur*	Open-grass	Sedentary
Small Tortoiseshell	*Aglais urticae*	*Agl.urt*	Ruderal-veg	Widespread
Large White	*Pieris brassicae*	*Pie.bra*	Ruderal-veg	Widespread

Table 3-3. The mean Bray-Curtis dissimilarity and 1 Standard Error (SE) of Lepidoptera communities between the highest quality chalk grassland fragment reference habitat patch (Luxenborough Bank) and the other land cover types. The total number of eight focal Lepidoptera species surveyed in different land-cover types of chalk grassland fragments (Chalk), barrow groups (Barrow), older grassland re-creation fields 7−10 years old (Older grass) and newer grassland re-creation fields 1−5 years old (Newer grass). The mean and 1 Standard Error of Lepidoptera individuals surveyed in transects extending from chalk grassland fragments into a matrix type of either newer grassland re-creation of 1-2 years old (Newer grass) or Arable land (Arable).

	Habitat transects				**Matrix transects**	
	Chalk	**Barrow**	**Older grass**	**Newer grass**	**Newer Grass**	**Arable**
Bray-Curtis dissimilarity	0.33	0.39	0.48	0.58	N/A	N/A
SE	0.03	0.09	0.09	0.05	N/A	N/A
Lysandra bellargus	1.334	2.00			0.50	
SE	0.88	2.00			0.29	
Coenonympha pamphilus	0.67	3.00			1.50	
SE	0.67	2.52			1.50	
Melanargia galathea	0.67	4.00	0.33			2.50
SE	0.33	3.06	0.33			0.87
Zygaena filipendulae	22.33	0.33	54.00	0.33		0.75
SE	16.70	0.33	45.71	0.33		0.48
Polyommatus icarus	12.67	30.00	9.67	2.33	20.50	
SE	2.85	25.51	4.48	1.86	10.37	
Maniola jurtina	33.67	34.33	16.67	1.33	10.75	5.75
SE	29.20	16.37	8.01	0.88	4.37	0.85
Aglais urticae	6.33	9.67			5.75	2.50
SE	3.38	9.67			3.33	0.87
Pieris brassicae	30.33	34.33	8.00	5.33	5.25	6.50
SE	18.66	17.02	5.69	2.03	1.49	2.63

There were higher, but not statistically significant Lepidoptera densities in chalk grassland reference habitat patches on slopes and Barrow groups compared to grassland re-creation fields of all ages (Wilcoxon test, W=30, p=0.0649 per 100 m of habitat transect). Out of all the grassland re-creation fields, Seven Barrows and Noice's Piece (sown in 2000 and 2003, respectively) had the highest densities indicating that they were approaching the conditions of the reference habitat. There was significantly higher Lepidoptera richness at target chalk grassland habitat patches compared to grassland re-creation habitat patches (Wilcoxon test, W=36, p=0.0022), but no significant difference in densities of different Lepidoptera ecological and mobility groups (p>0.05, Appendix B for full results and mixed-effect models) (Table 3.3, Figure 3-4).

For matrix transects surveys crossing from target chalk grassland fragments into adjacent matrix types, 582 individual Lepidoptera were recorded consisting of 16 butterfly species and three day-flying moth species; the 6-spot Burnet moth (*Zygaena filipendulae*), Forester moth (*Adscita statices* or possibly Cistus Forester *Adscita geryon*) and Hummingbird Hawk moth *(Macroglossum stellatarum*). There were no significant differences between mean densities of Lepidoptera, species richness or densities of the different ecological groups along transects from chalk grassland fragments into newer grassland re-creation of 1-2 years old compared to arable land mixed-effects models (p>0.05, Appendix B) .This result remained even when only Lepidoptera surveyed in the matrix part of the transect were used in the analysis (results not shown).

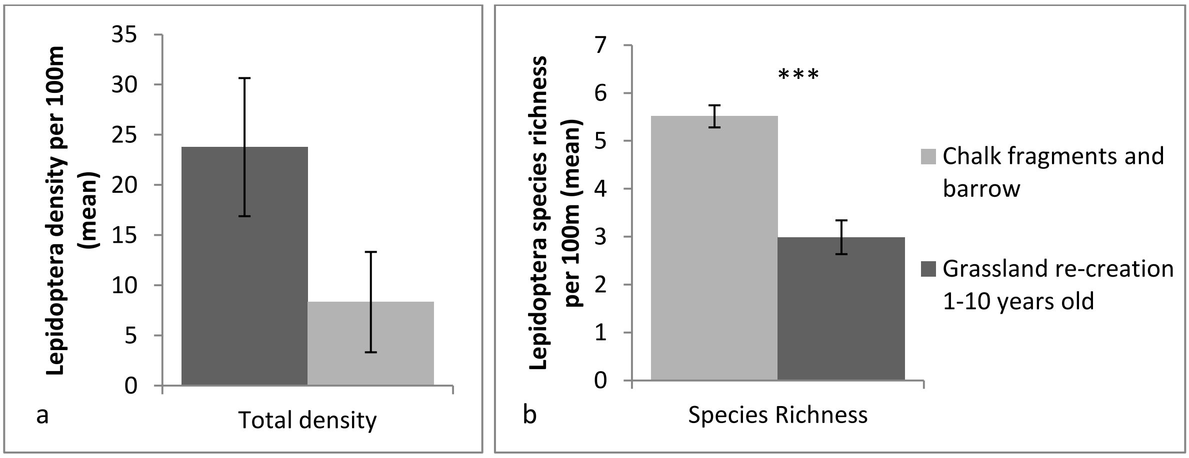


Figure 3-4. The, a) total Lepidoptera density (Wilcoxon sum rank test, W=30 p=0.0649) and, b) species richness (Wilcoxon sum rank test, W=36, p=0.0004) in broad habitat types of chalk grassland on slopes and barrows and grassland re-creation ages 1-10 years since sowing with regional seed mixtures. Significance p<0.001 ***.

Chalk grassland fragments (on slopes and barrows) had significantly higher mean densities of nectar flowers in the Asteraceae family and borderline significantly higher nectar flower richness (W=31, p=0.0411 and W=30, p=0.0649, respectively) and borderline significantly lower mean densities of Fabaceae nectar flowers (W=5.5, p=0.0542). Other variables were not significant (p>0.05) (see Appendix B for statistical comparison between all environmental variables).

A total of 234 Lepidoptera were recorded feeding on nectar plants in habitat transects. The nectar feeding interactions in the grassland re-creation were less diverse and dominated by a few individual species compared to the more complex interactions in the chalk grassland fragments, which also had the highest density of Lepidoptera feeding, followed by the barrow groups (Appendix B). The species that dominated the Lepidoptera-nectar plant interaction network were 6-spot Burnet moth (*Zygaena filipendulae*) and Meadow Brown (*Maniola jurtina*) and Geer Knapweed (*Centaurea scabiosa*), Creeping Thistle (*Cirsium arvense*) and Common Knapweed (*Centaurea nigra*) nectar plants.

3.4.2 Community compositions

3.4.2.1 Model, a) measures of habitat quality

(i) Habitat transects

Unconstrained PCA ordination on habitat transects showed that axes 1 and 2 explained 74.5% of the variation, which suggested strong gradients in the data. Transects in semi-improved pasture, arable land and new grassland re-creation (1-3 years old) were clustered to the mid left of the sample plot and grassland re-creation fields sown in the year 2000 and 2003 (h and j) were more similar to chalk grassland fragments on slopes (a and b) than to the other grassland re-creation fields as these were clustered close together(Figure 3-5. a).

The percentage coverage of linear features within a 100 m buffer of transects was selected for the habitat quality model as this variable had six significant species responses including *Maniola jurtina*, *Melanargia galathea*, *Pieris brassicae*, *Pieris napi*, *Polyommatus icarus* and *Zygaena filipendulae* (GLM positive linear response) compared to five at the 250 m scale (all species listed previously except *Melanargia galathea*) and was therefore used in the habitat transect model below (see Appendix B for all landscape RDA results).

In a constrained RDA, the environmental variables of mean coverage of bare ground, vegetation density, nectar flower richness, the age of the habitat (how many years it takes to restore) and percentage coverage of natural linear features within the 100 m buffer (all variables had a positive correlation) explained 63.8% (47.3% adjusted) of the variation (first axis p=0.004, all axes p=0.002). After interactive forward selection, the age, nectar richness and vegetation density were retained in the model and explained 55.1% (44.7% adjusted) of the variation (first and all axes p=0.002) (Figure 3-5, b, Table 3-4).

Age and vegetation density had significant conditional effects and a positive correlation once the shared variation had been removed from variation partitioning (p=0.035, 0.019, respectively). When constrained by ecological and then mobility group this model was borderline significant and significant, respectively (first axis p=0.056, all axes p=0.114 for ecology group and first axis p=0.024, all axes p=0.028 for mobility group).

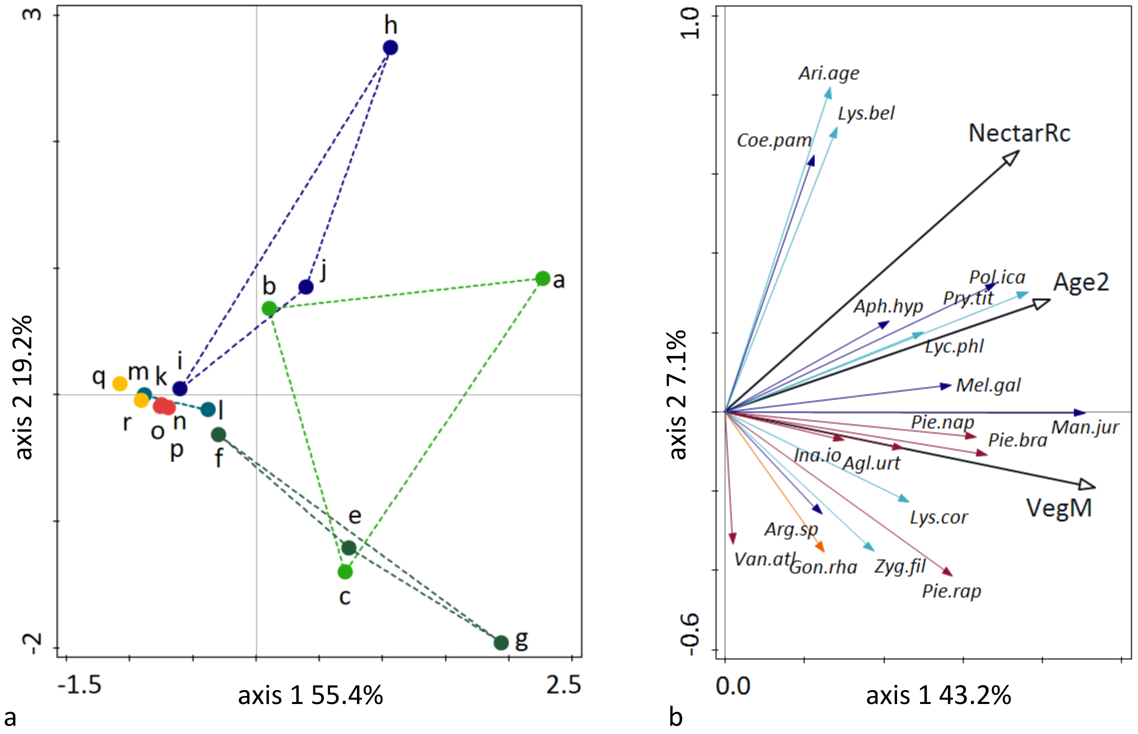


Figure 3-5. a) Principal Component Analysis, axis 1 and 2 explained 74.5% cumulatively of the variation for habitat transects. a-m relate to habitat patches/fields in Table 3-1 (note d not surveyed in habitat transects). b) Redundancy Analysis model (ai) of habitat quality in habitat transects explained 55.1% of the variation, axis 1 and 2 explained 50.34% of this cumulatively (first and all axes p=0.002). The ecological group of the Lepidoptera species response is illustrated by the colour of the arrows on, b) of ruderal-veg (dark blue), open-grass (pale blue), herb-rich (red) and woodland (orange).For non focal species abbreviations see Appendix B.

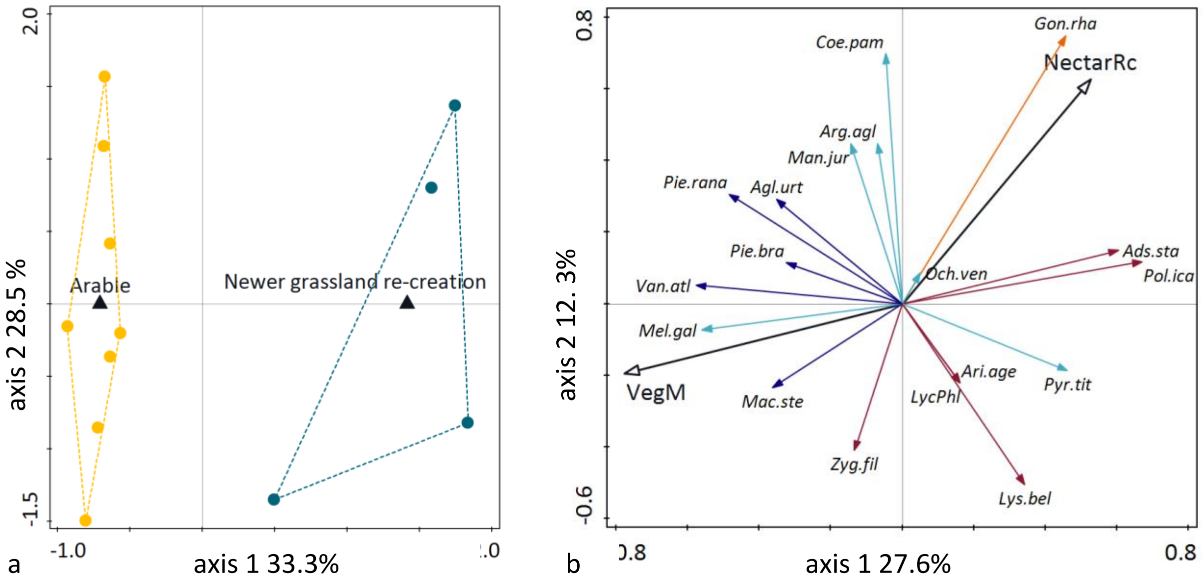


Figure 3-6. a) Redundancy Analysis model constrained by matrix type of arable or grassland re-creation explained 33.3% of the variation (all axes p=0.004), axis 1 and 2 explained 61.8% of this cumulatively. b) Redundancy Analysis model (aii) of habitat quality in matrix transects using the mean cloud coverage as a co-variable explained 39.6% of the variation (first axis p= 0.014, all axes p=0.004), axis 1 and 2 explained 39.9% of this cumulatively. Environmental variables (black arrows) were the age to re-create that habitat (Age2), nectar flower species richness (NectarRc) and vegetation density (VegM). The ecological group of the Lepidoptera species response illustrated by colour of arrows on, b) and, d) of ruderal-veg (dark blue), open-grass (pale blue), herb-rich (red) and Woodland (orange). For non focal species abbreviations see Appendix B.

(ii) Matrix transects

Unconstrained PCA ordination of matrix transects showed that axis 1 and 2 explained 6.9% of the variation cumulatively, suggesting that there were strong trends in the data. An RDA constrained by matrix type of arable or new grassland re-creation explained 33.3% (26.60% adjusted) of the variation (all axes p=0.004) (Figure 3-6, a, Table 3-4).

An RDA model using the mean percentage of cloud coverage as a co-variable and mean vegetation density, bare ground percentage coverage and nectar flower richness (all had negative correlations except nectar flower richness) as explanatory variables explained 51.6% (30.9% adjusted) of variation (first axis p=0.016, all axes p=0.002). Mean vegetation density and nectar flower richness were retained in the model after interactive forward selection resulting in a model that explained 39.6% (24.9% adjusted) of the variation (first axis p= 0.014, all axes p=0.004, Figure 3-6, b, Table 3-4).

The mean vegetation density and percentage coverage of cloud had significant conditional effects (negative correlation) when the shared variation was removed from variation partitioning (p=0.010

and p=0.066, respectively). When constrained by ecological and then mobility group the model was significant and not significant, respectively (first axis p=0.030, all axes p=0.002 and first axis p=0.280, all axes p=0.290).

Table 3-4. Summary of unconstrained (Principal Coordinate Analysis) and constrained (Redundancy Analysis) models including the full model containing all the environmental variables (Full) and after interactive forward selection (FS=) and the total (Total) and adjusted (Adj) variation explained. The cumulative explained variation of the first four axes (axis1-axis4) and the p value of the first and all axes from the Monte-Carlo permutation test. Whether the model was significant when constrained by ecological or mobility group (first axis p and all axes p=). Environmental variables include Age of the habitat (Age2), proportion of linear features in a 100m buffer (Lin100), Nectar flower species richness (NectarRc), mean percentage coverage of bare ground (BG%M), mean vegetation density (VegM) and mean percentage cloud coverage (CloudM).

	Variation explained %		**Explained variation (cumulative)**				**Permutation test p=**	
Model type	**Total**	**Adj**	**Axis1**	**Axis2**	**Axis3**	**Axis4**	**First**	**All**
Unconstrained models								
Unconstrained (habitat transect)			55.35	74.54	85.68	92.68		
Unconstrained (matrix transect)			38.45	64.89	77.94	84.01		
Matrix type (Arable and newer re-creation grassland)	33.30	26.60	33.29	61.75	74.91	82.20		0.004
a) Habitat quality								
i) habitat transects								
Age2, Lin100, BG%M, NectarRc, VegM	63.80	47.30	45.93	53.28	60.39	63.46	0.004	0.002
FS=Age 2, VegM, NectarRc	55.10	44.70	43.23	50.34	55.06	73.08	0.002	0.002
Ecological group	24.40	9.30	23.82	24.39	24.40	67.55	0.064	0.138
Mobility group	19.70	9.70	19.43	19.71	67.91	86.44	0.058	0.096
ii) matrix transects								
(CloudM), VegM, BG%M, NectarRc	51.60	30.90	28.98	42.6	51.62	69.37	0.016	0.002
FS=(CoudM), VegM, NectarRc	39.90	24.90	27.62	39.89	59.35	73.62	0.014	0.004
Ecological group	41.70	29.20	25.09	39.31	41.68	76.40	0.030	0.002
Mobility group	15.00	3.60	12.17	14.96	53.16	84.76	0.280	0.290

b) Nectar resources								
i) habitat transects								
NectarM, NectarRc, AstM, DipM, FabM	56.20	36.30	35.36	49.99	55.28	56.02	0.052	0.004
FS=NectarRc and DipM	42.70	34.50	32.99	42.66	69.97	82.41	0.004	0.002
Ecological group	37.40	24.80	24.28	37.36	80.24	100.00	0.082	0.024
Mobility group	24.30	14.80	23.96	24.26	69.87	100.00	0.038	0.064
ii) matrix transects								
NectarRc, AstM, DipM, FabM	62.70	41.40	34.53	53.51	60.65	62.73	0.008	0.002
FS= NectarRc, AstM	50.10	39.00	34.39	50.06	65.44	78.65	0.002	0.002
Ecological group	29.60	14.50	25.97	29.55	80.62	100.00	0.064	0.082
Mobility group	17.50	6.50	14.56	17.5	69.23	100.00	0.250	0.220
c) Vegetation characteristics								
i) habitat transects								
VegM, VegTranCV, VegSegCV, BG%M, BG%TranCV, BG%SegCV	57.40	31.80	40.85	53.93	56.14	57.02	0.028	0.028
FS= VegM, VegTranCV, BG%TranCV	52.40	41.40	39.03	51.20	52.40	71.80	0.002	0.002
Ecological group	12.00	0.00	9.78	11.18	12.04	63.55	0.666	0.702
Mobility group	4.70	0.00	4.02	4.72	63.30	96.49	0.830	0.838
ii) (matrix transects								
BG%M, VegM, BG%TranCV, VegTranCV	59.20	35.90	35.36	46.86	57.19	59.2	0.01	0.008
FS= BG%M, VegM	41.20	28.10	33.01	41.19	70.39	78.27	0.004	0.002
Ecological group	21.00	4.10	19.42	21.00	77.47	100.00	0.286	0.356
Mobility group	11.00	0.00	10.70	10.99	72.14	100.00	0.418	0.458

3.4.2.2 Model, b) measures of nectar resource

(i) Habitat transects

Nectar flower richness and the mean density of Asteraceae, Fabaceae and Dipsacaceae flowers (all positive correlation) explained 56.2% (36.3% adjusted) of the variation in RDA (first axis p=0.052, all axes p=0.004). Nectar flower richness and the mean density of Dipsacaceae flowers were retained in the model after interactive forward selection and explained 42.7% (34.5% adjusted) of the variation (first axis p=0.004, all axes p=0.002) (Figure 3-7, a, Table 3-4).

Nectar flower richness and the mean density of Dipsacaceae flowers had significant conditional effects and positive correlation once the shared effect had been removed from variation partitioning (p=0.017, 0.015, respectively). Variation partitioning of the three nectar plant families showed that Dipsacaceae had significant conditional effects and Fabaceae and Asteraceae did not once the shared variation was taken out (p=0.018, 0.094 and 0.131, respectively). When constrained by ecological and then mobility groups, the model was borderline significant and significant, respectively (first axis p=0.082, all axes p=0.038 and first axis p=0.024, all axes p=0.064).

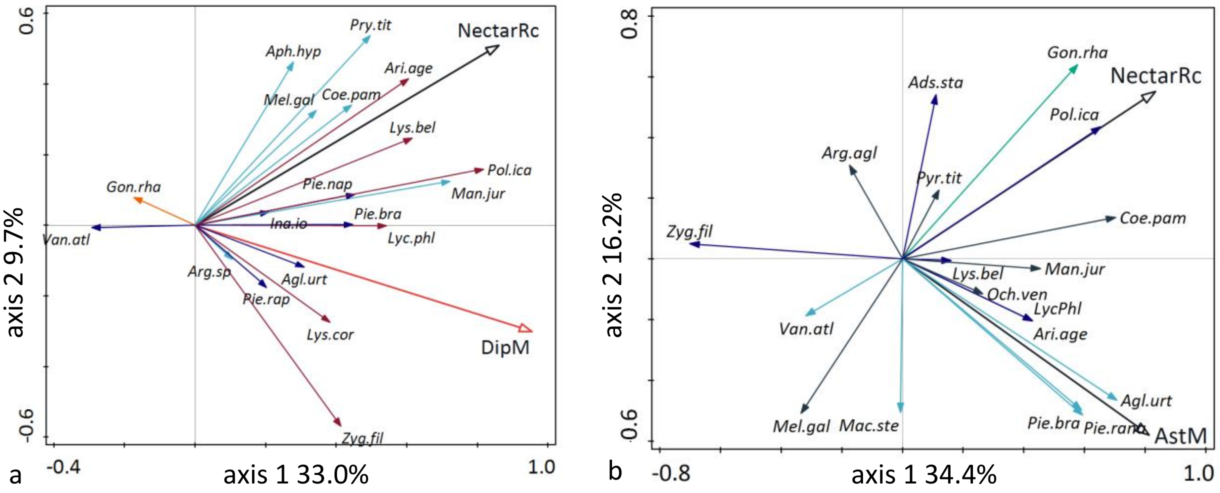


Figure 3-7. a) Redundancy Analysis model (bi) of nectar resources in habitat transects explained 42.7% of the variation (first axis p=0.004, all axes p=0.002), axis 1 and 2 explained 42.7% of this cumulatively. b) Redundancy Analysis model (bii) of nectar resources in matrix transects explained 50.1% of the variation (first axis p=0.002, all axes p=0.002), axis 1 and 2 explained 50.1% of this cumulatively. Ecological group of the Lepidoptera species response illustrated by the colour of the arrows of ruderal-veg (dark blue), Open-grass (pale blue), Herb-rich (red) and Woodland (orange). For non focal species abbreviations see Appendix B

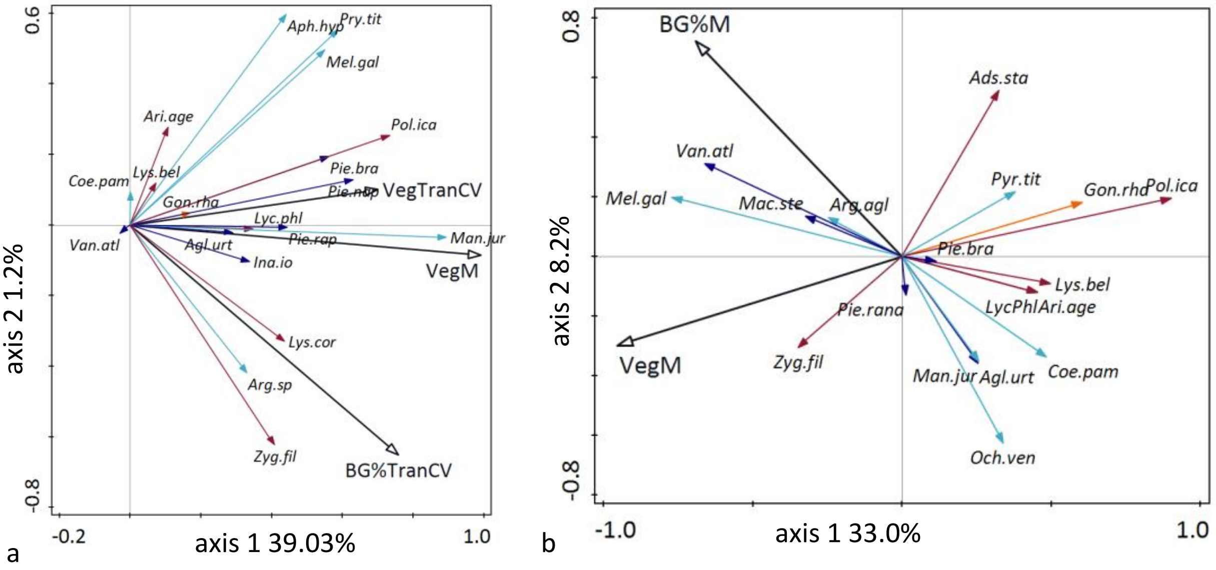


Figure 3-8. (a) Redundancy Analysis model (ci) of vegetation characteristics in habitat transects explained 52.40% of variation (first and all axes p=0.002), axis 1 and 2 explained 51.2% cumulatively. (b) Redundancy Analysis model (cii) of vegetation characteristics in matrix transects explained 41.2% of the variation (first axis p=0.004, all axes p=0.002), Axis 1 and 2 explain 41.2% cumulatively. Environmental variables (black arrows) were nectar flower species richness (NectarRc), mean density of Dipsacaceae flowers (DipM), mean density of Asteraceae flowers (AstM), mean vegetation density (VegM) and the within transect variation of vegetation density (VegTranCV) and bare ground percentage coverage (BG%TranCV). Ecological group of the Lepidoptera species response is illustrated by the colour of the arrows of ruderal-veg (dark blue), Open-grass (pale blue), Herb-rich (red) and Woodland (orange). For non focal species abbreviations see Appendix B

(ii) Matrix transects

Nectar flower richness and the mean densities of Asteraceae, Dipsacaceae and Fabaceae nectar plant families (all positive correlation) explained 62.7% (41.4% adjusted) of the variation in RDA (first axis p=0.008, all axes p=0.002). After interactive forward selection the mean nectar flower richness and the mean number of Asteraceae flowers were retained in the model, explaining 50.1% (39.0% adjusted) of variation (first axis p=0.002, all axes p=0.002) (Figure 3-7, b, Table 3-4).

The mean number of Asteraceae flowers and nectar flower species richness had significant conditional effects and positive correlation once the shared variation had been removed from variation partitioning (p=0.006 and 0.008, respectively). Variation partitioning of the three nectar flower families showed that only Asteraceae had significant conditional effects (p=0.044). When constrained by ecological and then mobility group the nectar resource models were not significant.

3.4.2.3 Model, c) vegetation characteristics models

(i) Habitat transect

Vegetation characteristics of vegetation density and bare ground percentage coverage mean and within transect and within segment variation (all positive correlation) explained 57.4% (31.8% adjusted) of variation in RDA (first and all axes p=0.028). Vegetation density and bare ground within transect variation and mean vegetation density were retained after interactive forward selection and explained 52.4% (41.40% adjusted) of variation (first and all axes p=0.002) (Figure 3-8, a, Table 3-4).

Mean vegetation density and variation in the percentage coverage of bare ground had significant conditional effects and negative correlations after the shared variation had been removed from variation partitioning (p=0.004 and 0.014, respectively). The model was not significant when constrained by ecological or mobility group.

(ii) Matrix transects

The mean percentage coverage of bare ground and vegetation density (negative correlation)and the within transect variation of bare ground coverage and vegetation density (positive correlation) explained 59.2% (35.9% adjusted) of the variation (RDA, first axis p=0.01, all axes p=0.008). The mean bare ground coverage and vegetation density were retained in the model after interactive forward selection resulted in a model explaining 41.2% (28.1% adjusted) of the variation (RDA, first axis p=0.004, all axes p=0.002) (Figure 3-8, b Table 3-4).

Vegetation density had significant conditional effects once the shared variation had been removed from variation partitioning (p=0.014). The model was not significant when constrained by ecological or mobility group.

3.4.2.4 Individual species response to the environmental variables

There were species-specific responses to the environmental variables, with all focal species associated with the increasing age of the habitat except the 6-spot Burnet moth (*Zygaena filipendulae*), whose response was explained significantly better by a quadratic function. All focal species were associated with increases in nectar flower richness except for Small Tortoiseshell (A*glais urticae*) and the 6-spot Burnet moth (*Zygaena filipendulae*) in habitat transects and all except Adonis Blue (*Lysandra bellargus*) and Large White (*Pieris brassicae*) in matrix transects. The species most associated with increased nectar flower families were *Aglais urticae*, *Lysandra bellargus*, Meadow Brown (*Maniola jurtina), Pieris brassicae* and Common Blue (*Polyommatus icarus*) to Dipsacaceae and *Aglais urticae*, *Maniola jurtina*, *Pieris brassicae* and *Zygaena filipendulae* to Asteraceae (Table 3-5).

All focal species were significantly positively associated with measures of increased vegetation density in habitat transects except *Lysandra bellargus* and Small Heath (*Coenonympha pamphilus*) (although these two species had low densities so may have not been sufficient to fit a GLM). For matrix transects, *Lysandra bellargus* and *Pieris brassicae* did not have a significant response to vegetation density but the other six focal species had significant responses but differed in their positive or negative correlations to this environmental variable (Table 3-5).

In habitat transects all of the significant environmental variables in the final models had a positive correlation with butterfly response, however, in the matrix transects these variables had a negative correlation. These include the density of Asteraceae flowers for *Zygaena filipendulae*, the percentage coverage of bare ground for *Aglais urticae*, *Maniola jurtina* and *Polyommatus icarus*, the richness of nectar flowers for *Melanargia galathea* and *Zygaena filipendulae* and mean vegetation density for all but *Melanargia galathea* (positive correlation) and *Lysandra bellargus* and *Maniola jurtina* (no effect).

Table 3-5. Individual species response to the significant environmental variables in habitat transects of age of habitat (Age2), mean density of Dipsacaceae flowers (DipM), mean vegetation density (in cm, VegM) and the within transect coefficient of variation of vegetation density (VegTranCV) and percentage coverage of bare ground (BG%TranCV). Individual species response to the significant environmental variables in matrix transects of mean density of Asteraceae flowers (AstM), percentage coverage of bare ground (BG%M), nectar flower richness (NectarRc), mean vegetation density (cm) (VegM) and percentage cloud coverage (CloudM used as a covariable in RDA analysis). R^2(%) of linear GLM (Poisson distribution, log-link function, only significant R^2 shown) and p value Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). Direction of linear response either positive (+) or negative correlation (-). For individual species response to all environmental variables see Appendix B.

Variable		***Aglais urticae***	***Coenonympha pamphilus***	***Lysandra bellargus***	***Maniola jurtina***	***Melanargia galathea***	***Pieris brassicae***	***Polyommatus icarus***	***Zygaena filipendulae***
Habitat transects									
Age2	R^2	48.40(+)	(+)	52.90(+)	45.60(+)	(+)	50.60(+)	42.70(+)	
	p=	**	(*)	*	***	(*)	***	***	
BG%TanCV	R^2				40.30(+)		16.30(+)		38.30(+)
	p=				***		**		***
DipM	R^2			43.60(+)	15.20(+)		8.50(+)	17.10(+)	
	p=			*	**		*	**	
NectarRc	R^2		(+)	63.00(+)	36.10(+)	(+)	17.60(+)	71.40(+)	
	p=		(*)	*	***	(*)	**	***	
VegM	R^2	(+)			79.90(+)	(+)	48.20(+)	38.70(+)	11.10(+)
	p=	(*)			***	(*)	***	***	**
VegTranCV	R^2				47.50(+)	52.2(+)	44.90(+)	30.40(+)	
	p=				***	*	***	***	
Matrix transects									
AstM	R^2	81.70(+)			36.30(+)		48.50(+)		43.40(-)
	p=	***			**		**		**
BG%M	R^2	30.10(-)			20.40(-)	35.50(+)		19.60(-)	

	p=	**			*	*		***	
CloudM	R^2	62.50(-)	50.70(-)		18.80(-)		32.80(-)	7.70(-)	
	p=	***	**					***	
NectarRc	R^2	27.60(+)	100.00(+)		26.50(+)	28.70(-)		29.70(+)	39.30(-)
	p=	**	*		*	*		***	**
VegM	R^2	14.90(-)	28.80(-)			47.00(+)		70.00(-)	12.50(+)
	p=	*	*			**		**	*

3.5 Discussion

3.5.1 Biodiversity enhancement as a result of the grassland re-creation at the landscape scale for Lepidoptera

3.5.1.1 Lepidoptera density, richness and community compositions

There was evidence of biodiversity enhancement within the relatively short time period of under a decade in terms of Lepidoptera density, richness and community compositions in response to the grassland re-creation in the Stonehenge landscape. There was a borderline significant difference between the density of Lepidoptera in the grassland re-creation compared to chalk grassland fragments. There were increases in community similarity (Bray-Curtis index) and older grassland re-creation sown in 2000 and 2003 were more similar to chalk grassland fragments on slopes than to the other grassland re-creation fields (multivariate analysis).

Previous surveys of the botanical characteristics of this grassland restoration and re-creation project have shown that the re-creation fields have approached similar ecological conditions to the donor habitat patches within 7-10 years (Campbell 2009; Pemberton 2011; Twiston-Davies *et al. in press*) and other calcareous grassland studies (Piqueray *et al.* 2011; Prach *et al.* 2013), supporting these results for relatively rapid colonisation. Invertebrates are likely to lag behind botanical colonisation and are expected within 10 years for butterfly communities (Woodcock *et al.* 2012a), although invertebrates characteristic of the target habitat can colonise new grasslands in as little as 2 years and some generalist species colonise newly restored habitats at the early stages (Deri *et al.* 2011).

Biodiversity enhancement is limited by low Lepidoptera species richness in grassland re-creation and the community compositions of newer grassland re-creation. Grassland re-creation overall had significantly lower species richness compared to chalk grassland fragments and a matrix of newer grassland re-creation 1-2 years old adjacent to chalk grassland fragments was not significantly different in Lepidoptera density or species richness compared to arable land. Newer grassland re-creation was more similar in terms of community compositions to semi-improved pasture and arable land in multivariate analysis.

Results from the nectar feeding interactions showed differences between chalk fragments and older and newer grassland re-creation with less diverse networks that were dominated by some individual species in grassland re-creation habitat patches (Appendix B).

3.5.1.2 Species specific response

Many Lepidoptera species surveyed across the Stonehenge Landscape were characteristic of calcareous grasslands in Europe, including the Brown Argus (*Arica agestis*), *Coenonympha pamphilus*, Small Copper (*Lycaena phlaeas*), Marbled White (*Melenargia galathea*), *Polyommatus icarus* and *Lysandra bellargus* (van Swaay 2002). Some of these species, such as *Coenonympha pamphilus* and *Melanargia galathea*, are more associated with open-grass and mesotrophic conditions in the UK (Shreeve *et al.* 2001).

The response of Lepidoptera to the significant environmental variables in terms of fit, direction and function was species specific and their distributions across the habitats of the Stonehenge Landscape were most likely attributed to their larval host specificity and the presence of these plants in the grassland re-creation fields. The colonisation of the less specialist species such as *Zygaena filipendulae* and *Melanargia galathea* in the older grassland re-creation fields is likely due to the establishment of their larval host plants (*Lotus corniculatus* and *Festuca* sp. respectively, Campbell 2009; Pemberton 2011). These species also have weaker associations with short-turf, herb-rich grassland habitats which are characteristics associated with chalk grassland (Shreeve *et al.* 2001; van Swaay 2002) and therefore further expansion of these Lepidoptera species into younger grassland re-creation fields would be predicted in the future.

Lysandra bellargus did not have a significant linear relationship with nectar flower species richness and this is more likely due to its overall low numbers in matrix transects rather than a changed association with nectar flower richness in the matrix compared to the habitat.

The more specialist species such as *Lysandra bellargus*, associated with chalk grassland and short-turf, herb rich habitats were absent from grassland re-creation fields (Shreeve *et al.* 2001; van Swaay 2002). This is probably due to the restriction of their larval host plant Horseshoe Vetch (*Hippocrepis comosa*) to chalk grassland fragments, potentially inhibiting colonisation (although this species was in the original seed mixture sown into the 2000 grassland re-creation field) and *Lysandra bellargus* adults and eggs have been surveyed on *Hippocrepis comosa* on these fragments (Appendix B). Individuals of *Lysandra bellargus* were recorded twice in matrix transects of newer grassland re-creation under 40 m from the chalk grassland fragment, indicating the potential of this new grassland habitat for additional nectar resources. Additionally, there were plans to extend the grassland re-creation to encompass the chalk grassland fragments on slopes at Full-moon Bank and Luxenborough Bank which went ahead at the end of the year 2012. The restriction of *Lysandra bellargus* to chalk grassland fragments may also be due to their symbiotic relationship with ants (*Myrmica sabuleti* and *Lasius alienus* Forster, Thomas 1983) which may need to colonise these new habitats along with *Lysandra bellargus* in order to achieve for biodiversity enhancement for these species.

3.5.1.3 Summary

It is vital to evaluate grassland re-creation and biodiversity enhancement using a variety of measures such as Lepidoptera density, richness, the distributions of individual Lepidoptera species and the community compositions as made evident by differences in these measures of biodiversity enhancement in this study. Biodiversity enhancement measured on Lepidoptera densities or richness alone may be inaccurate as communities may be different, for example in a previous study, d higher densities of Lepidoptera surveyed in sown wildflower meadow strips and no differences between species richness but the community compositions were however, different (Haaland & Bersier 2011). The Lepidoptera species specific responses indicate that grassland re-creation may only result in biodiversity enhancement for some species; whether this relates to different ecological classifications or mobility groups is discussed (section 3.5.3). Biodiversity enhancement should also be measured in terms of ecological interactions and a pilot study to investigate Lepidoptera nectar feeding was conducted in the different habitats types of Lepidoptera feeding on nectar plants (Appendix B).

3.5.2 The habitat and landscape traits that encourage colonisation of new habitats and the movement of species from isolated chalk grassland fragments

3.5.2.1 Habitat scale environmental variables

The age of the habitat (or age to re-create that habitat) explained a large proportion of the variation in the multivariate analyses for habitat transects, significantly explaining Lepidoptera density and richness in GLMs (Appendix B), Lepidoptera occurrence in the RDA analysis and had significant conditional effects (along with vegetation density) after variation partitioning.

Multivariate analysis results indicated the importance of environmental variables that could be managed for, such as increased nectar flower richness and variation in vegetation density for Lepidoptera occurrence. Vegetation density, nectar flower richness and nectar flowers in the Dipsacaceae and Asteraceae families were the environmental variables significantly explaining Lepidoptera occurrence for both habitat and matrix type transects. Although these environmental variables were positively correlated with the age of the habitat (correlation coefficient of 0.51 for vegetation density and 0.69 for nectar flower richness in habitat transects, (data not shown), vegetation density explained more variation than the age of the habitat and was also significant after variation partitioning. Nectar flower richness was not significant after variation partitioning but was significantly positively correlated with Lepidoptera density and richness whereas vegetation density was only significant for density (richness was borderline significant) in habitat type GLMs (Appendix B). In addition to this, the effect of increasing vegetation density in matrix transects was significantly negative.

Nectar source abundance and diversity are important variables in explaining Lepidoptera occurrence (Clausen *et al.* 2001; Haaland & Bersier 2011) and flower visitor diversity (Ebeling *et al.* 2008), although does not necessarily reflect pollinator diversity (King *et al.* 2013). The abundance of nectar rich sources in composite flowers such as Field Scabious (*Knautia arvensis*) in the Dipsacaceae family for example were the preferred nectar plant in uncultivated habitats of organic farms for butterflies and burnet moths (Clausen *et al.* 2001).

Responses to the environmental variables were species specific but species within the same ecological and mobility groups responded similarly. All species that had a significant response to increased nectar flower richness and densities of nectar flowers in the Dipsacaceae family had a positive correlation with these variables. Lepidoptera individual species response was more variable for in terms of significance and direction in response to increased vegetation density.

Botanically, differences between chalk grassland fragments habitat patches and grassland re-creation fields of all ages were significant in terms of nectar plant richness and the densities of Asteraceae and Fabaceae families (Appendix B). In chalk grassland fragment reference habitat patches there were significantly higher mean densities of nectar flowers in the Asteraceae family (dominated by knapweeds such as Common Knapweed, *Centaurea nigra* as well as Smooth Hawksbeard, *Crepis capillaris*), borderline significantly higher nectar flower richness and significantly lower mean densities of Fabaceae (dominated by Sainfoin, *Onobrychis viciifolia* and Bird's-foot Trefoil, *Lotus corniculatus*). These differences in nectar resources between grassland re-creation and reference habitat patches were significant in explaining Lepidoptera community compositions and the responses of individual species (RDA, GLM).

3.5.2.2 The influence of the landscape

The results presented suggest that linear features were not as important for Lepidoptera occurrence as habitat characteristics in this study as they were not retained in habitat type models after interactive forward selection. These findings are supported by some previous studies that concluded that habitat patch quality is more important for overall species conservation actions and for butterflies in calcareous grasslands and (Hodgson *et al.* 2011; Hodgson *et al.* 2009; Rosin *et al.* 2012).

The influence of the landscape is nonetheless important to invertebrates for facilitating movement (Delattre *et al.* 2010b), enhancing biodiversity (Vergnes *et al.* 2012), affecting patch characteristics (Ockinger *et al.* 2012) and supporting populations in fragmented landscapes (Oliver *et al.* 2010; Steffan-Dewenter & Tscharntke 2002) and therefore should not be overlooked. Due to the importance of the landscape in effecting Lepidoptera occurrence, and therefore the effect of restoration on biodiversity enhancement is likely to be a combination of habitat quality and landscape characteristics such as connectivity (Haaland & Bersier 2011; Heer *et al.* 2013; Ouin *et al.* 2008; Thomas *et al.* 2001b).

3.5.2.3 Summary

The species-specific responses to the environmental variables examined here reinforce the importance of management designed for heterogeneity in vegetation structure and nectar resources for enhancing the conservation value of grassland re-creation habitats. It should be noted that interpretations of these results are limited by the linear methods used especially as Lepidoptera response to habitat characteristics may be more appropriately explained by a quadratic function which describes an optimum vale of that variable rather than a linear relationship. For example, individual species responses to vegetation height differed and the high vegetation density of arable matrix transects resulted in a negative effect on community compositions as measured as a different community composition from the target chalk grassland habitat.

Despite the weak effect of landscape in this study it is important to consider conservation at large spatial as well as temporal scales to understand plant and insect interactions and populations in fragmented landscapes (Tscharntke & Brandl 2004) and to consider the landscape as dynamic rather than static for butterfly populations (Aviron *et al.* 2007). These aspects were not addressed in this study and are appropriate avenues for future studies. Additionally, it needs to be highlighted that the lack of a landscape effect may also be due to the experimental design which was restricted by the study area. The constraints of the study area meant that there was low replication as well as confounding variables such as the age of habitat, size and isolation of chalk fragments, grazing regime and density and seed source of grassland re-creation. In addition to this, due to the small study site many habitat patches may have not been spatially independent and the landscape characteristics are highly variable. Due to these reasons future research recommendations are made in Chapter 7 in order to overcome some of the challenges of working in real landscapes.

3.5.3 The species traits that encourage the colonisation of new habitats and the movement from isolated chalk grassland fragments

3.5.3.1 Ecological group

Open-grass associated species responded positively to grassland re-creation with high abundances of *Maniola jurtina* and *Melanargia galathea* in grassland re-creation fields of all ages. Herb-rich associated species colonised older grassland re-creation fields; especially *Polyommatus icarus* and *Zygaena filipendulae*. New grassland re-creation potentially encouraged the colonisation of some herb-rich species as illustrated by the matrix transect results, potentially due to high nectar plant abundance.

Models were significant (and borderline significant) when constrained by ecological group in cases when they included environmental variables relating to nectar resources. When the models were constrained by ecological group they were borderline significant for the habitat quality and nectar resource models in habitat transects (Table 3-4), significant for the habitat quality in matrix transects and borderline significant for nectar resources in matrix transects.

3.5.3.2 Mobility group

Lepidoptera species of sedentary, intermediate and widespread mobility were surveyed in grassland re-creation fields although the species restricted to chalk grassland and barrows in habitat transects *Lysandra bellargus* and *Coenonympha pamphilus* were mainly sedentary. There were no significant differences between chalk grassland fragments and grassland re-creation fields or between matrixes of arable or new grassland re-creation in species density due to the species specific responses to these habitat and matrix types. For example *Zygaena filipendulae* and *Melanargia galathea* are classified as sedentary and were recorded in older restoration and arable matrix types.

Models constrained by mobility group were borderline significant for habitat transects in terms of the habitat quality and nectar resources. Models constrained by mobility group were also borderline significant for matrix transects in terms of nectar resources depending on the mobility classification of the Green-veined/Small White (*Pieris napi/Pieris rapae*) combined group (was borderline significant when *Pieris napi/Pieris rapae* were classed as widespread and reported in the Appendix B).

3.5.3.3 Summary

It is crucial to consider different ecological and mobility groups of Lepidoptera as these can be responsible for changes in community compositions due to trait specific responses to habitat and landscape characteristics (Ockinger *et al.* 2009; Thomas 2000) and lags in the colonisation times of particular groups and species (Woodcock *et al.* 2012a; Woodcock *et al.* 2012b). Overall, ecological and mobility groups did not significantly differ between reference and grassland re-creation habitat patches or between arable and new grassland re-creation matrix in terms of mean densities; however, in multivariate analysis there were significant differences. This was potentially due to species specific responses as well as high variation between the mean densities of Lepidoptera in different habitats and the low number of replicate surveys per habitat type. When constrained by ecological group more models were significant compared to when constrained by mobility group; however, these groups are not completely independent of one another and the use of these broad classifications may not remain static as fragmentation-caused selection can alter Lepidoptera traits and host plant specificity (Hardy *et al.* 2007; Ockinger & Van Dyck 2012).

3.6 Conclusion

This case study of chalk grassland at the landscape scale in the UK provides evidence that biodiversity enhancement as a result of grassland re-creation can be obtained within a decade for some Lepidoptera groups and species. The colonisation of specialist species may lag behind, requiring additional time and specific habitat management. Habitat conditions that can be managed for can be as important as the age of the restoration habitat patch and therefore prescribing the appropriate management is vital to encourage colonisation by a range of groups and species.

Limitations of biodiversity enhancement at this landscape restoration project at the Stonehenge Landscape arise from the complexity of restoring invertebrate communities. Such restoration projects will not achieve biodiversity enhancement without the establishment of species specific and habitat patch characteristic host plants. Insect colonisation will inevitably lag behind vegetation in restoration projects, but the rate of this can be managed for if the group and species specific requirements of the target taxa are understood and appropriate management is undertaken.

The main assumption of this study is that butterfly biodiversity as measured by species richness, abundances and community assemblages can be an indicator for other groups, but this is not always the case (Biesmeijer *et al.* 2006; Carvalheiro *et al.* 2013). Also, this study did not show a landscape effect on butterfly community assemblages, this may be due to the confounded survey site and low replication and therefore conclusions relating to landscape effects can not be confidently made here. This could be addressed in future studies by comparing a number of study landscapes undergoing restoration. Additionally, species richness and abundances were measured, this is not always the best measure for biodiversity enhancement and association to a targeted habitat may be more appropriate, e.g. habitat affinity indices (Deri *et al.* 2011).

Despite the potential of habitat re-creation to restore connectivity to our fragmented landscapes, protected areas are still important for biodiversity (Thomas *et al.* 2012) and this means that habitat re-creation and restoration is just one of a range of methods for landscape conservation and protection. Overall habitat restoration at the landscape scale is promoted as conservation policy as an effective method alongside habitat conservation to enhance landscape connectivity, biodiversity and facilitate the migration of species in response to climate change (Lawton *et al.* 2010; Pfadenhauer 2001).

Chapter 4 Impacts of habitat creation on boundary-crossing behaviour of grassland butterflies

4.1 Introduction

Measuring the effect of habitat restoration and re-creation projects on biodiversity is complex (Ruiz-Jaen & Aide 2005; SER 2004). Just as different taxa respond differently to habitat fragmentation (Aviron *et al.* 2005; Diekotter *et al.* 2008; Hendrickx *et al.* 2007; Keller *et al.* 2013; Ricketts 2001), their response also differs in relation to restoration measures. This means that the effect of restoration on biodiversity and on the behaviour of organisms may depend on the measures and identity of species groups studied.

A variety of studies have documented invertebrate responses to habitat fragmentation, habitat edges and the intervening matrix land cover that separates habitat patches for example, (Conradt & Roper 2006; Delattre *et al.* 2013; Matter & Roland 2002). Many of these are species specific, either focussing on a species of conservation concern (Pickens & Root 2009; Severns *et al.* 2013; Skorka *et al.* 2013) or a model organism for example, Meadow Brown butterfly (*Maniola Jurtina*) in fragmented agricultural systems (Delattre *et al.* 2013; Ouin *et al.* 2008). Whilst these studies give insight into specific conservation actions or conclusions based on the study organism that could be transferable to others, responses to fragmentation, matrix and habitat edges are species-specific (Clausen *et al.* 2001; Ouin *et al.* 2004; Prevedello & Vieira 2010; Ricketts 2001; Ries & Debinski 2001). Very few look at a range of species and consider the differing responses of groups based on traits or habitat and resource associations (but see van Noordwijk *et al.* 2012a; Woodcock *et al.* 2012a; Woodcock *et al.* 2012b).

Many recent reviews have investigated the influence of the intervening matrix land cover in dispersal, mainly studying broad contrasting land cover types and have concluded that overall a matrix more homogenous in vegetation structure is more permeable to movement (Eycott *et al.* 2012; Prevedello & Vieira 2010; Prugh *et al.* 2008). However, the matrix can provide resources, for example, supplementary and complementary resources (Ouin *et al.* 2004) and therefore permeability is likely to be influenced by a combination of vegetation structure (density and height) and available resources. The matrix can provide additional resources, facilitate connectivity and buffer habitat patches (Clausen *et al.* 2001; Ouin *et al.* 2004; Rosin *et al.* 2012) and a dichotomous view of habitat and matrix may not be appropriate.

A key area in studying the effects of habitat fragmentation and its mitigation involves examining the behaviour of individuals at habitat boundaries for example, (Ricketts 2001; Ries & Debinski 2001; Schtickzelle & Baguette 2003; Schultz *et al.* 2012). Boundary crossing is not random or dependant on the probability of encountering the habitat boundary and can be modelled and predicted depending on habitat, boundary and matrix characteristics (Conradt *et al.* 2000; Conradt & Roper 2006; Delattre *et al.* 2010a; Ries & Sisk 2008). An individual's decision to cross a boundary is the first step towards migration to new habitats (Clobert *et al.* 2004), the first component in measuring landscape connectivity (Tischendorf & Fahrig 2000). Individual behaviour is also vital in evaluating metapopulation persistence (Heinz *et al.* 2006). However, not all crossing behaviour will result in immigration, for example, some butterflies exhibit foray loop behaviour where they will cross a habitat boundary, fly through the matrix for a few metres and then return to the original habitat patch (Conradt & Roper 2006; Delattre *et al.* 2010a).

Current nature conservation policy advocates management for the enhancement of landscape connectivity to increase biodiversity and mitigate some of the negative effects associated with habitat fragmentation (Filz *et al.* 2013; Lawton *et al.* 2010; Wagner *et al.* 2013). Habitat re-creation is an important component of this, but it can take decades to reach the specific conditions of the target or source habitat (Fagan *et al.* 2008) and the colonisation of animals may lag behind (Woodcock *et al.* 2012a; Woodcock *et al.* 2012b). However, transitional land cover types that have similar vegetation structure in terms of height and density and offer resources to the target organisms can be cost effective for increasing biodiversity value and dispersal over short time periods (Deri *et al.* 2011; Diepenbrock & Finke 2013; Donald & Evans 2006; Ockinger & Smith 2007b; Ouin *et al.* 2004) and eventually given time and management may reach the target conditions.

Management of new habitats is a vital factor that influences their species richness and composition (Batary *et al.* 2012; Buri *et al.* 2013; Jacquemyn *et al.* 2011; Mitchley & Xofis 2005) especially regarding grasslands (review by Rook *et al.* 2004). Understanding the response of organisms to both structural characteristics and resource availability across habitat boundaries may provide insight into management options that could encourage colonisation of new habitats and provide management options targeted at encouraging dispersal. The distribution, abundance and behaviour of mobile insects can be influenced by a range and interaction of environmental and ecological variables which includes vegetation height and density as well as available nectar and host-plant resources, weather conditions, time of the years and can be density dependent (Berg *et al.* 2011; Clausen *et al.* 2001; Heer *et al.* 2013; Ries & Debinski 2001; Schultz *et al.* 2012).

4.2 Aims and Hypotheses

Aims;

- To investigate the behaviour of Lepidoptera at habitat boundaries in relation to their different ecological and mobility groups.
- To compare boundary behaviour for Lepidoptera in their habitat compared to that in the adjacent land cover types.
- To study Lepidoptera boundary behaviour in relation to the adjacent land cover types of new grassland re-creation or arable land.
- To determine whether boundary behaviour is affected by variables relating to vegetation characteristics, nectar plants, density dependence and weather conditions.

Hypotheses;

i. New grassland re-creation will increase with functional connectivity for Lepidoptera species associate with grasslands.
ii. There will be more crossing behaviour by species that are less specialist in larval host-plants compared to those species with specialist larval host-plants.
iii. There will be more crossing behaviour by species with higher mobility compared to those species with lower mobility.
iv. There will be more crossing behaviour and a higher permeability value with an adjacent land cover more similar in vegetation structure and nectar resources to the chalk grassland fragment.

4.3 Methods

4.3.1 Study site

The study site was the Stonehenge World Heritage Site (WHS), Wiltshire, UK (see Chapter 2 for full details) where over 500 hectares of former arable land are currently undergoing management for habitat creation using species-rich locally-sourced chalk grassland seed mixtures. This landscape consists of small fragments (ranging from 0.22-1.98 ha) of ancient chalk grassland on slopes and groups of burial mounds (barrows) which have retained many of the characteristic chalk grassland plant and butterfly species. Surveys were located at four of these chalk grassland fragments; Full-moon Bank, Luxenborough Bank, Winterbourne Stoke Group and Fargo Barrow, all within the Stonehenge Landscape estate owned by the National Trust.

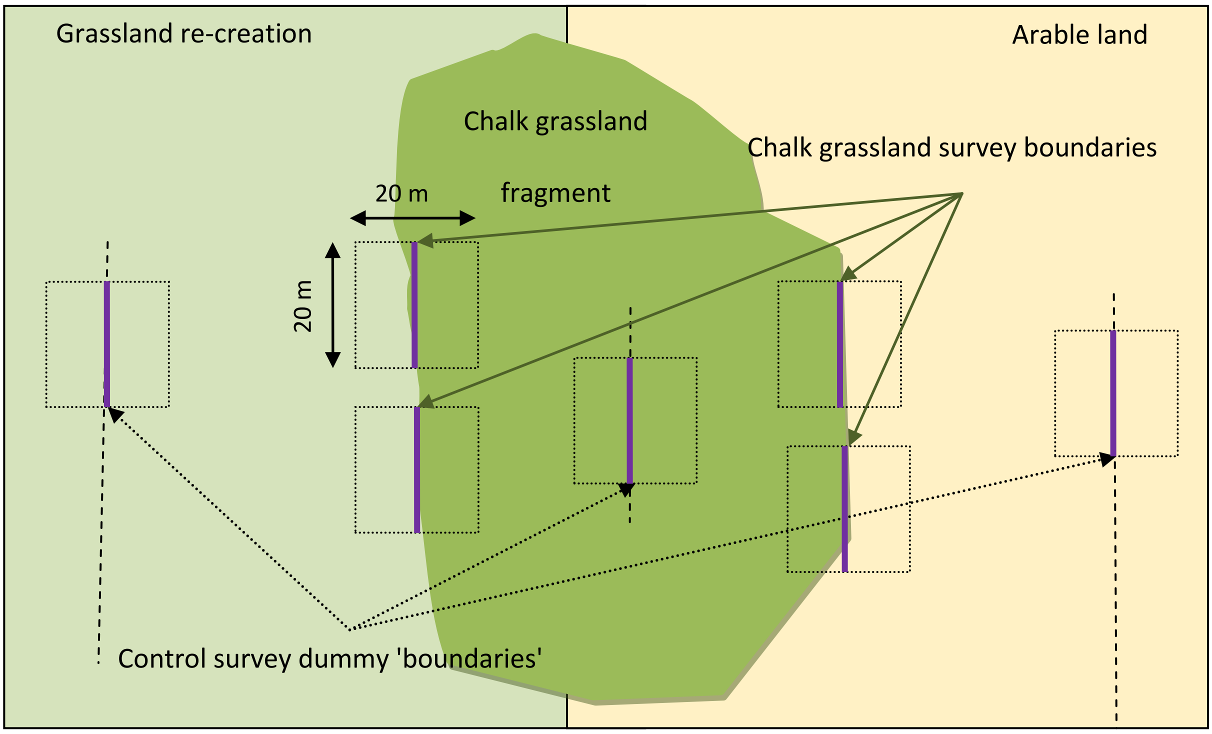


Figure 4-1. Schematic of habitat boundary surveys at a chalk grassland fragment. This shows boundary surveys located at the edge of the chalk grassland fragment and control surveys in the centre of the chalk grassland fragment and the adjacent land cover with dummy 'boundaries'. Survey area around each boundary survey is 20 m by 20 m.

At each chalk grassland fragment, four 20 m long survey boundaries, were set up on boundaries with adjacent land cover of either arable land or new grassland re-creation sown in the years 2009 or 2010 (Figure 4-1, Table 4-1). For those fragments with long edges running north to south, two survey boundaries were set up on the western edge of the fragment and two on the eastern edge. At Fargo Barrow only two survey boundaries were set up (western and northern edges) due to its small size. A total of fourteen survey boundaries were set up (Table 4-1). Control surveys were also carried out in areas of continuous habitat within the chalk grassland fragment and in the adjoining land cover type. In these control surveys a dummy 'boundary' was assigned parallel to the corresponding fragment boundary (Figure 4-1). Boundary and control surveys were not paired but control surveys were used to give an indication of Lepidoptera behaviour in continuous land cover.

Table 4-1. Survey boundary location, chalk grassland fragment, side of chalk grassland fragment and adjacent land cover type for year 2011-2012.

Chalk fragment Location	Side	Adjacent land cover (2011)	Adjacent land cover (2012)
Full-moon bank	West	Arable (Wheat)	Arable (Oil-seed rape)
Full-moon bank	West	Arable (Wheat)	Arable (Oil-seed rape)
Full-moon bank	East	Arable (Wheat)	Arable (Oil-seed rape)
Full-moon bank	East	Arable (Wheat)	Arable (Oil-seed rape)
Luxenborough bank	West	Arable (Wheat)	Arable (Oil-seed rape)
Luxenborough bank	West	Arable (Wheat)	Arable (Oil-seed rape)
Luxenborough bank	East	Arable (Oil-seed rape)	Arable (Wheat)
Luxenborough bank	East	Arable (Oil-seed rape)	Arable (Wheat)
Winterbourne Stoke group	West	Semi-improved pasture	Semi-improved pasture
Winterbourne Stoke group	West	Semi-improved pasture	Semi-improved pasture
Winterbourne Stoke group	East	Grassland habitat re-creation (09)	Grassland habitat re-creation (09)
Winterbourne Stoke group	East	Grassland habitat re-creation (09)	Grassland habitat re-creation (09)
Fargo Barrow	West	Grassland habitat re-creation (11)	Grassland habitat re-creation (11)
Fargo Barrow	North	Grassland habitat re-creation (11)	Grassland habitat re-creation (11)

4.3.2 Lepidoptera surveys

Surveys of Lepidoptera behaviour were carried out from May to July2011 and 2012. Due to unsuitable weather conditions in May-July 2012, only 39 individual Lepidoptera flight paths were recorded within the chalk grassland fragments (Table 4-2). Therefore, only surveys from 2011 are hereafter reported on. Surveys were conducted between 10am and 4pm and effort was taken to survey the same site at different times of the day in order to minimise the effect of survey time on behaviour.

Lepidoptera behaviour may be different at arable boundaries with adjacent oil-seed rape crop compared to winter wheat crop and therefore the aim was to compare these differences between the two years of data (2011, 2012). However, this was not possible due to unsuitable weather conditions in 2012 and as comparison with just 1 year would be confounded by variables relating to the different locations of theses boundaries, behaviour comparisons between these two crops was not investigated but is acknowledged.

Table 4-2. Summary of the numbers of Lepidoptera recorded in 2011 and 2012, in chalk grassland fragment control plots (Control) and at chalk grassland fragment boundaries (Boundary) with flight paths starting at the chalk grassland side of the boundary or dummy 'boundary' (in brackets). Numbers in total and recorded in each survey month of May, June or July. Whether vegetation surveys were conducted after Lepidoptera flight path surveys are also indicated (Yes).

	Survey 2011			**Survey 2012**		
	Lepidoptera behaviour		**Vegetation**	**Lepidoptera behaviour**		**Vegetation**
	Control	**Boundary**		**Control**	**Boundary**	
Total	428	682		55	75	
1 May	16 (16)	76 (51)		13	41 (17)	Yes
2 June	130 (54)	197 (133)	Yes	42	34 (22)	Yes
3 July	282 (213)	409 (293)	Yes			

Survey protocols were based on those used by Ries & Debinski (2001), adapted to the restrictions of the survey site and aims and objectives of the study. A survey area of 20 m by 20 m was set up over each boundary (and control) survey which were centred on the boundary between the chalk grassland fragment and the adjacent habitat (Figure 4-1). Bamboo poles were used to mark the corners of the survey area and a 10 m grid within each to enable butterfly positions within the survey area to be estimated and flight paths to be recorded. Due to the small size of the fragments, larger survey areas were not feasible.

Surveys were conducted by the researcher standing at the chalk grassland fragment edge and tracking the flight path of individual Lepidoptera in the survey area. Each individual Lepidoptera flight path were surveyed for three minutes, until the individual became stationary for more than three minutes or if they moved more that 20 m from the edge of the survey area (more than 40 m from the survey boundary). Each survey boundary was surveyed by visually searing the area for a total of 20 minutes on three occasions, once in May, June and July, with equal survey effort allocated to visually searching the adjacent land cover and chalk grassland fragment side of the boundary.

The species, start and finish location (in the chalk grassland fragment or the adjacent land cover) and flight path of Lepidoptera within the survey area were recorded and the survey area exiting behaviour was subsequently allocated to a category, either 'crossing', 'following' or 'avoiding' the boundary. Individuals were allocated to a further category, 'staying', if they did not exit the survey area or their flight path was too convoluted to assign to a single behaviour (Figure 4-2). These categories were mainly assigned by the survey edge by which the individual exited the survey area by; if by the habitat boundary they would be assigned as "crossing", if by the edge perpendicular to the boundary as "following", if by the edge parallel to the boundary as "avoiding" and if they did not exit the survey area or their flight path was too complicated to assign just one behaviour they were assigned as "staying".

The survey methodology of this study did not include the capture, mark and recapture of individuals, which would have eliminated the risk of recording the flight path of the same individual. However, to minimise the risk of this type of pseudoreplication, effort was taken to select a different species or sex of Lepidoptera for each recorded flight path and there was an average of approximately 15 days between survey replicates at each site. Estimation of flight path was appropriate to assign categorical survey area exiting behaviour and the start and end location of individuals. Alternative methods involving the capture and marking of Lepidoptera, or that measure precise step length and turning angles and consequently require accurate following of individuals, were beyond the resources of this study.

Surveys were carried out in weather and conditions defined as acceptable for similar surveys by the UK Butterflies Monitoring Scheme (Pollard & Yates 1993, Chapter 2).

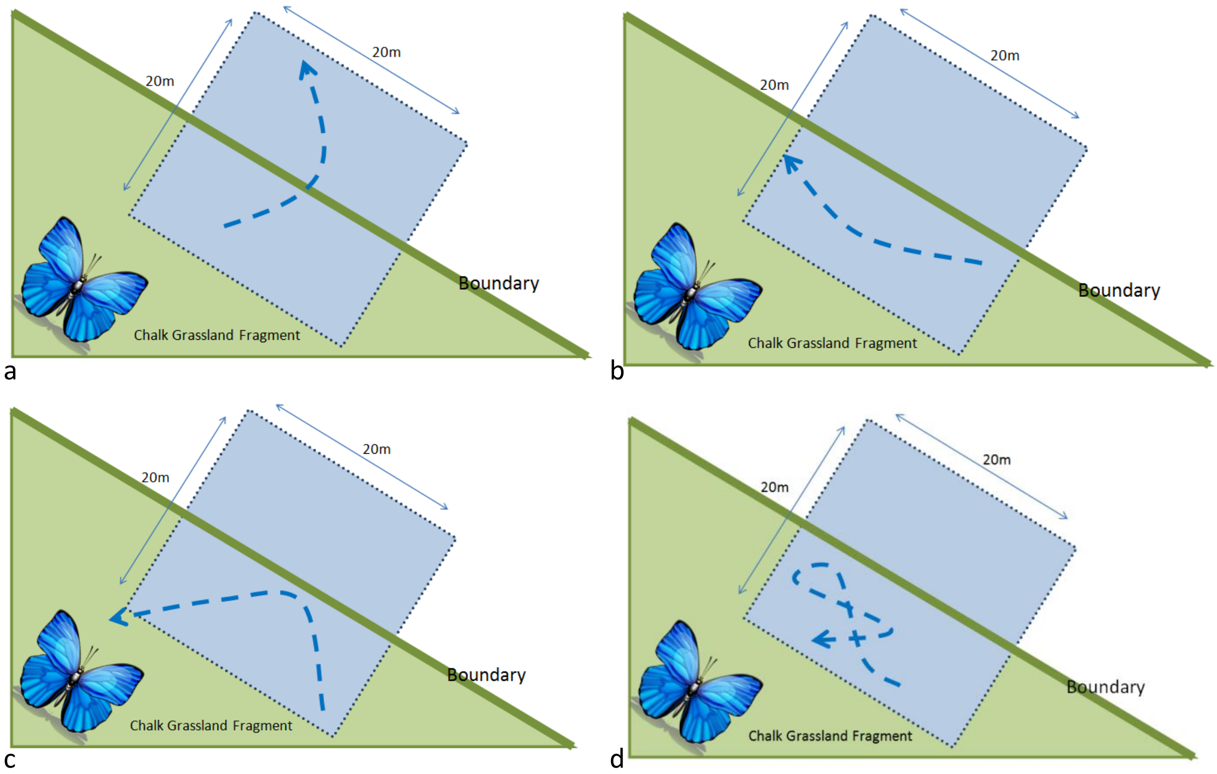


Figure 4-2. Graphical representation of a Lepidoptera survey area exiting behaviour showing an example of the flight path and the subsequent allocation of behaviour categories, a) 'crossing', b) 'following', c) 'avoiding' and, d) 'staying'.

Measures of vegetation characteristics and nectar flower availability were recorded for each plot using eight, 0.5 m by 0.5 m quadrats (four on the adjacent land cover side and four on the chalk side of the boundary chosen ad hoc). Recorded vegetation characteristics included the mean and variation (coefficient of variation) in vegetation height and density (using the drop disc method described by Stewart *et al.* 2001, henceforth referred to as vegetation density), at a rate of one drop per quadrat) and percentage cover of bare ground. Nectar flower availability was measured as the number of flowering units of nectar flowers, species richness and numbers of those in the Asteraceae, Fabaceae and Dipsacaceae families. Nectar flowers were selected based on the nectar plant database (Hardy *et al.* 2007). Botanical characteristics were surveyed on two occasions between May and August.

The average wind speed and wind direction (see Chapter 4, section 5.3.3 for categorisation of wind direction) were recorded using measurements from the nearest meteorological station at Boscombe Down, Wiltshire, UK, which was located 6.5 km SW of the site to the nearest hour.

4.3.3 Statistical analysis

Data were analysed for all Lepidoptera regardless of species, and after categorisation into ecological associations and mobility categories. The butterflies surveyed were grouped using ecological classifications of species associated with: a) ruderal vegetation, b) short-grass herb-rich vegetation, c) open grassland with medium to tall sward or warm open grassland with short-sward and, c) woodland (Shreeve *et al.* 2001). The difference between the two grassland ecological groups was that those associated with short-grass herb-rich vegetation were not dependant on grasses for any part of their life-cycle, whereas, those associated with short, medium or tall warm open grassland were (Shreeve *et al.* 2001). The larval host plants of the herb-rich grasslands associated group were Legumes and they were likely to have a symbiotic relationship with ants. The ruderal-vegetation group is not associated with a particular family of larval host plants, but is likely to be associated with tall and/or mature herbs and to overwinter as pupae and the woodland group utilised trees and/or shrubs for larval host-plants and adult feeding.

Day flying moths were categorised based on their association with different habitat types: the Six-spot Burnet (*Zygaena filipendulae*) was more associated with herb-rich grassland as its larval host plant is legume species *Lotus corniculatus*, (although this species will use tall grass stems and pupation sites), the Forester moth (*Adscita statices*) as it is associated with herb-rich chalk grassland where its larval host plant Common Rock-rose (*Helianthemum nummularium*) is abundant (Heath & Emmet 1985). Both of these moth species were also categorised as sedentary in mobility (Naumann *et al.* 1999). The Hummingbird Hawk moth (*Macroglossum stellatarum*) was categorised as associated with ruderal vegetation as it is a widespread immigrant species associated with a variety of habitat types (Heath & Emmet 1985; Langmaid *et al.* 1989).

Categories of Lepidoptera mobility used were sedentary, intermediate and widespread (Pollard & Yates 1993). Species categorised as sedentary are unlikely to move outside the habitat patch and are considered to have a closed population structure, whereas, species categorised as widespread are wide-ranging and frequently move between habitat patches and have an open population structure. species categorised as intermediate are somewhere in-between sedentary and widespread. The 6-spot Burnet Moth (*Zygaena filipendulae*) was categorised as being in the sedentary mobility groups (Naumann *et al.* 1999).

Wind speed was categorised by speed (Low: < 10 mph High: > 10 mph, wind direction, and relationship to the Lepidoptera flight path direction. For example, if the Lepidoptera crossed an edge and the wind was in the same direction it would be classed as ‘with’ the flight path (See Chapter 5, for examples). Mean values per survey boundary (and control boundary) were calculated for response and environmental variables. Response variables were Lepidoptera densities in total and the different boundary behaviours. Explanatory variables were the different ecological and mobility groups, vegetation characteristics, nectar flower availability and weather conditions.

Pearson's Chi-squared test with Yates' continuity correction and Fisher's Exact test in R (version 3.0, R Core Team 2013) were used to compare the differences between observed and values expected for total Lepidoptera and for each of the different ecological and mobility groups separately. The three comparisons were;

a) between the control and boundary surveys,
b) between Lepidoptera flight paths that started in the adjacent land cover side and the chalk grassland fragment side of the boundary.
c) between adjacent land cover types of arable land or new grassland re-creation when Lepidoptera flight paths started in the chalk grassland fragment side of the boundary.

4.3.3.1 Comparisons between different boundary surveys and side of edge and matrix type

Differences in the observed and expected behaviours of Lepidoptera in the three comparisons were based on; (i) the proportion that crossed the fragment boundary (or control dummy 'boundary') compared to the proportion exhibiting other behaviours, and (ii) the proportion that followed the boundary compared to those exhibiting other behaviours.

For comparisons between observed and expected behaviours in the survey boundaries at chalk grassland fragments and the control boundaries in continuous land cover (comparison a) , a total of 1110 individual behaviour recordings were used. For comparisons between observed and expected behaviours according to whether the Lepidoptera flight path observation started in the chalk grassland fragment or the adjacent land cover type (comparison b), a total of 644 were used. Observations where the Lepidoptera flight path originated at the boundary of the fragment were excluded as their origin (i.e. what side of the boundary they started from) could not be determined. For comparisons between observed and expected behaviours according to adjacent land cover type (arable land or new grassland re-creation, comparison c) a total of 402 individual behaviour recordings were used, excluding those flight paths that originated at the boundary..

4.3.3.2 Behaviour probability and edge permeability measures

The behaviour probability was calculated by comparisons of observed and expected Lepidoptera boundary behaviours between different adjacent land cover types (arable land or new grassland re-creation) and were based on the proportion exiting the survey area compared to if the probability of exiting by a particular survey area 'edge' was random. This method was adapted from that of Ries & Debinski (2001), but in this current study the square survey area is bisected by the fragment boundary into two rectangles, one in the chalk grassland fragment and one on the adjacent land cover side of the boundary. As the behaviour category was assigned by the survey edge by which the butterfly exited the survey area, this means that if butterfly behaviour is random, the probability of exiting the survey area by crossing the boundary is 33.3%, by the opposite 'edge' of the survey area is 33.3% and by one of the perpendicular survey area 'edges' is 33.3% (Figure 4-3). A total of 402 individual plot exiting behaviours were recorded and used for this analysis which excluded those who flight paths started at the boundary or who's flight path was categorised as "staying) in the survey area.

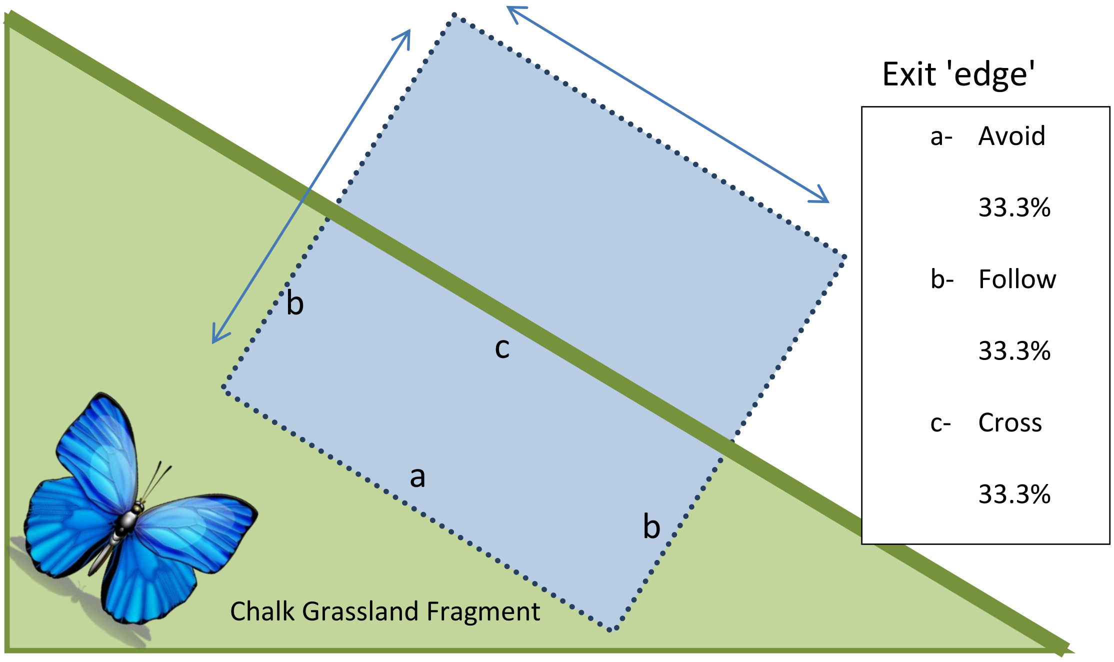


Figure 4-3. Probability of exiting the survey area for Lepidoptera on the chalk grassland fragment side of the boundary is 33.3% for exiting the survey area by avoiding (exit at a), following (exit at b) and crossing (exit at c) the boundary.

Edge permeability was defined as the proportion that approach the boundary and then cross it (Stamps *et al.* 1987) and was calculated using the estimated flight path data recorded during the survey. Comparisons between adjacent land cover type behaviour probabilities and edge permeability were done for Lepidoptera flight paths that originated in the adjacent land cover side and the chalk grassland fragment side of the boundary separately .

4.3.3.3 Logistic models

To model the effect of environmental variables on the behaviour of Lepidoptera in chalk grassland fragments at survey boundaries for Lepidoptera in total and for the different ecological and mobility groups, logistic stepwise regression models were conducted in R (version 3.0, R Core Team 2013) using Generalized Linear Models (GLM) and Generalized Linear Mixed Models (GLMM) with binomial errors. These included only Lepidoptera flight paths that originated in the chalk grassland fragment side of the boundary and excluded Lepidoptera that did not exit the survey area and whose flight path started at the chalk grassland fragment boundary.

GLMM used the proportion of Lepidoptera exiting the survey area as the response variable and boundary behaviour category (cross, follow or avoid), survey month, unique survey boundary identifier (related to position in the chalk grassland fragment and given a number 1-4), Lepidoptera density (including those that stayed in the survey area), adjacent land cover type, wind speed and wind direction (with or against the flight path of the individual) as explanatory variables. The interaction of Lepidoptera density with adjacent land cover type, month with boundary behaviour and wind speed with wind direction were also explanatory variables. These interactions are important as behaviour can be effected by an interaction of species density, month and the strength and direction of the wind (Ries & Debinski 2001). The unique survey boundary identifier was nested within the location (chalk grassland fragment) as a random effect. These used fixed and random effect; a fixed effect influences only the mean of the response variable and a random effect influences only the variance of the response variable (Crawley 2007).

GLM used the proportion of Lepidoptera exiting the survey area and the boundary behaviour of crossing and following were analysed separately as response variables. These included Lepidoptera data from June and July where vegetation characteristics and nectar resources were surveyed and therefore variables relating to vegetation density and nectar flower richness could be included in the models. Lepidoptera behaviour results from May were excluded as they did not have corresponding vegetation characteristics and nectar resources surveyed, this included four recordings of Lepidoptera crossing boundaries and 30 following boundaries. Explanatory variables were the month of survey, variation in vegetation density (Coefficient of Variation), nectar flower richness, the density of Asteraceae and Dipsacaceae nectar plants, wind speed, wind direction (as before), Lepidoptera density and matrix type. Interactions of wind speed with wind direction and Lepidoptera density with adjacent land cover type were also explanatory variables.

Interactive backwards step wise selection of explanatory variables was used to retain those variables with p <0.1 until the Minimum Adequate Model that did not increase significantly in residual deviance from the previous model and that was significantly different from the Null model was produced.

4.4 Results

A total of 1,110 Lepidoptera flight paths were recorded at boundary and control surveys consisting of observation of 22 butterfly and four moth species (Forester moth or Cistus Forester *Adscita stacies,* Hummingbird hawk moth, *Macroglossum stellatarum, Tyria jacobaeae* and the 6-spot Burnet moth, *Zygaena filipendulae). Table 4-3* shows the statistical analysis of the proportions of Lepidoptera displaying boundary crossing and boundary following behaviour in the boundary and control plots, for the adjacent matrix land cover side and the chalk grassland fragment side of the boundary, and for the fragment side of the boundary with adjacent matrix restoration grassland or arable land (for comparisons between the proportions of different ecological and mobility groups see Appendix C).

Table 4-3. Results of comparison between observed and expected proportions of Lepidoptera displaying boundary crossing and boundary following behaviour in total and for different ecological groups and mobility groups of control and boundary survey areas, the chalk grassland fragment and adjacent matrix land cover side of the boundary and at edges with adjacent matrix of restoration or arable. What plots were compared (Compare between), behaviour tested (Behaviour), Test used (Test) Chi-Squared value (X^2), significance (p=) those p<0.05 are in bold and whether the observed proportion was higher or lower than the expected (Comments).

Behaviour	**Test**	**Test**	**X^2**	**p**	**Comments**
Comparison a- Edge and Control plots n=1110					
Cross n=389	Cross/not Cross	Chi-squared	40.94	**<0.0001**	Cross lower at boundaries
Follow n=434	Follow/not Follow	Chi-squared	27.96	**<0.0001**	Follow higher at boundaries
NA	Ecological group	Fisher's Exact		**<0.0001**	Open-grass proportion higher at boundaries
NA	Mobility group	Fisher's Exact		**<0.0001**	Sedentary proportion higher at boundaries
Comparison b- Chalk and Matrix side of the edge n=644					
Cross n=154	Cross/not Cross	Chi-squared	75.53	**<0.0001**	Cross lower for those in chalk grassland side of boundary
	Ecological group	Fisher's Exact		0.2159	No difference
	Mobility group	Fisher's Exact		0.2974	No difference
Follow n=309	Follow/not Follow	Chi-squared	18.73	**<0.0001**	Follow higher for those in chalk grassland side of boundary
	Ecological group	Fisher's Exact		**<0.0001**	Herb-rich follow higher for those in chalk grassland side of boundary
	Mobility group	Fisher's Exact		**<0.0001**	Sedentary follow higher for those in chalk grassland side of boundary
Comparison c- Restoration and Arable matrix n=402					
Cross n=63	Cross/not Cross	Chi-squared	8.09	**0.0442**	Cross higher for boundaries with adjacent grassland re-creation
	Ecological group	Fisher's Exact		**0.0219**	Herb-rich cross higher at boundaries with adjacent

					grassland re-creation
	Mobility group			**0.0219**	Sedentary cross higher at boundaries with adjacent grassland re-creation
Follow n=229	Follow/not Follow	Chi-squared	0.52	0.4698	Follow lower for boundaries with adjacent grassland re-creation
	Ecological group	Fisher's Exact		0.6229	No difference
	Mobility group	Fisher's Exact		0.1501	No difference

4.4.1 Comparison, a) Lepidoptera density and behaviour between boundaries and controls

Results indicate that there are differences in the proportions, behaviour and ecological or mobility groups of Lepidoptera at survey boundaries compared to the expected values. Comparison between observed and expected proportions of the different boundary behaviours shown by Lepidoptera and of different ecological and mobility groups using Fisher's exact and Chi-Squared test (Table 4-3, Figure 4-4.) showed that there were lower Lepidoptera crossing and higher following at boundaries than expected (X^2= 40.94 and 27.96 respectively, p<0.0001). There were higher numbers of individuals in the open-grass ecological group and in the sedentary mobility group at survey boundaries than expected (Fisher's exact p<0.0001, Figure 4-5, Appendix C for all results).

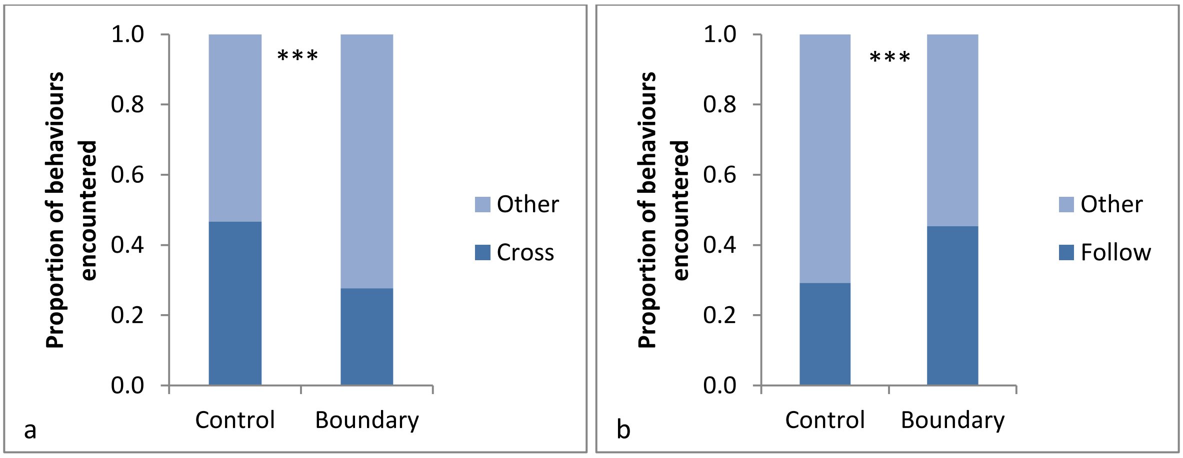


Figure 4-4. Comparison of behaviours observed between boundary and controls survey areas, a) crossing and, b) following Chi-squared and Fisher's Exact p<0.0001 comparing observed to expected for all. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

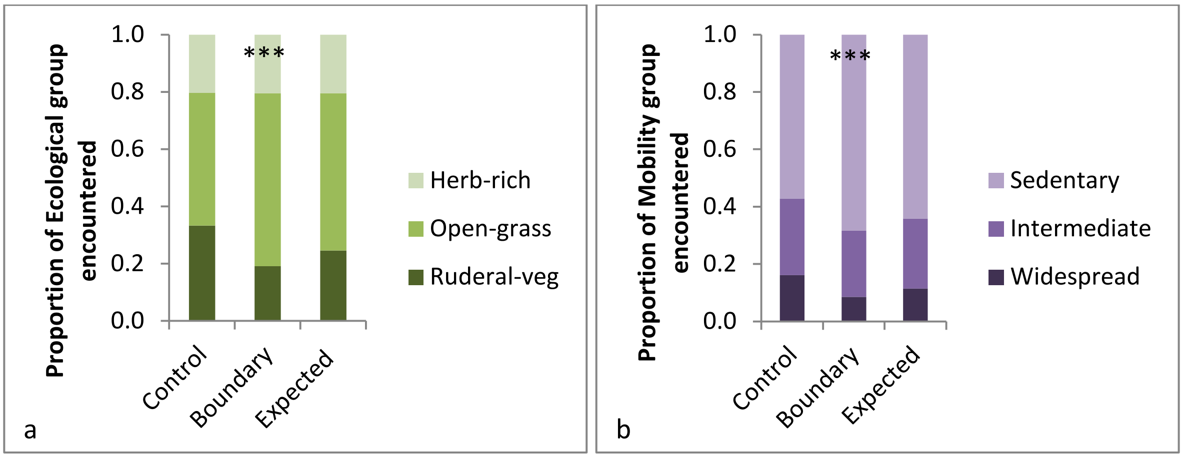


Figure 4-5. Comparison of behaviours observed between boundary and control survey areas the proportions in different, a) ecological and, b) mobility groups. Chi-squared and Fisher's Exact $p<0.0001$ comparing observed to expected for all. Significance $p<0.001$ ***, $p<0.01$ **, $p<0.05$ *, $0.1<p>0.05$ (*).

When investigating the proportion of Lepidoptera at control boundaries located in the chalk grassland fragment, arable land and new grassland re-creation there were significant differences between ecological and mobility groups with higher proportions of open-grass associated Lepidoptera at chalk grassland controls than grassland re-creation or arable and the converse for species of intermediate dispersal ability (X^2=145.67, $p<0.0001$ and X^2 150.76, $p<0.0001$ for ecological and mobility group, respectively, Figure 4-6). There were significant differences in the proportion of Lepidoptera in different ecology groups crossing the dummy 'boundary' in chalk grassland controls but not in arable land or grassland re-creation (X^2=17.14, $p<0.0001$, Figure 4-7) There were no significant differences between control dummy 'boundary' crossing in mobility groups or following dummy 'boundaries' in ecological and mobility groups ($p>0.05$, Appendix C).

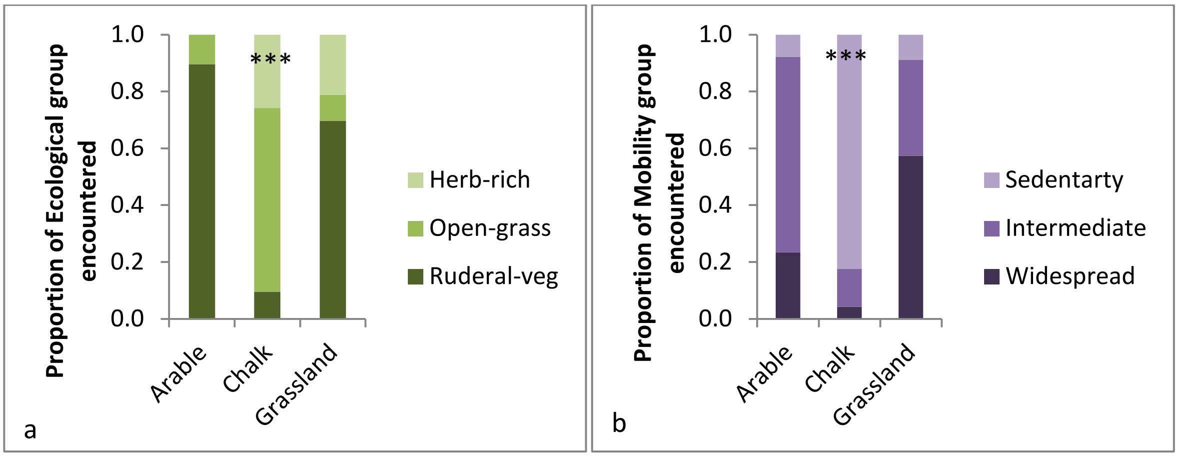


Figure 4-6. Proportions of Lepidoptera flight paths recorded of different, a) ecological and, b) mobility groups in control survey areas in the centre of arable land (Arable) , chalk grassland fragment (Chalk) and grassland re-creation (Grassland). Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

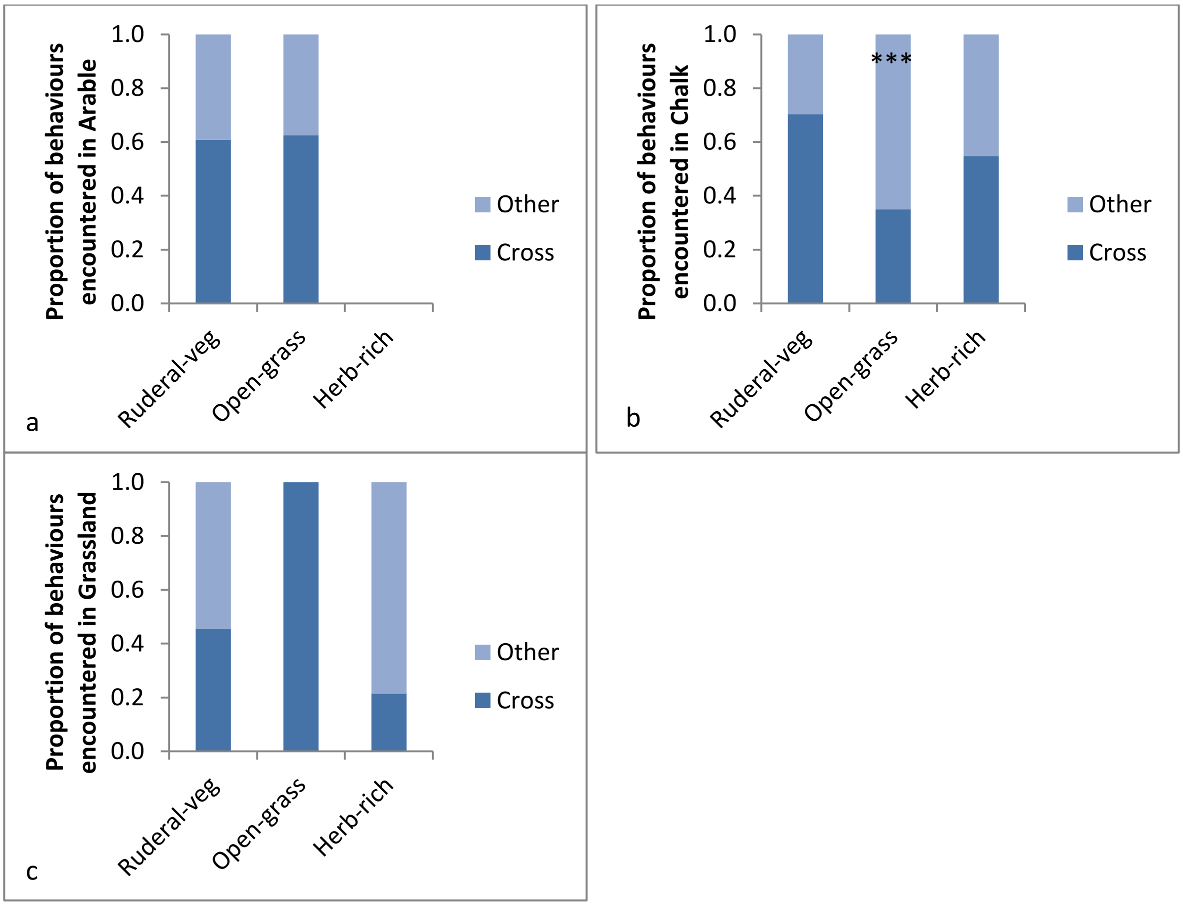


Figure 4-7. Proportions of Lepidoptera in different ecological groups recorded crossing the dummy 'boundary' in control survey areas in, a) arable land for, b) in chalk grassland fragments for (c) new grassland re-creation. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

4.4.2 Comparison, b) Lepidoptera behaviour on either side of the boundary

Results indicate that there are overall differences between the proportions of different boundary behaviours exhibited and between different ecological and mobility groups despite the small scale of the 20 m by 20 m survey area. For flight paths that originated in the chalk fragment side of the boundary there were higher proportions of Lepidoptera following and lower crossing boundaries than expected (Table 4-3, Figure 4-8, X^2= 18.73 and 75.53 respectively, p<0.0001). In the chalk grassland fragment side of the boundary there were higher proportions of open-grass and sedentary species than expected (Fisher's Exact test, p<0.0001). Of those that crossed the boundary from the chalk grassland fragment, there were no significant differences according to ecological or mobility group (Fisher's Exact test, p=0.2159, p=2974, respectively). However, for those that followed the boundary there were higher representation of herb-rich, open-grass and Sedentary species than expected when flight paths originated in chalk fragment side of the boundary (Figure 4-9, Fisher's Exact test, p<0.0001, Appendix C).

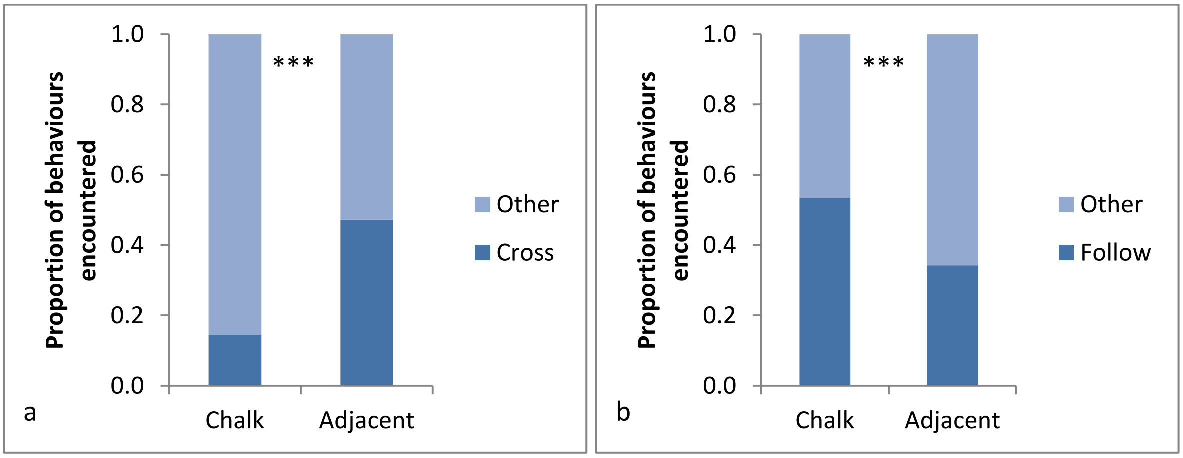


Figure 4-8. comparisons of behaviours according to whether the observation started in the adjacent matrix land cover and the chalk fragment side of the boundary for, a) crossing and, b) following. Chi-squared and Fisher's Exact p<0.0001 comparing observed to expected for all. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

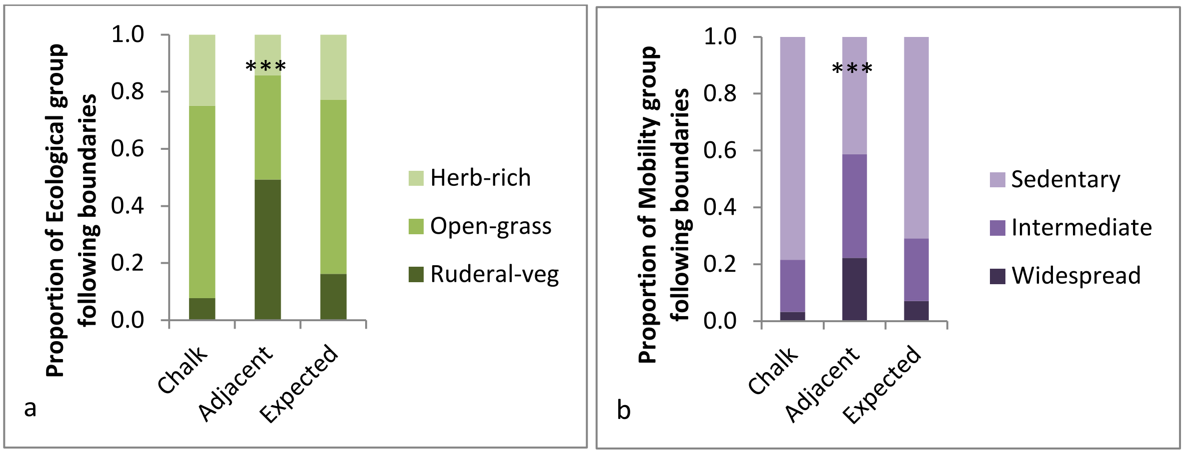


Figure 4-9. Comparisons of behaviours according to whether the observation started in the matrix and the chalk fragment side of the edge for proportions in different, a) ecological and, b) mobility groups for those individuals following edges. Chi-squared and Fisher's Exact p<0.0001 comparing observed to expected for all. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

4.4.3 Comparison, c) Lepidoptera behaviour to adjacent land cover of arable land or new grassland re-creation

Results showed that an adjacent land cover of new grassland re-creation significantly increased boundary-crossing behaviour (Table 4-3, Figure 4-10). At boundaries with grassland re-creation there were higher proportions of Lepidoptera crossing than expected (Chi-squared, X^2=8.09, p=0.0440) and no difference between matrix types for edge following behaviour. At boundaries with grassland re-creation there were higher proportions of Intermediate and lower of sedentary mobility groups than expected but no difference for ecological groups (Fisher's Exact, p=0.1718). At boundaries with grassland re-creation, there were higher open-grass ecological group and sedentary mobility group crossing (X^2= 6.17, p=0.01, and X^2= 7.79, p=0.0053 respectively) and lower herb-rich associated group crossing than expected (X^2= 3.3747, p=0.0662, Figure 4-11). At boundaries with arable land there were higher herb-rich ecological group following edges (X^2= 3.23, p=0.07) than expected and no difference for open-grass, sedentary and intermediate groups (Chi-squared, p>0.05, Table 4-3, Appendix C).

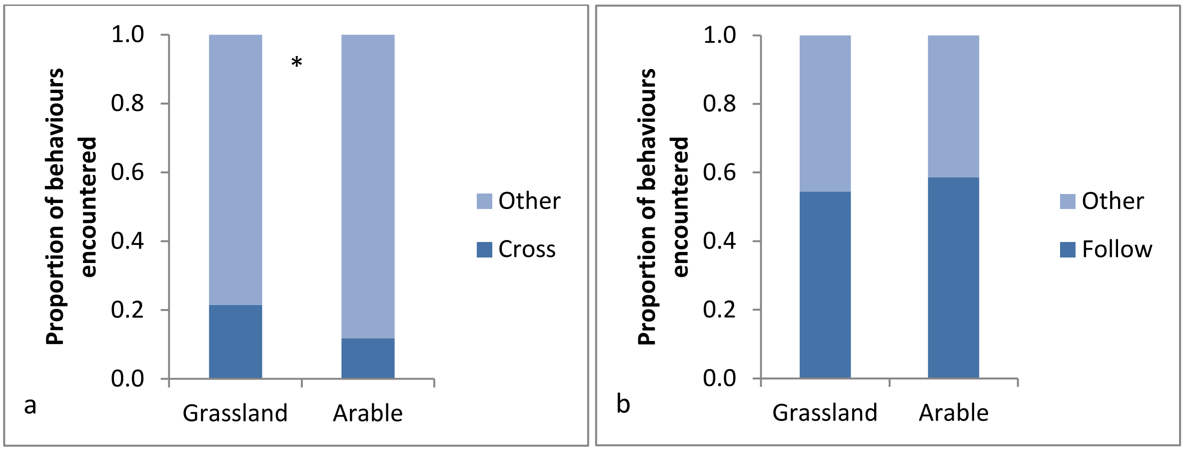


Figure 4-10. Comparisons of proportions between behaviours of individuals originating in chalk grassland fragments with adjacent land cover matrix of grassland re-creation and semi improved pasture (Grassland) or arable land (Arable) matrix of behaviours, a) crossing and, b) following. Chi-squared and Fisher's Exact p<0.05 comparing observed to expected for all. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

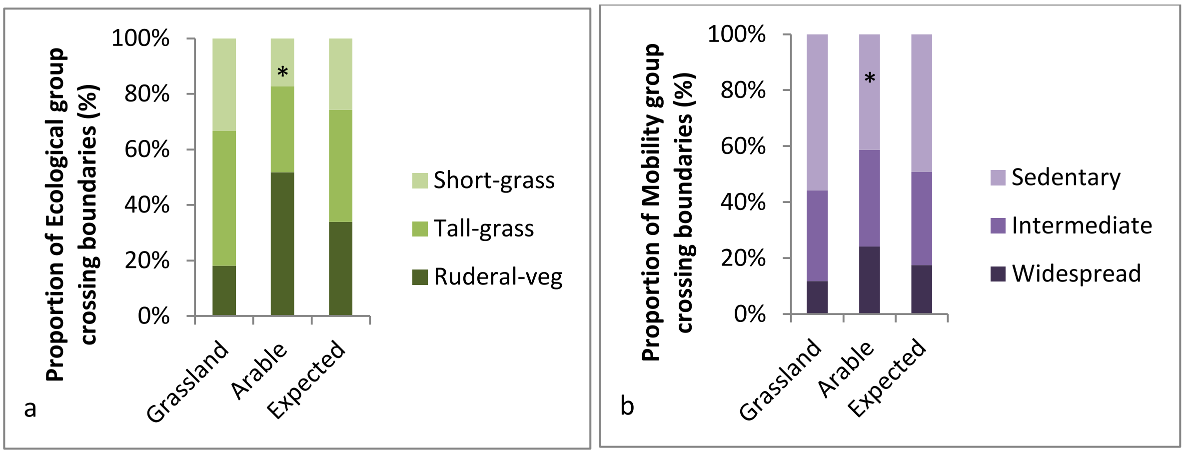
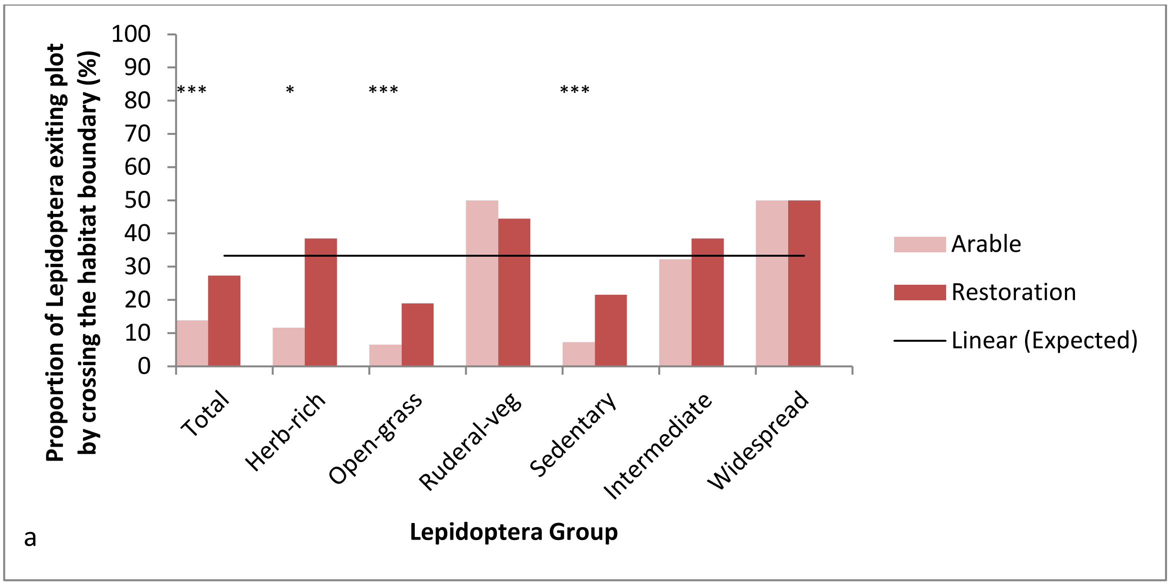


Figure 4-11. Comparisons of proportions between behaviours of individuals originating in chalk grassland fragments with adjacent matrix of grassland re-creation and semi improved pasture (Grassland) or arable land (Arable) matrix between, a) ecological and, b) mobility groups crossing edges. Chi-squared and Fisher's Exact p<0.05 comparing observed to expected for all. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

4.4.4 Behaviour probability and edge permeability measures

4.4.4.1 Behaviour probabilities

The proportion of Lepidoptera exiting the chalk grassland fragment by crossing the boundary was lower than expected when the adjacent land cover was arable land for all Lepidoptera, herb-rich, open-grass, and sedentary groups (Figure 4-12, p<0.05), but was not different from random when the adjacent land was grassland re-creation. The proportion of Lepidoptera exiting the survey area by following the boundary was higher than expected for both adjacent land cover types if movement was random for all Lepidoptera and all groups except the ruderal-veg and widespread groups (Figure 4-12, p<0.05).



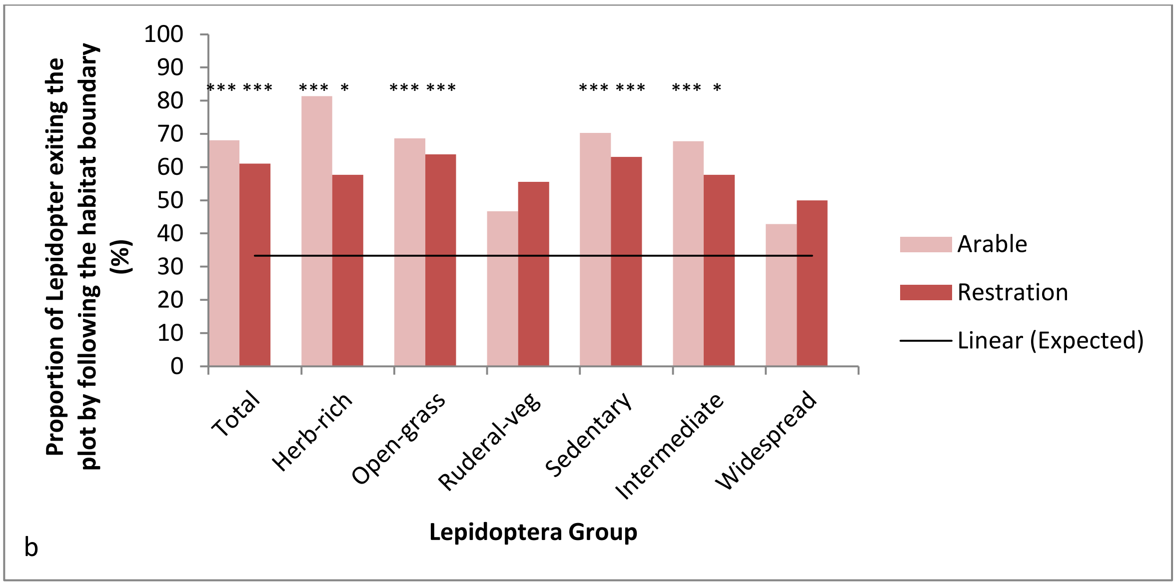


Figure 4-12. The proportion (%) of Lepidoptera exiting the survey area by, a) crossing the boundary and, b) following the boundary and results of Chi-squared test to compared this proportion to the 33.33% that would be expected if exit route was random (for example, 33% would exit the plot by crossing the edge, 33% would exit by avoiding the edge and 33% would exit by following the edge). For Lepidoptera in total and for the different ecological groups of ruderal-veg, herb-rich and open-grass associated species and mobility groups of intermediate, sedentary and widespread. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*).

4.4.4.2 Edge permeability

Edge permeability values were calculated as the percentage of Lepidoptera flight paths that approached the boundary and then crossed it. This was done for boundary crossing behaviour and for following behaviour (approached the 'edge' of the survey area that was perpendicular to the fragment boundary). This was calculated for flight paths originating in the chalk grassland fragment side of the boundary (for flight paths originating in the matrix side of the chalk grassland fragment boundary see Appendix C). Table 4-4 shows that for all ecological and mobility groups except for ruderal-veg and widespread species, grassland re-creation had a higher permeability value which meant that individuals were more likely to approach the boundary and then cross it. Open-grass species had the lowest permeability to both grassland re-creation and arable edges, intermediate species had the highest permeability to grassland re-creation edges after ruderal-veg associated species.

Table 4-4. Mean and 1 Standard Error (SE) for boundary permeability estimates with adjacent land cover of grassland re-creation (Grassland) and arable land (Arable) for all Lepidoptera and the different ecological and mobility groups. Only for Lepidoptera on the chalk grassland fragment side of the boundary (see Appendix C for the adjacent land cover side of the boundary and avoiding behaviour). This is the proportion of Lepidoptera that approached the edge that then crossed it and compared the boundary (Crossing) to the perpendicular edge (Following).

Response	**Grassland**	**Arable**	**Grassland**	**Arable**
	Cross (%)		**Follow (%)**	
All Lepidoptera	82.46	39.01	92.78	97.75
SE	14.11	6.37	3.89	1.31
Ecological group				
Ruderal-veg	66.67	83.93	100.00	88.89
SE	33.33	11.80	0.000	7.85674
Herb-rich	61.11	48.21	79.26	100.00
SE	30.93	20.49	11.57	0.00
Open-grass	51.52	22.63	65.33	98.53
SE	28.91	11.04	32.69	1.47
Mobility group				
Intermediate	61.91	58.33	88.89	97.22

SE	31.23	22.05	5.56	2.78
Sedentary	51.52	21.67	94.00	99.29
SE	28.91	10.26	3.24	0.71
Widespread	33.33	87.50	66.67	62.50
SE	33.333	12.50	33.33	23.94

4.4.5 Modelling the behaviour of Lepidoptera

4.4.5.1 GLMM of all boundary behaviours

The Minimum Adequate Model from GLMM for all Lepidoptera in total showed that there were higher proportions exiting the survey area by following the boundary and when there was an interaction of month and exit behaviour with higher proportion crossing the boundary in June.

For Lepidoptera in the herb-rich ecological group there were higher proportions exiting the survey area by following the boundary, an interaction of exit behaviour and survey month where in June there were higher proportions crossing. For the open-grass ecological group there were higher proportions following and lower proportions crossing boundaries.

For Lepidoptera species in the intermediate mobility group there were higher proportions crossing and following the boundary and for the sedentary group there were lower proportions crossing and higher proportions following. Survey month and the interaction of boundary behaviour and month were retained in the Minimum Adequate Model but were not significant individually (Table 4-5).

Table 4-5. Minimum Adequate Model for GLMM for all boundary behaviours (crossing, following and avoiding the boundary), Variable estimate, Standard error (Std.Error), z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*), See Appendix C for all model iterations.

	Variables	**Estimate**	**Std.Error**	**Z**	**p**	
All Lepidoptera	Model iteration 8 compared to Null				**<0.0001**	***
	(Intercept)	-1.48	0.18	-8.10	**<0.0001**	***
	Month June	-0.60	0.36	-1.69	0.0907	(*)
	Month May	-0.44	0.51	-0.86	0.3903	
	Behaviour Cross	-0.14	0.26	-0.53	0.5986	
	Behaviour Follow	2.09	0.24	8.88	**<0.0001**	***
	Month June: Behaviour Cross	1.07	0.46	2.31	**0.0207**	*
	Month May: Behaviour Cross	-0.11	0.76	-0.15	0.8815	
	Month June: Behaviour Follow	0.60	0.44	1.38	0.1665	
	Month May: Behaviour Follow	1.03	0.66	1.56	0.1149	
Ecological group						
Ruderal-veg	Null					
Herb-rich	Model iteration 10 compared to Null				**<0.0001**	***
	(Intercept)	-2.77	1.03	-2.69	**0.0072**	**
	Behaviour Cross	0.76	1.28	0.59	0.5528	
	Behaviour Follow	4.31	1.21	3.56	**0.0004**	***
	Behaviour Avoid: Month June	-0.78	1.45	0.541	0.5883	
	Behaviour Cross: Month June	1.44	0.83	1.74	0.0814	.
	Behaviour Follow: Month June	-1.09	0.72	-1.51	0.1318	
	Behaviour Avoid: Month May	1.11	1.17	0.96	0.3393	
	Behaviour Cross: Month May	-1.16	1.27	-0.92	0.3591	
	Behaviour Follow: Month May	-0.15	0.81	-0.19	0.8489	
Open-grass	Model iteration 10 compared to Null				**<0.0001**	***
	(Intercept)	-1.33	0.16	-8.12	**<0.0001**	***
	Behaviour Cross	-0.75	0.27	-2.79	**0.0053**	**
	Behaviour Follow	2.09	0.22	9.59	**<0.0001**	***

Mobility group						
Intermediate	Model iteration 10 compared to Null				**<0.0001**	***
	(Intercept)	-3.45	0.72	-4.80	**<0.0001**	***
	Behaviour Cross	2.71	0.77	3.54	**<0.0001**	***
	Behaviour Follow	4.05	0.76	5.31	**<0.0001**	***
Sedentary	Model iteration 8 compared to Null				**<0.0001**	***
	(Intercept)	-1.27	0.19	-6.84	**<0.0001**	***
	Month June	-0.52	0.39	-1.34	0.1813	
	Month May	-0.23	0.59	-0.40	0.6905	
	Behaviour Cross	-0.74	0.30	-2.44	**0.0148**	*
	Behaviour Follow	1.95	0.25	7.88	**<0.0001**	***
	Month June: Behaviour Cross	0.85	0.56	1.51	0.1311	
	Month May: Behaviour Cross	-16.08	2029.42	-0.01	0.9937	
	Month June: Behaviour Follow	0.69	0.50	1.40	0.1629	
	Month May: Behaviour Follow	1.06	0.82	1.29	0.1957	
Widespread	Null					

4.4.5.2 GLM for boundary crossing

The Minimum Adequate Model from GLM for Lepidoptera crossing the chalk grassland fragment boundary showed that there were higher proportions of all Lepidoptera crossing boundaries in May and July, when there was a low nectar flower richness, lower variation in vegetation density, when the wind direction was towards the chalk grassland fragment boundary, when the adjacent land cover was new grassland re-creation and an interaction of when the wind was high and towards the chalk fragment edge.

For Lepidoptera in the open-grass ecological group there was a higher proportion of boundary crossing when the wind speed was low (<10 mph), when there was lower densities of other open-grass species in the fragment but when there was an interaction of high species density at the fragment boundary next to a grassland re-creation. For species in the sedentary mobility group there were higher proportions crossing boundaries when species density was low or when it was high with an interaction of adjacent grassland re-creation (Table 4-6).

Table 4-6. Minimum Adequate Model results from GLMs for Lepidoptera crossing the grassland fragment boundary, Variable estimate, Standard error, z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). Appendix C for all model iterations.

	Variable	**Estimate**	**Std.Error**	**Z**	**p**	
All Lepidoptera	Model iteration 4 compared to Null				**0.0024**	**
	(Intercept)	-0.13	1.11	-0.12	0.9037	
	Month July	-1.31	0.50	-2.61	**0.0092**	**
	N1	-0.38	0.18	-2.05	**0.0407**	*
	Drop Disc CV	-0.04	0.01	-2.09	**0.0367**	*
	Wind direction towards boundary	2.43	0.88	2.77	**0.0057**	**
	Wind speed low	1.38	0.62	2.23	**0.0270**	*
	Adjacent grassland re-creation	1.64	0.49	3.37	**0.0008**	***
	Wind direction towards boundary: Wind speed low	-2.67	1.05	-2.54	**0.0110**	*
Ecological group						
Ruderal-veg	Null					
Herb-rich	Null					
Open-grass	Model iteration 8 compared to Null				**0.0018**	**
	(Intercept)	-1.80	0.71	-2.56	**0.0116**	*
	Wind speed low	1.28	0.66	1.95	0.0518	(*)
	Open-grass Sp density	-0.18	0.06	-2.92	**0.0035**	**
	Open-grass Sp density: Adjacent grassland re-creation	0.12	0.04	2.69	**0.0072**	**
Mobility Group						
Widespread	Null					
Intermediate	Null					
Sedentary	Model iteration 9 compared to Null				**0.0115**	*
	(Intercept)	-1.10	0.44	-2.50	**0.0123**	*
	Sedentary Sp density	-0.12	0.05	-2.39	**0.0167**	*
	Sed Sp density: Adjacent re-creation	0.10	0.04	2.52	**0.0117**	*

4.4.5.3 GLM for boundary following

The Minimum Adequate Model of GLM for Lepidoptera following the boundary of the chalk grassland fragment showed that there were higher proportions when nectar flower richness was higher and lower proportions when the wind direction was towards the boundary. For species in the herb-rich ecological group, lower proportions followed boundaries in June and when the density of other herb-rich species was higher. For the open-grass ecological group, there was borderline significance for higher proportions following when nectar flower richness was higher. For species in the sedentary mobility group there was borderline significance for high proportions followed the boundary when nectar flower richness was higher and for intermediate mobility group there was borderline significance for lower proportions following when the wind direction was towards the boundary (Table 4-7).

Table 4-7. Minimum Adequate Model results from GLMs for Lepidoptera following the grassland fragment boundary, Variable estimate, Standard error, z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). Appendix C for model iterations.

	Variables	**Estimate**	**Std.Error**	**Z**	**p**	
All Lepidoptera	Model iteration 9 compared to Null				0.0377	*
	(Intercept)	0.02	0.32	0.05	0.9626	
	N1	0.28	0.12	2.30	0.0212	*
	Wind direction towards boundary	-0.47	0.28	-1.67	0.0953	(*)
Ecological group						
Ruderal- veg	Null					
Herb-rich	Model iteration 10 compared to Null				0.0012	**
	(Intercept)	4.98	1.55	3.21	0.0013	**
	Month June	-2.67	1.07	-2.51	0.0121	*
	Herb-rich Sp density	-0.31	0.11	-2.82	0.0048	**
Open-grass	Model iteration10 compared to Null				0.0692	(*)
	(Intercept)	-0.09	0.45	-0.20	0.8387	
	N1	0.28	0.16	1.78	0.0753	(*)
Mobility group						
Intermediate	Model iteration 10 compared to Null				0.0851	(*)
	(Intercept)	0.92	0.42	2.19	0.0285	*
	Wind direction towards boundary	-1.00	0.59	-1.70	0.0896	(*)
Sedentary	Model iteration 10 compared to Null				0.0638	(*)
	(Intercept)	0.04	0.39	0.12	0.9185	
	N1	0.25	0.14	1.81	0.0703	(*)
Widespread	Null					

4.5 Discussion

4.5.1 Comparison of the proportions of Lepidoptera in total and of ecological and mobility groups in different survey areas and edge permeability

Overall there were lower proportions of Lepidoptera in total crossing boundaries, and higher proportions following boundaries than expected at chalk grassland fragment boundaries, when flight paths originated in the chalk grassland fragment and when the adjacent land cover was arable land (Table 4-3). This indicated that in this landscape, Lepidoptera were affected by, and responding to, the chalk grassland fragment boundary, an effect supported by many other studies (Ries & Debinski 2001; Schtickzelle & Baguette 2003; Schultz *et al.* 2012).

There were significantly higher proportions of Lepidoptera crossing chalk grassland fragment boundaries when the adjacent land cover was new grassland re-creation, when flight paths originated in both the fragment and in the adjacent land cover side of the boundary for all Lepidoptera (Table 4-3). A matrix that is similar in structure to the habitat patch has been shown to have higher permeability values which increases functional connectivity. A review by (Prevedello & Vieira 2010) summarised this affect, concluding that in 88% of studies, functional connectivity was increased when the matrix was more similar in structure to the habitat patch. Reeve *et al.* (2008) and Haynes & Cronin (2006) used experiments, observations and models of plant hoppers in habitat patches and a matrix of different grass species and mudflat to illustrate that when the adjacent matrix was similar in structure to the habitat edge, crossing behaviour occurred from both sides of the edge and that the grass matrix was three times more permeable than mudflat.

Overall, grassland associated butterflies and those with sedentary and intermediate mobility groups responded similarly to chalk grassland fragment boundaries with lower proportions crossing and higher proportions following than expected if movement was random. This was supported by the behaviour probabilities results whereby, these groups crossed significantly less at boundaries with adjacent arable land but was no different from random when there was adjacent new grassland re-creation. This is likely to be because they are associated with grasslands for larval hot plants and nectar sources they are more reluctant to leave an area which contains the resources they require. Those in the ruderal-veg ecological and widespread mobility groups did not show a similar significant trend to the other groups as these species are less specialist in their habitat requirement and not ecologically restricted to grassland habitats (Langmaid *et al.* 1989), therefore these groups will not be discussed further.

There were some differences between these groups, indicating that new grassland re-creation may be more effective for some groups. An adjacent matrix type of new grassland re-creation affected the herb-rich ecological and the sedentary groups with significantly higher proportions crossing when boundaries were adjacent to this matrix type, indicating the importance of even this new habitat on the behaviour of these group. Although, herb-rich associated Lepidoptera species had higher overall permeability values at boundaries, there were lower proportions crossing and more following boundaries than expected and this may have been a result of those individuals in the survey areas were more likely to cross whereas others may have already avoided the boundary before they entered the survey area and this is supported by the fact that there were significantly higher proportions of open-grass group and lower proportions of herb-rich at boundaries.

A chalk grassland fragment boundary with an adjacent land cover of grassland re-creation was more permeable than one adjacent to arable land for all grassland ecological and intermediate to low mobility groups (Table 4-4). Chalk grassland fragment boundaries adjacent to grassland re-creation had the highest permeability value for the herb-rich ecological group and sedentary mobility group. These results support similar results reported for the Mountain Parnassian butterfly (*Parnassius smintheus*) where the forest matrix was twice as resistant to movement as meadows (Matter & Roland 2002). Also for the specialist prairie Lepidoptera species the Regal Fritillary (*Speyeria idalia*) where significantly different crossing than expected was reported when the matrix land cover was crop and/or field (Ries & Debinski 2001).

Results considering the permeability of the chalk grassland fragment boundary to Lepidoptera located in the adjacent land cover showed higher permeability values compared to those in the chalk grassland fragment especially for open-grass ecological and Sedentary mobility groups (Appendix C). This is unlikely to represent species immigration into the chalk grassland fragment and more likely due to foray loop behaviour where Lepidoptera will cross the habitat boundary and fly into the matrix for some distance before returning to the habitat. This behaviour has been studied in *Maniola jurtina and Pyronia tithonus* (Meadow brown and Gatekeeper butterflies respectively, open-grass ecological and sedentary mobility groups) where 70%-80% of edge crossing behaviours were foray loops (Conradt & Roper 2006) and similarly in Delattre *et al.* (2010a) showed that although 27% of *Maniola Jurtina* went into the arable matrix, 16% were foray loops. This means that edge permeability can’t be used as a measure of dispersal or connectivity alone but this behaviour is at least the first step in dispersal.

There were reasonably high permeability values for boundaries with adjacent arable land for herb-rich associated and intermediate mobility Lepidoptera (48% and 58%, respectively, Table 4-4). There were also high permeability values for the boundaries when Lepidoptera from these groups were recorded in the arable land cover as a high proportion crossed back over to the chalk grassland fragments (Appendix C). This may be attributed to the foray loop behaviour descried in *Maniola jurtina* (Delattre *et al.* 2010a). However, due to the survey methodology, the mechanism behind this result cannot be determined as butterfly flight paths were not surveyed for more than 40 m from the habitat boundary.

There were some differences between the grassland associated mobility groups and the sedentary and intermediate mobility groups. For flight paths that originated in either the chalk grassland fragment or the adjacent land cover side of the boundary, there was no difference for ecological or mobility groups that crossed boundaries. However, for those that followed boundaries, there were higher proportions of herb-rich associated Lepidoptera and the sedentary mobility group and lower proportions of intermediate mobility Lepidoptera (Table 4-3). Also for boundary permeability values, there were lower permeability values for open-grass group compared to the herb-rich group and lower permeability for sedentary compared to intermediate

Boundary response, behaviour probabilities and boundary permeability values differ between ecological and mobility groups, these results are supported by a review by (Prevedello & Vieira 2010) which showed that matrix land cover type effects are species specific and even closely related species of butterfly respond to matrix differently (Ricketts 2001). For example, Ries & Debinski (2001) showed that the more prairie specialist Lepidoptera species, *Speyeria idalia* had significantly different proportions of crossing behaviour than expected when the matrix was crop and field with a quarter of individuals crossing edges that had first approached them, however for the more generalist species, Monarch butterfly (*Danaus plexippus)* edge crossing behaviour did not differ from expected and doubled in edge permeability values.

4.5.1.1 limitations

The grouping of all species together does not allow for the species specific differences to be identified, however grouping does allow for robust statistical analysis and grouping into ecological associations and mobility does enable for differences between species that have similar life history traits to be analysed and rare species to be include. For this study arable land of either oil-seed rape or winter wheat was grouped due to low replication, however, it is likely that there would be differences between butterfly behaviour at these two matrix types as oil-seed rape can provide early flowering sources of nectar for many nectar feeding insects (Bartomeus *et al.* 2014; Riedinger *et al.* 2014; Woodcock *et al.* 2013) as well as microclimate an larval host plants for *Pieris.* sp. of butterfly (Langmaid *et al.* 1989).

4.5.1.2 Summary

Overall, behaviour of Lepidoptera in and at boundaries of grassland re-creation which was only 1 or 2 years old was significantly different from arable for all grassland and intermediate to low mobility groups indicating that this new habitat can encourage the dispersal of these groups.

Lepidoptera boundary crossing behaviour is affected by many variables and not just the type of land cover adjacent to habitat patches, behaviour may also be affected by vegetation characteristics, nectar and host plant resources, and the month of study, weather conditions and co-specific density for example and these variables are discussed below.

4.5.2 Environmental variables that increased the proportion of Lepidoptera crossing edges

Models showed the importance of new grassland re-creation adjacent to chalk grassland fragments, a low variation in vegetation structure, nectar richness, the effect of weather (wind direction) and density dependence on Lepidoptera behaviour at chalk grassland fragment boundaries (Table 4-5, Table 4-6, Table 4-7).

A low variation in vegetation structure as measured by vegetation density, low nectar flower species richness across the boundary and an adjacent land cover of grassland re-creation were significant explanatory variables (variables indicating a similar structure and nectar flower composition to the chalk grassland fragments) for all Lepidoptera with a positive effect on the proportion crossing boundaries (Table 4-5, Table 4-6, Table 4-7). An increase in nectar flower species richness increased the proportion of herb-rich Lepidoptera following boundaries, this potentially indicates that there were different nectar sources in the adjacent land cover to the chalk grassland fragment which weren't attractive to this group. This is an interesting result, especially as the surveys in Chapter 3 have shown that these new grassland re-creation fields at the Stonehenge Landscape are providing many nectar resources and some host plant for Lepidoptera). Overall, butterfly species richness is positively affected by plant species richness (Rosin *et al.* 2012) and variables effecting the dispersal and as a result the abundance and richness of Lepidoptera in habitat patches in fragmented landscapes are affected by the quality and abundance nectar flowers (Binzenhofer *et al.* 2005; Clausen *et al.* 2001; Matter & Roland 2002) and host plant patches (Berg *et al.* 2011; Heer *et al.* 2013; Menendez *et al.* 2002; Schultz *et al.* 2012). The effect of floral resources is species-specific and not all species will respond, (Clausen *et al.* 2001; Ricketts 2001). For example Clausen *et al.* (2001), showed that the abundance of Skippers (*Thymelicus* sp.) and Ringlet (*Aphantopus hyperantus)* were positively affected by the number of nectar plants but the abundance of *Maniola jurtina* was not, despite these species all belonging to the same open-grass ecological and sedentary mobility group.

Model results showed no effect of the density of nectar plants in the Asteraceae and Dipsacaceae families in contrast to previous results (Chapter 3) and other studies for example, composite nectar flowers (Ricketts 2001) and nectar plant species of Field Scabious (*Knautia arvensis)*, Small Scabious (*Scabiosa columbaria)*, Greater Knapweed (*Centurea scabiosa*), Thistles *(Cirsium.* sp*)* and Mouse-ear Hawkweed (*Hieracium pilosella)* (Binzenhofer *et al.* 2005; Clausen *et al.* 2001). Similarly, the effect of vegetation height on butterfly presence is dependent on species specific preferences. For example, the abundance of *Aphantopus hyperantus* was positively affected by increased vegetation height and species that were less mobile were more significantly affected than more mobile species (Clausen *et al.* 2001).

Models showed that when the wind was with the direction of the crossing flight path, a higher proportion crossed than expected and this is supported by results from generalist Lepidoptera *Danaus plexippus* (Ries & Debinski 2001). Temperature and solar radiation are also important for butterflies which are thermoregulating insects shown in studies where immigration can be dependent on temperature (Ricketts 2001) and the abundance and site (habitat patch) occupancy can be associated with rates of solar radiation at sites (Clausen *et al.* 2001; Heer *et al.* 2013). Models also highlighted more crossing and less avoiding behaviour for herb-rich Lepidoptera in July most likely Common Blues (*Polyommatus icarus*) which emerged at the end of May and then August, perhaps low numbers of individual in July increased crossing behaviours and this is supported by the generalist *Danaus plexippus* where boundary crossing was affected by survey week with more crossing at the end of the season (Ries & Debinski 2001). Conversely, some studies have shown that flight times can be significant in explaining differences in abundance and species richness between habitat types for the early season (May to the middle of June) (Berg *et al.* 2011). More crossing behaviour in July also coincided with lower total numbers of nectar flowers in July compared to June across the survey area (mean 14.0 and 41.5, respectively) and lower nectar flower species richness (mean 2.6 and 3.2, respectively, data not shown), the main contributor to this was nectar flowers in the Fabaceae family which had higher abundance in June compared to July (9.3 and 0.4, respectively) and potentially individuals were crossing more to find additional nectar resources.

Models showed that as the Lepidoptera ecological or mobility group density in the survey area decreased there was an increase in the proportion of Lepidoptera crossing for open-grass and Intermediate groups except when group density was high at boundaries with adjacent grassland re-creation which increased the proportion crossing. Similarly, Alpine meadow species Mountain Parnassian (*Parnassius smintheus)* were more likely to stay at habitat patches with high numbers of conspecifics (members of the same species) and migrate when there were low numbers (Roland *et al.* 2000) and for the prairie specialist *Speyeria idalia* plot exiting was affected by a species density interaction with habitat types where crossing was less likely as co-specific density increased and higher when the matrix was a grassy field than when it was crop or woodland (Ries & Debinski 2001). The effect of density dependence varies between species and depends on the sex of the individual, for example, immigration of the male alpine meadow butterfly *Parnassius smintheus* was positively affected by number of females (Matter & Roland 2002).

4.5.2.1 Limitations

Models did not consider aspects of the surrounding landscape, for example measures of fragment connectivity or the different habitat types in the landscape and studies have shown that these aspects are important for example, site/patch occupancy for Iolas Blue (*Iolana iolas*) was dependent on connectivity (Heer *et al.* 2013), *Zygaena filipendulae* presence was dependant on dry grassland close by (Binzenhofer *et al.* 2005) and linear features in the landscape such as hedgerows, lanes and grassy field margins are important for Lepidoptera abundance (Clausen *et al.* 2001; Delattre *et al.* 2013). Also shelter and woodland are important, for example, Lepidoptera species richness and abundance were affected by shelter (Rosin *et al.* 2012) and *Maniola jurtina* were affected by shelter and tree species (Clausen *et al.* 2001). The management of the landscape is also important such as the type and intensity of grazing (Clausen *et al.* 2001). Additionally, patch size may be an important variable as there may be more crossing in smaller patches a individuals are more likely to encounter an edges, however studies have shown that behaviour that the probability of encountering an edge is related to the probability of crossing it (Conradt *et al.* 2000; Conradt & Roper 2006).

Weather conditions can be important at effecting butterfly behaviour however, microclimate too is very important especially considering the ground temperature for oviposition and thermoregulation (Beyer & Schultz 2010) and this study did not sure this variable, this mean that future studies would benefit from this additional variable .

These results show that not all groups respond similarly to chalk grassland fragments boundaries and different environmental variables, there is also difference within species with males and females responding differently, an aspect that was not analysed in this study as a sex could not be allocated to all individuals in the passive observational study. Even though males and females may respond to resources and structural similarly e.g. vegetation density, the strength of the response, movement rates, foraging strategy and flight characteristics may differ. Studies have shown that females are more affected by resources and males by habitat types (Schultz *et al.* 2012) and for Adonis Blue *(Lysandra bellargus)* even though there was high selectivity in both males and females for nectar plants but their foraging strategies were different, females utilised a higher range of nectar plants but in a shorter distance to the habitat patch than males (Rusterholz & Erhardt 2000). For *Parnassius smintheus*, 52% of males and 35% females moved between meadows (Matter & Roland 2002).

4.5.2.2 Summary

Boundary crossing and following behaviour was influenced by a mixture of vegetation characteristics such as vegetation density and nectar plant availability, weather conditions and group density. Results show that boundaries with similar vegetation density and nectar plant species to the habitat fragment can encourage crossing behaviour. Some of these variables could be managed for example, flowering plant species richness and structural similarity of restoration habitat patches to reflect that of the target habitat and source fragments. The different responses of ecological and mobility groups indicate that managing habitat patches and landscape for heterogeneity is also important.

4.6 Conclusion

The results from this study illustrate the utility of new grassland re-creation adjacent to chalk grassland fragments. There were significantly higher proportions of Lepidoptera associated with grasslands and low to intermediate mobility groups crossing boundaries at new grassland re-creation compared to if movement and therefore behaviour was random. This indicates that grassland re-creation that was only 1-2 years old was significantly different from arable land when Lepidoptera boundary behaviour was investigated and therefore may increase the functional connectivity of isolated habitat patches. There were higher proportions of herb-rich associated Lepidoptera crossing at boundaries with adjacent grassland re-creation, than the open-grass associated group. However, higher proportions of species associated with herb-rich habitats followed rather than crossed boundaries and therefore were potentially more isolated to the chalk grassland fragments.

Results showed that variables relating to vegetation characteristics and nectar resources may increase boundary crossing behaviour and these could be managed for. However, specialist species would require either targeted management or more time for restoration grasslands to mature, before functional connectivity was enhanced for this group.

Chapter 5 The effects of mowing on the boundary behaviour of two grassland associated Lepidoptera species

5.1 Introduction

The behavioural response of an individual to features of a fragmented landscape is dependent on species traits, their functional group and landscape context (Debinski & Holt 2000; Prevedello & Vieira 2010; Ricketts 2001; Ries & Debinski 2001; Steffan-Dewenter *et al.* 2002). It is important to understand how these behavioural responses change with habitat loss, fragmentation and climatic and land use change in order to predict future behaviour and make recommendations for conservation actions. Boundary features can also be important for habitat, resources and dispersal for many insect species, for example, crop edges and grassy margins (Delattre *et al.* 2010b; Driscoll & Weir 2005; Ouin *et al.* 2008).

Examining behaviour at habitat boundaries can give insights into dispersal, immigration and emigration rates as, for an individual, crossing a habitat boundary is the first factor in dispersal (Clobert *et al.* 2004). Management practices and spatial targeting of habitat restoration can be used to encourage certain types of behaviour such as boundary crossing by increasing the permeability of the adjacent matrix (for example, Haynes & Cronin 2003). Conservation approaches can also take account of certain types of behaviour such as boundary following and the usage of linear features as corridors (for example, Berggren *et al.* 2001; Driscoll & Weir 2005; Duelli & Obrist 2003; Ockinger & Smith 2007b).

Behaviour at habitat boundaries has been studied in observational studies in real landscapes (Conradt & Roper 2006; Delattre *et al.* 2013; Matter & Roland 2002; Pither & Taylor 1998; Ries & Debinski 2001) and in experiment settings (Haynes & Cronin 2006; Reeve *et al.* 2008). In observational studies it is difficult to control for environmental and landscape variables at different sites and therefore experiments can be used to investigate boundary behaviour whilst controlling for these variables. However, the transferability of results derived from experimental set ups may be limited to the species, habitat and landscapes studied. Additionally, some behaviour can be misleading, for example, not all crossing behaviour will result in immigration, for example, some butterflies exhibit foray loop behaviour where they will cross a habitat boundary, fly through the matrix for a few metres and then return to the original habitat patch (Conradt & Roper 2006; Delattre *et al.* 2010a).

Management of grasslands influences their conservation value especially grazing and mowing regimes which have a significant effect on plant and insect species richness, community compositions and interactions (Buri *et al.* 2013; Clausen *et al.* 2001; Maccherini & Santi 2012). The structural similarity of habitat and matrix land cover is a key component in increasing matrix permeability and therefore increasing the colonisation of new habitat patches . timing and extent of mowing and grazing should be late and varied in order to increase insect biodiversity (Berg *et al.* 2013; Lenoir & Lennartsson 2010), leaving uncut refuges utilised by many insect species (Berggren *et al.* 2002; Buri *et al.* 2013; Humbert *et al.* 2012).

To explore boundary behaviour the Stonehenge World Heritage Site (WHS), Wiltshire, UK (see Chapter 2) was used as the study site. Here, over 500 hectares of species-rich grassland are being re-created and restored on former arable land. These ex-arable fields have been sown with species-rich locally-sourced chalk grassland seed mixtures from the year 2000 to 2012, creating a chronosequence of grassland re-creation fields across the landscape.

The Meadow Brown (*Maniola jurtina*) butterfly is used as an indicator and model species in experiments (Conradt *et al.* 2000; Delattre *et al.* 2010a; Merckx *et al.* 2003) due to high local abundance in fragmented agricultural landscapes, wide distribution, and reliance on grassland habitats (Asher *et al.* 2001; Shreeve *et al.* 2001).The 6-spot Burnet moth, *Zygaena filipendulae* occurs in species-rich grasslands where its larval host plant Bird's-foot Trefoil (*Lotus corniculatus*) (Heath & Emmet 1985) and pupation sites (often long grass stems) are abundant, but has been less widely used as a study organism (but see Menendez *et al.* 2002). These species were the most abundant on the study site at the time of the experiment. Other species were recorded but data were combined in an 'all Lepidoptera species' category due to low individual species abundances in order to allow for statistical analysis.

5.2 Aims and Hypotheses

Aims;

- To investigate Lepidoptera behavioural response to small scale alterations in habitat structure at experimental boundaries.
- To determine whether Lepidoptera response to the physical attributes of the mown boundary itself or the lack of resources in the mown area.
- To determine if there are differences in boundary behaviour between Lepidoptera species.
- To inform the spatial targeting of grassland re-creation.

Hypotheses;

i. Mowing will reduce boundary crossing behaviour and increase boundary following and avoiding behaviour.
ii. Behaviour at mown boundaries will be species specific due to differences in larval host-plant specialism and mobility.
iii. Differences in behaviour at mown boundaries will be due to difference in structure rather than lack of resources.

5.3 Methods and materials

5.3.1 Experimental set up

The experiment was set up in the Seven Barrows grassland re-creation field which was sown with chalk grassland seed sourced from Salisbury Plain in 2000 (Figure 5-1, Chapter 2), this field was species-rich and was the most similar in plant community assemblages to the chalk grassland target habitat. Here, two large areas of grassland (40 m by 50 m) were mown and eight 20 m long survey boundaries were set up and given a unique boundary identifier number from 1-8. Four of these were set up on the edge of one of two mown areas (treatment boundaries) and four were set up in areas of continuous un-mown grass which had dummy 'boundaries' parallel to the mown boundaries (control boundaries, Figure 5-2). Two 'blocks' were set up, one next to a small fragment of woodland with the un-mown side of the boundary to the west , and the other with the un-mown side of the boundary to the east; these are referred to as 'sheltered' and 'exposed' block respectively (Figure 5-2). The two mown areas were 15 m from one another, treatment boundaries within the same block were separated by 5 m, control boundaries within the same block were separated by 5 m and treatment and control boundaries were separated by 25 m (Figure 5-2). Boundaries were surveyed from 24th July- 23rd August 2012.

The close proximity of the survey boundaries and blocks aimed to minimise the variation in grassland species composition, structure and climatic conditions, and was designed to fit within the area that was allocated for the experiment by the tenant farmer. To reduce the impact of the experiment on ongoing and subsequent sheep grazing in the field, the tenant farmer limited the area of mown grass to no more than 400 m^2 (0.04 hectares) in total and a fenced off experimental area of no more that 100 m across. The main limitations of this experimental set up were that treatment survey boundaries were 2.5 m from the perpendicular edge of the mown area and that there was a minimum distance of 15 m from survey boundaries and the fences in the field (Figure 5-2).This means that Lepidoptera may have been responding to the perpendicular edge of the mown area at transect boundaries and/or the fences at control boundaries. Treatment boundaries were located in the centre of the field to minimise the possible confounding effects of the fences and woodland.

Map produced by Grace Twiston-Davies 2013 © Natural England copyright (2013). Contains Ordnance Survey data © Crown copyright and database right 2013. LCM2007 © and database right NERC (CEH) 2011. All rights reserved. © third party licensors.

Figure 5-1. The location of the Seven Barrows grassland re-creation field (sown in the year 2000) within the National Trust Stonehenge Landscape in 2012 and the set up of the experimental survey boundaries within the Seven Barrows field. Treatment survey boundaries located at the edge of the mown area and control survey dummy 'boundaries' in continuous grassland.

Survey protocols were based on those used by Ries & Debinski (2001), adapted to the survey site and aims and objectives of the study. Treatment boundary surveys were conducted at the edge of the mown area and control boundary surveys were conducted on the corresponding dummy 'boundary' and the area surveyed was 10 metres either side of the 20 m survey boundary (survey area of 20 m by 20 m). Bamboo poles were used to mark the corners of the survey area and a 10 m grid within each to enable butterfly positions within the survey area to be estimated and flight paths to be recorded (method also described in Chapter 4). The characteristic flora of the experimental area was associated with species-rich chalk grassland, most similar to the Upright Brome dominant grassland community (*Bromopsis erecta* grassland, CG3 in Rodwell 1992) with Quaking Grass (*Briza media*), Glaucous Sedge (*Carex flacca*), Ribwort Plantain (*Plantago lanceolata*) and Bird's-foot Trefoil (*Lotus corniculatus*) constant throughout the sward as well as a high abundance of Sainfoin (*Onobrychis viciifolia*) which is not characteristic of a chalk grassland community but successfully established in this re-creation filed (Campbell 2009; Pemberton 2011).

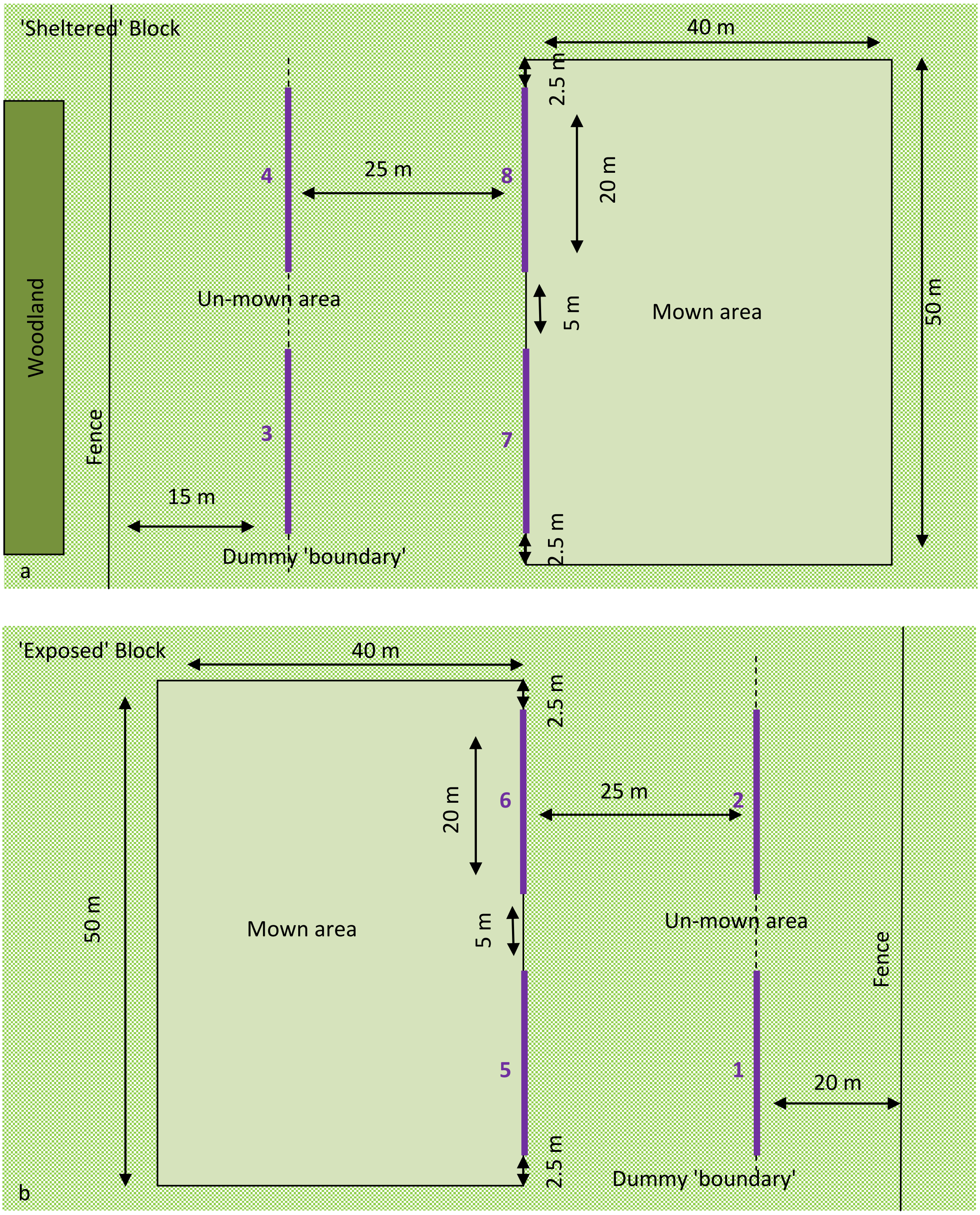


Figure 5-2. Schematic of the experimental set up of survey boundaries (not to scale) in the , a) Sheltered Block (un-mown side to the west) and, b) Exposed block (un-mown side to the East). Four control survey boundaries (1-4) with dummy 'boundaries' shown for control and four treatment survey boundaries (5-8) with the mown area adjacent. For controls the 'mown' side of the boundary was to the east in the 'sheltered' block and to the west in the 'exposed' block. The close proximity of survey boundaries to each other and to fences aimed to minimise within site variation and fit the experimental design within the area that was allocated for the experiment although does require careful interpretation of results.

For survey boundaries in the 'exposed' block the un-mown side of the boundary was on the on the east side of the boundary and therefore on the east side of control in that block. For survey boundaries in the 'sheltered' block the un-mown side of the boundary was on the west side of the boundary and therefore the west side for the control for that block.

5.3.2 Lepidoptera surveys

The survey was conducted by the surveyor standing at the survey boundary (or dummy 'boundary' in controls) and tracking the flight path of individual Lepidoptera in the area 10 m either side of the survey boundary. Each individual Lepidoptera flight path was surveyed for three minutes, until the individual became stationary for more than three minutes, moved further than 20 m from the edge of the survey area (Lepidoptera returning to the survey area could also be recorded). Each boundary was surveyed for a total of 20 minutes on three occasions over the five week period (referred to as survey period). The sequence of boundaries surveyed was chosen randomly and equal survey effort was allocated to visually searching both sides of the boundary. The order and time of day for surveying each survey area was random so to spread surveys throughout the survey period and throughout the day.

The species, start and finish location (in the un-mown or mown side of the boundary or the corresponding control 'boundary') and flight path of Lepidoptera within the 20 m by 20 m survey area around were recorded. The behaviour by which the Lepidoptera exited the 20 m by 20 m survey area was categorised as either 'crossing', 'following' or 'avoiding' the boundary (or dummy 'boundary'). Individuals were allocated to a further category, 'staying', if they did not exit the survey area or their flight path was too convoluted to assign to a single behaviour.

For each survey period, each boundary survey (boundaries 1-8) were completed before the next survey period began, the first being was between 24th July-9th August , the second between 10th-11th August and the third between 14 -23rd August. This was a short window of the overall butterfly flight season but coincided with the peak abundance of adult (imago) *Maniola jurtina* and *Zygaena filipendulae at* the Stonehenge landscape which were shown in previous transect surveys from 2010-2011 (Chapter 3, the peak occurrence for both of these species were the last week in July to the first week in August, *data not shown*), although imago of both of these species may start emerging from pupa from June. The number of days it took to complete each survey period varied as was dependant on weather conditions. There was an average of 10 days between each survey at the same survey transect throughout the study minimising the possibility of pseudoreplication by recording the flight path of the same individual which may have been increased by the close proximity of survey transects and blocks in the experiment.

Surveys were carried out in weather and conditions defined as acceptable for similar surveys by the UK Butterflies Monitoring Scheme (Pollard & Yates 1993).

5.3.3 Environmental variables

Measures of vegetation characteristics and nectar flower availability were recorded for survey area (20 m by 20 m) using eight, 0.5 m by 0.5 m quadrats placed in homogenous vegetation representative of the survey area (four in the un-mown side of the boundary, four in the mown side and the corresponding sides of the control dummy 'boundary'). Recorded vegetation characteristics included the mean and variation (coefficient of variation) in vegetation height and density (using the drop disc method described by Stewart *et al.*,(2001) 1 drop per quadrat, henceforth referred to as vegetation density). Nectar flower availability was measured as the number of flowering units of nectar flowers, species richness and numbers of those in the Asteraceae, Fabaceae and Dipsacaceae families. Nectar flowers were selected based on the nectar plant database ((Hardy *et al.* 2007). Botanical characteristics were surveyed on three occasions (19th July, 10th August and 23rd/24th August).

Variables relating to vegetation height and density and the coverage of bare ground and leaf litter are important for butterflies, as they effect the microclimate and can be used as a resource for oviposition, pupation, courtship and thermoregulation (e.g. Beyer & Schultz 2010; Lawson *et al.* 2014; NCC 1986; Thomas *et al.* 2009). Different butterfly species are associated with different vegetation heights (NCC 1986) for example, the recovery of a threatened Butterfly species, the Large Blue (*Maculinea arion*) can be determined by the vegetation height as this effects the microclimate and the subsequent establishment of a successful symbiotic relationship (Thomas *et al.* 2009). The cover and height of grasses and depth of leaf litter can determine the selection of oviposition sites for Skipper species (*Pokes mardon*) (Beyer & Schultz 2010) and in cooler sites, bare ground may provide a warmer microclimate for oviposition site for *Heperia comma* (Lawson *et al.* 2014).

The average wind speed and wind direction were recorded using measurements from the nearest meteorological station at Boscombe Down, Wiltshire, UK (Chapter 2) to the nearest hour; cloud coverage by eye and average microclimate conditions of humidity, wind speed and air temperature using a digital recorder held at one metre from the ground for three minutes at the start of the survey.

Wind direction was categorised by the relationship to the boundary. For example, if the wind was in the same direction or less than 45° it would be classed as 'with' the orientation of the boundary , if the wind was in the opposite direction or equal to or more than 45° to the boundary it was classed as 'against' (Figure 5-3).

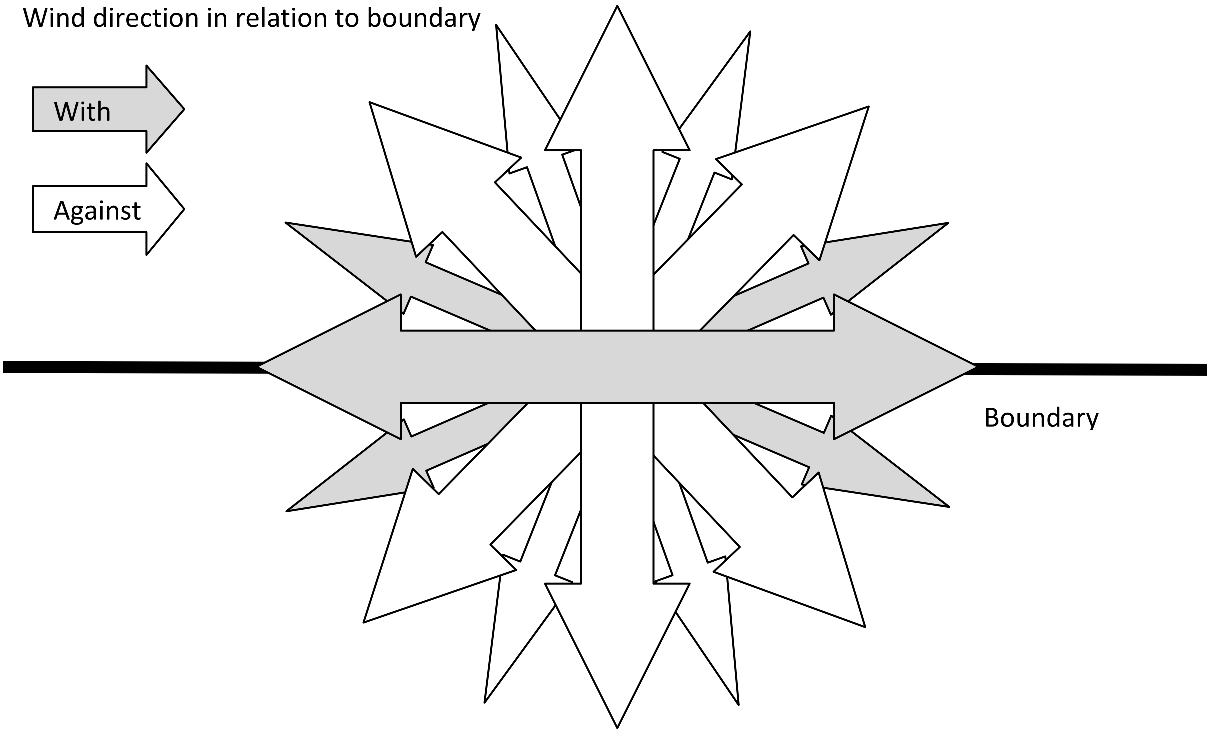


Figure 5-3. Examples of how the relationship of wind direction and boundary edge was categorised as the wind either with or against the orientation of the survey area boundary. If the wind direction was less than 45° to the boundary than it was categorised as "with" the boundary orientation and if it was equal or more than 45° it was categorised as "against" the boundary orientation.

5.3.4 Statistical analysis

The mean values per survey boundary were calculated for the following response variables: total number of Lepidoptera, *Maniola jurtina* and *Zygaena filipendulae* and different survey area exiting behaviours. Mean values were also calculated for the explanatory variables of weather, microclimate, nectar resource and vegetation characteristics. These were calculated for each survey boundary overall and for each side of the survey boundary (mown and un-mown side of the treatment boundary and the corresponding 'mown' and un-mown side of the control dummy 'boundary'). Statistical comparison was conducted using Pearson's Chi-squared test with Yates' continuity correction and Fisher's Exact test in R (version 3.0, R Core Team 2013) and Students T-test (Wilcoxon sum rank for non normal distribution) for Lepidoptera/environmental variables in:

a) either side of the boundary (whole survey area) between;
   i. treatment boundaries and control boundaries,
   ii. the 'sheltered' and the 'exposed' block,

b) in the un-mown side of the treatment boundary or corresponding side of the dummy 'boundary' between;
    i. treatment boundaries and control boundaries,
    ii. the 'sheltered' and the 'exposed' block,
c) in the un-mown side of the boundary compared to the mown (or 'mown' side for control dummy 'boundaries') side of the boundary for treatment and control boundaries separately.

5.3.5 Behaviour probability and boundary permeability measures

The probability of different behaviours and boundary permeability were measured for all Lepidoptera and for *Maniola jurtina* and *Zygaena filipendulae* separately and used the methodology described in Chapter 4.

Behaviour probabilities were calculated by comparing observed and expected proportions of survey area exiting behaviours (by crossing, following or avoiding the boundary) at treatment and control boundaries. This method was adapted from that of Ries & Debinski (2001), but in this study the square survey area was bisected by the boundary or dummy 'boundary' into two rectangles, one in the un-mown side of the boundary and one in the mown side (and corresponding 'mown' sides for controls). As the behaviour category was assigned by the survey edge by which the butterfly exited the survey area, this means that if butterfly behaviour is random, the probability of exiting the survey area by crossing the boundary is 33.3%, by the opposite 'edge' of the survey area is 33.3% and by one of the perpendicular survey area 'edges' is 33.3% (Figure 5-4).

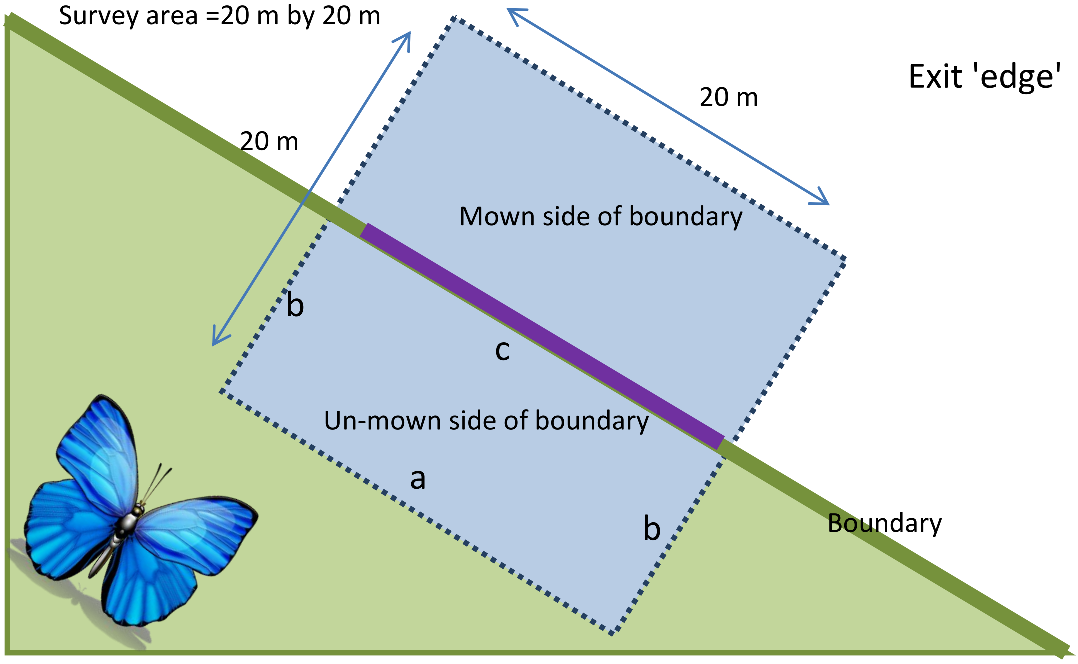


Figure 5-4. Probability of exiting the survey area on the un-mown side of the boundary is 33.3% for exiting by, avoiding (exit at a), following (exit at b) and crossing (exit and c) the survey boundary.

Boundary permeability was defined as the proportion that approach the boundary and then cross it (Stamps *et al.* 1987) and was calculated using the estimated flight path data recorded during the survey.

Comparisons between behaviour probabilities and boundary permeability were done for flight paths that originated in the un-mown and mown side of the boundary separately (or corresponding control side of the dummy 'boundary').

5.3.6 Generalised Linear Mixed Models

To investigate the differences between Lepidoptera behaviour at the mown boundaries and on either side of the boundaries, two models were created that used all Lepidoptera responses on both sides of the boundary and just those on the un-mown or corresponding side of the control boundaries. This also enabled the effect of wind speed and direction to be investigated. The proportion of all Lepidoptera, *Maniola jurtina* and *Zygaena filipendulae* crossing boundaries and following boundaries separately were response variables in two different Generalised Linear Mixed Models (GLMM, Table 5-1). These used fixed and random effect; a fixed effect influences only the mean of the response variable and a random effect influences only the variance of the response variable (Crawley 2007). So random effects are variables that may affect the variation in the data but that we are not interested in testing the effects of these on the response variable specifically.

The first model (Table 5-1, a) used Lepidoptera flight paths which originated on either side of the boundary and had treatment (mown area next to boundary or control), survey period, block ('sheltered' or 'exposed'), species density, individual survey boundary identifier (1-8) and interaction of treatment with survey period and species density with treatment as explanatory variables. The individual survey boundary identifier was a random effect in model.

The other model (Table 5-1, b) used Lepidoptera flight paths originating in the un-mown side of the survey boundary with the corresponding side in controls as the response variable. For survey boundaries in the 'exposed' block the un-mown side of the boundary was on the on the east side of the boundary and therefore on the east side of control in that block. For survey boundaries in the 'sheltered' block the un-mown side of the boundary was on the west side of the boundary and therefore the west side for the control for that block. These models had treatment, survey period, block, species density, individual survey boundary identifier (1-8), wind direction, wind speed and interactions of treatment with survey period, species density with treatment and wind direction with wind speed as explanatory variables. Individual survey boundary identifier was a random effect in model. This was done for all Lepidoptera/boundary behaviour combinations except for *Zygaena filipendulae* with boundary following which only had interaction of treatment and survey period due to zero proportions in some combinations. Models were also created as described above but with survey period as a random effect along with individual boundary identification.

Table 5-1. Model response variable and explanatory variable fixed and random effects.

Model	**Reponses variables**	**Explanatory variables**	
	Flight path starting from	**Fixed effects**	**Random effects**
a	both sides of boundary (whole survey area) behaviour to boundary	treatment, survey period (survey week), block and species density. Interaction of treatment X survey period and species density X treatment	Individual survey boundary identifier
b	un-mown side of boundary (half the survey area) behaviour each side of the boundary	treatment, survey period, block, species density, wind direction and wind speed. Interaction of treatment X survey period, species density X treatment and wind direction X wind speed	individual survey boundary identifier

5.4 Results

5.4.1 Comparison, a) Lepidoptera between treatment and control survey areas

A total of 389 Lepidoptera were surveyed at control and treatment plots consisting of 148, *Maniola jurtina* and 195 *Zygaena filipendulae.* Of these totals, 159 crossed, 74 followed and 36 avoided boundaries and 120 stayed within the survey are and therefore no behaviour could be assigned (Table 5-2).

Table 5-2. Summaries of the numbers of all Lepidoptera and of *Maniola* and *Zygaena filipendulae* exhibiting different behaviours (crossing, following, avoiding and staying) at control and treatment boundaries on either the un-mown or mown side of the boundary (or "mown" side of the control boundary).

	Control			**Treatment**		
	un-mown	**"mown"**	**Total**	**un-mown**	**mown**	**Total**
Totals						
All Lepidoptera	105	92	197	125	67	192
Maniola jurtina	36	37	73	47	28	75
Zygaena filipendulae	58	47	105	62	28	90
Crossing						
All Lepidoptera	57	33	90	32	37	69
Maniola jurtina	15	13	28	9	15	24
Zygaena filipendulae	34	17	51	19	18	37
Following						
All Lepidoptera	6	15	21	32	21	53
Maniola jurtina	3	7	10	10	6	16
Zygaena filipendulae	3	6	9	19	8	27
Avoiding						
All Lepidoptera	7	11	18	15	3	18
Maniola jurtina	3	6	9	9	2	11
Zygaena filipendulae	3	5	8	5	1	6
Staying						
All Lepidoptera	35	33	68	46	6	52
Maniola jurtina	15	11	26	19	5	24
Zygaena filipendulae	18	19	37	19	1	20

Initial comparison was conducted between the mean number of Lepidoptera at treatment survey boundaries with the adjacent mown area and control survey boundaries that had not been mown (Figure 5-5). There was no significant difference between mean numbers of Lepidoptera at treatment compared to control boundaries, (Student's T-test, $p>0.05$, Figure 5-6). There were higher proportions of Lepidoptera 'crossing' at the control dummy 'boundary' compared to the treatment boundary (with an adjacent mown area) but the significance was borderline (Figure 5-7 a, X^2=3.43, p=0.0640). There were significantly higher proportions of boundary following at treatment boundaries for all Lepidoptera and for *Zygaena filipendulae* compared to expected (Figure 5-5, b, full results in Appendix D).

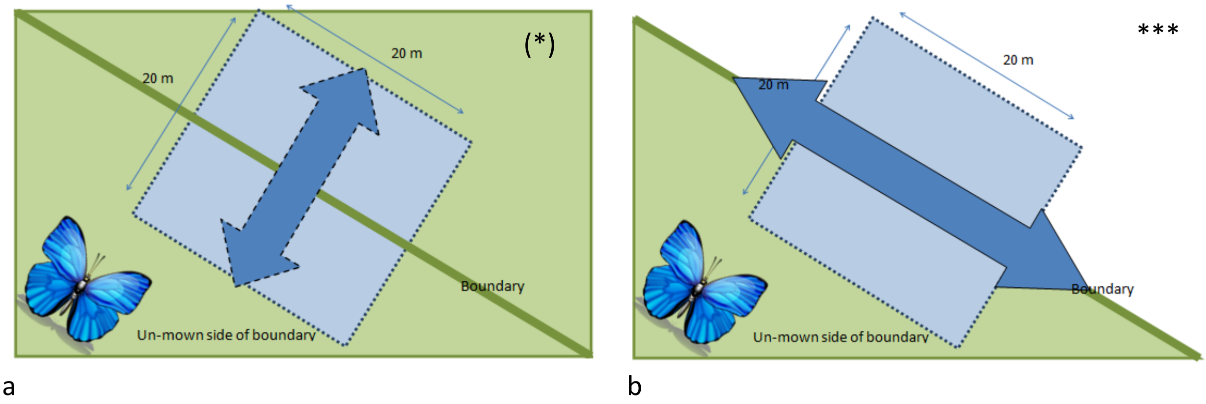


Figure 5-5. There were significantly (and borderline) more numbers of all Lepidoptera in total crossing the control dummy 'boundary' than expected (a) and more following the treatment boundary than expected (b) if movement was random (p=0.0640 and <0.0001, respectively). There were more *Zygaena filipendulae* following the treatment boundary than expected if movement was random (p=0.0003) and no significant difference for *Maniola jurtina*.

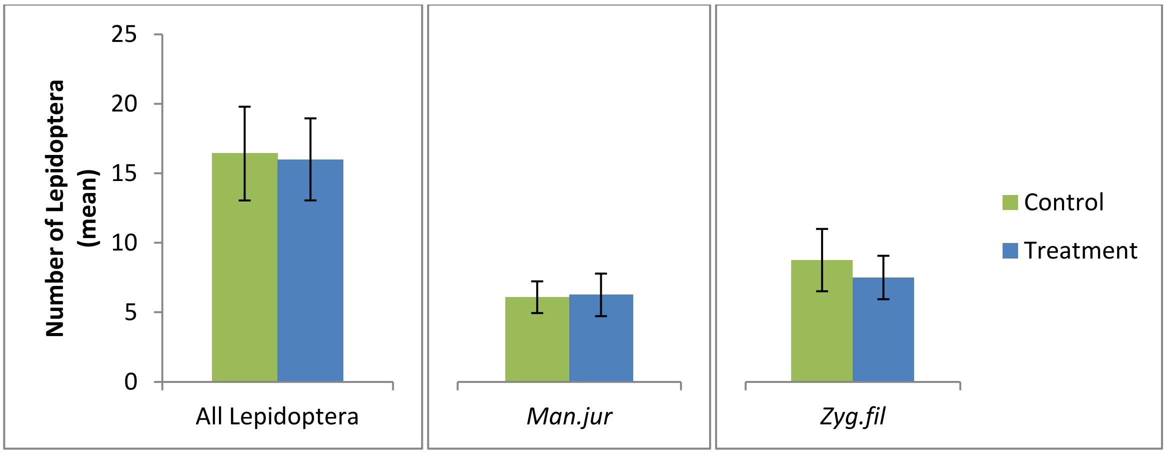


Figure 5-6. Mean number of all Lepidoptera, *Maniola jurtina* (*Man.jur*) and *Zygaena filipendulae* (*Zyg.fil*) between treatment (experimentally mown) boundaries and control boundaries that were not mown. Error bars show 1 Standard Error of the mean.

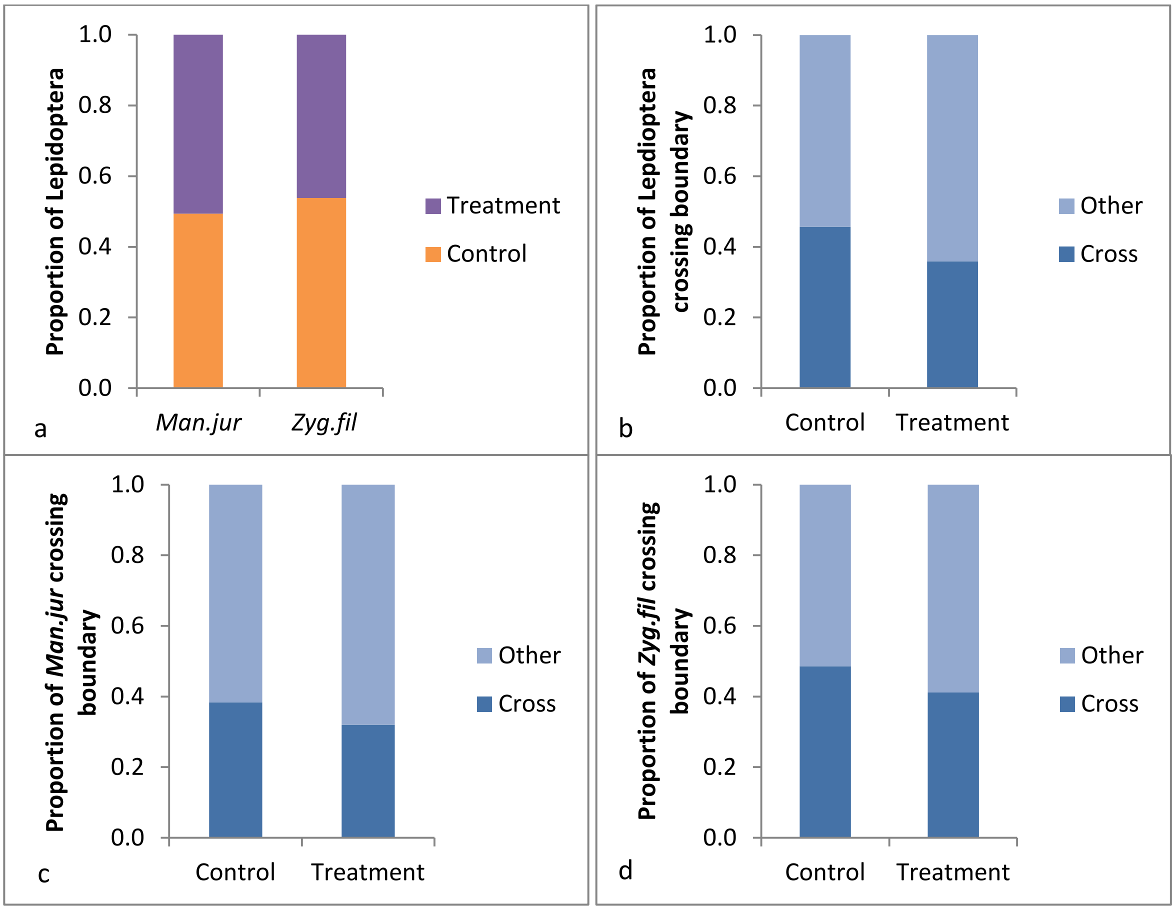


Figure 5-7. Proportion of, a) *Maniola jurtina* and *Zygaena filipendulae* (*Man. jur* and *Zyg. fil* respectively), proportion crossing boundaries for, b) all Lepidoptera p=0.0640, c) *Maniola jurtina* and, d) *Zygaena filipendulae* separately at treatment boundaries (adjacent to mown area) and control boundaries (not mown). Chi-squared test p>0.05.

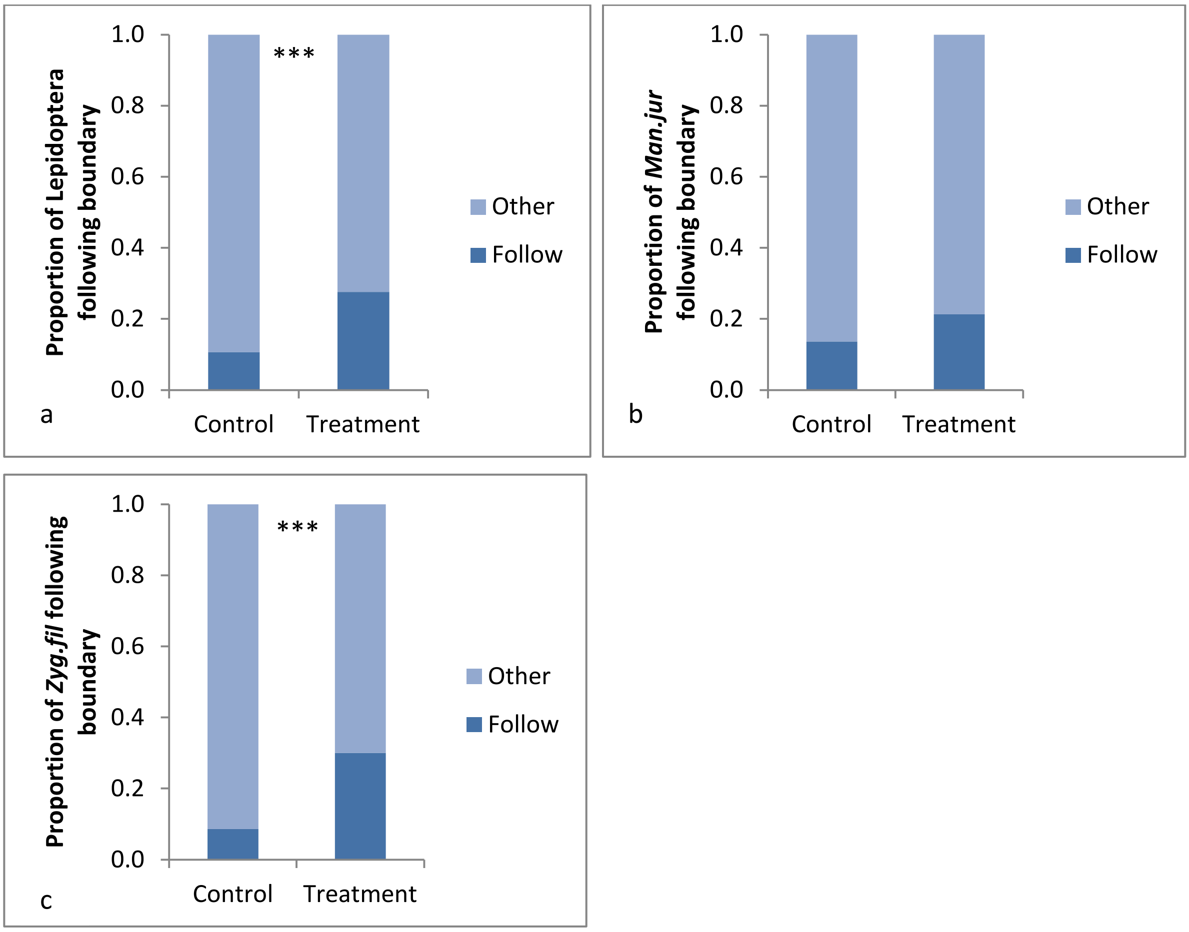


Figure 5-8. Proportion of Lepidoptera following boundaries for, a) all Lepidoptera, b) *Maniola jurtina* (*Man.jur*) and, c) *Zygaena filipendulae* (*Zyg.fil*) separately at treatment boundaries (adjacent to mown area) and control boundaries (not mown). Chi-squared test p<0.0001, 0.3153 and 0.0003, respectively. Significance p<0.001 ***, p<0.01 **, p<0.05 *.

5.4.2 Comparison, b) Lepidoptera between sheltered and exposed blocks

Comparison was conducted between the mean number of Lepidoptera in the two different blocks to investigate if the adjacent woodland in the 'sheltered' block affected the distribution and behaviour of Lepidoptera. There was no significant difference between mean numbers of Lepidoptera in the two different blocks (more exposed and more sheltered locations, Figure 5-9). There was no significant difference between proportions of *Maniola jurtina* and *Zygaena filipendulae* (Figure 5-10, a). There were no significant differences between the proportions crossing boundaries for all Lepidoptera, *Maniola jurtina* or *Zygaena filipendulae* separately (Figure 5-10, a) or following boundaries for *Zygaena filipendulae* (Figure 5-11,d) and *Maniola jurtina* following boundaries between the sheltered and exposed blocks (Figure 5-11, Appendix D for full results).

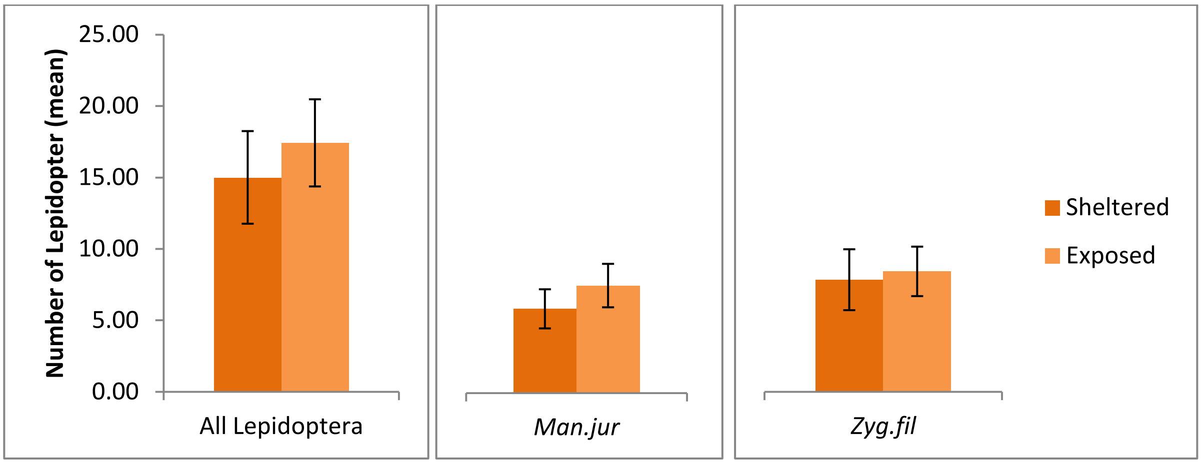


Figure 5-9. Mean number of all Lepidoptera, *Maniola jurtina* (*Man. jur*) and *Zygaena filipendulae* (*Zyg.fil*) at the exposed and sheltered block. $p>0.05$. Error bars show 1 Standard Error of the mean.

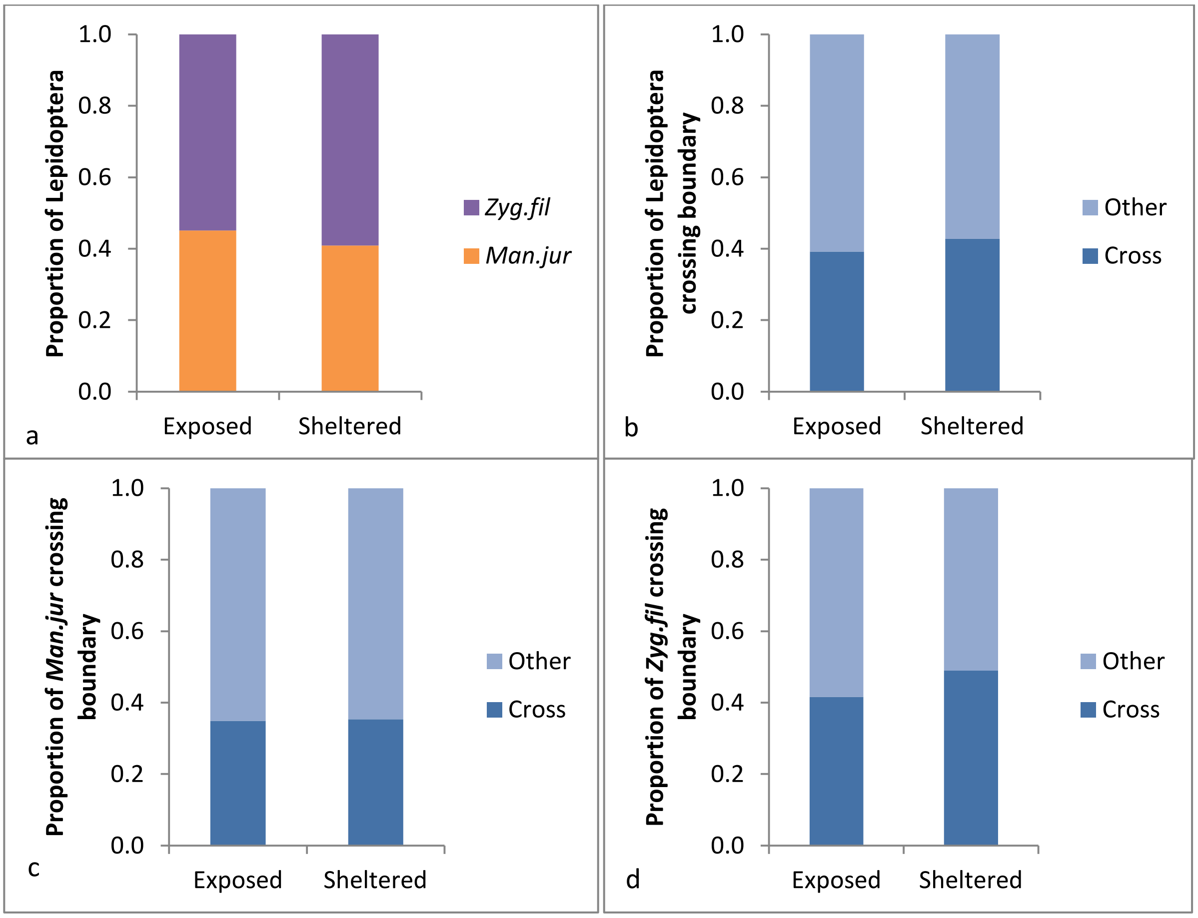


Figure 5-10. Proportion of, a) *Maniola jurtina* and *Zygaena filipendulae* (*Man.jur* and *Zyg.fil* respectively), proportion crossing boundaries for, b) all Lepidoptera, c) *Maniola jurtina* and, d) *Zygaena filipendulae* separately at survey boundaries in more exposed block (Exposed) and more sheltered block (Sheltered) (includes treatment and control boundary surveys). Chi-squared test $p>0.05$.

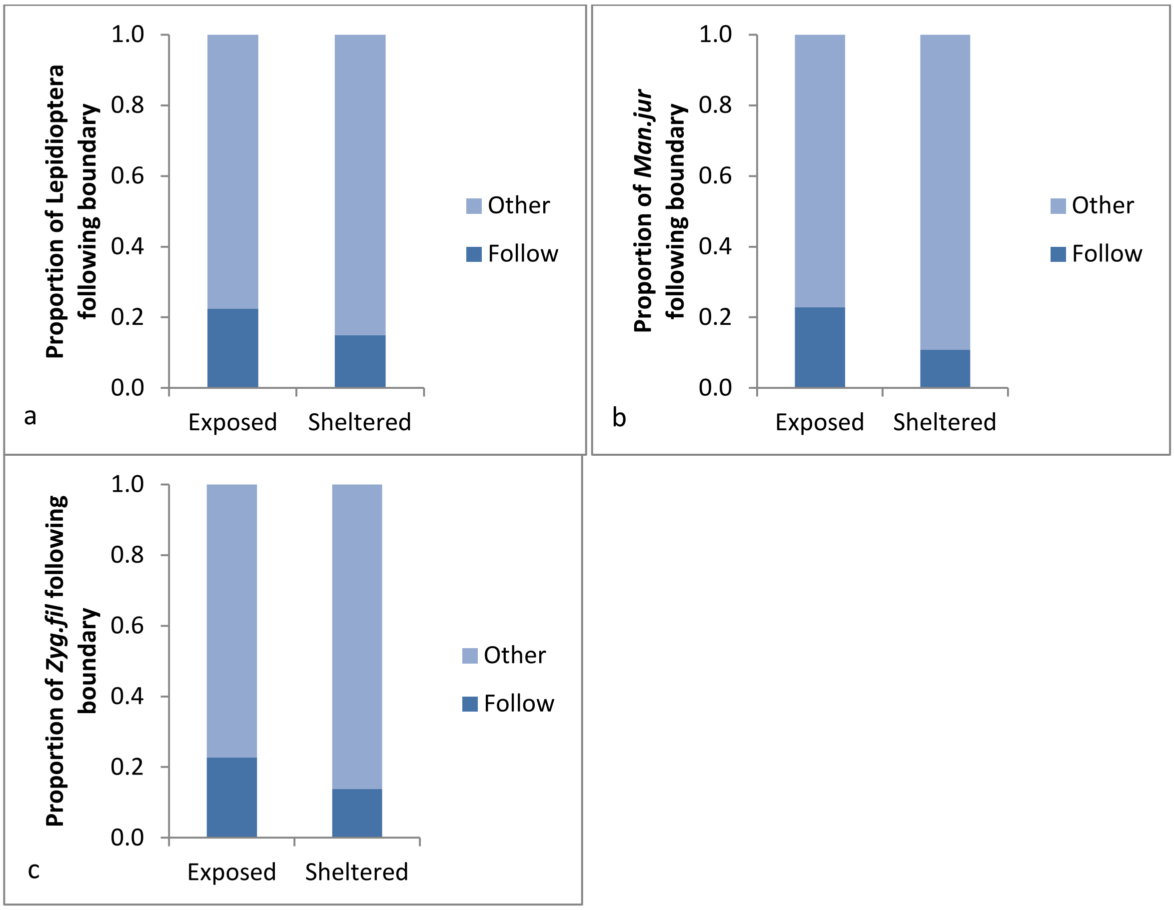


Figure 5-11. Proportion of Lepidoptera following boundaries for, a) all Lepidoptera, b) *Maniola jurtina* (*Man.jur*) and, c) *Zygaena filipendulae* (*Zyg.fil*) separately and expected in more exposed block (Exposed) and more sheltered block (Sheltered) (includes treatment and control boundary surveys). Chi-squared test p>0.05.

5.4.3 Comparison, c) Lepidoptera behaviour either side of the boundary

Statistical comparisons were made to investigate if there was a difference in the number or behaviour of Lepidoptera either side of the survey boundaries and are summarised in Figure 5-14. Results comparing the behaviour of Lepidoptera on either side of the boundary showed that there was no significant difference between the proportion of *Maniola jurtina* and *Zygaena filipendulae* on different sides of the boundaries at both control and treatment boundaries (Figure 5-12, p>0.05). There was no significant difference between boundary crossing at control boundaries or boundary following at treatment boundaries (p>0.05), but there were significant differences between boundary crossing at treatment boundaries for total Lepidoptera (X^2= 5.02, p=0.0251) and boundary following at control boundaries (X^2=7.29, p=0.01, Figure 5-13, Appendix D for full results). The significant difference between following at control boundaries is anomalous.

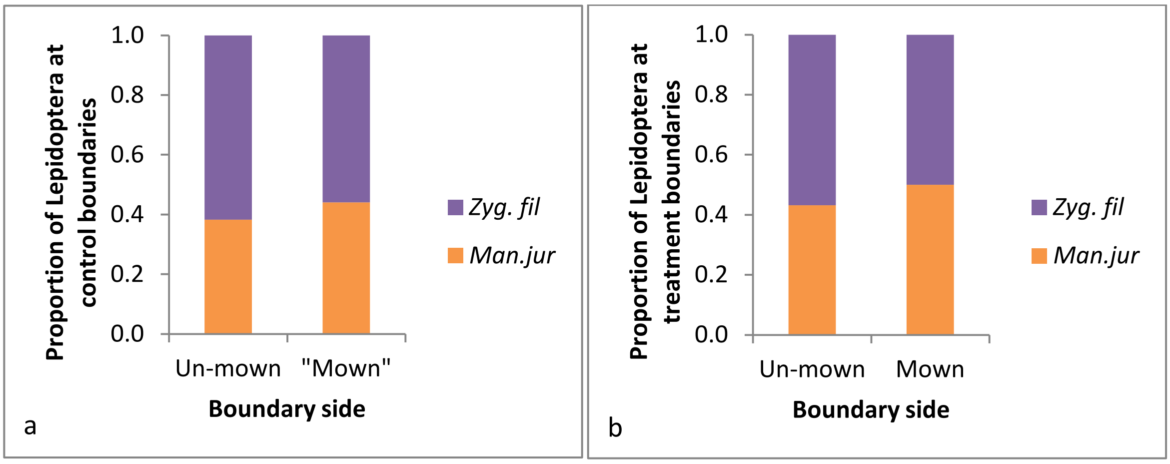


Figure 5-12. The proportion of *Maniola jurtina* and *Zygaena filipendulae* (*Man.jur and Zyg.fil, respectively*) in the un-mown and mown side of the boundary for, a) controls ('Mown' side refers to corresponding side of the boundary to the treatment but was not mown) and , b) treatments. p>0.05.

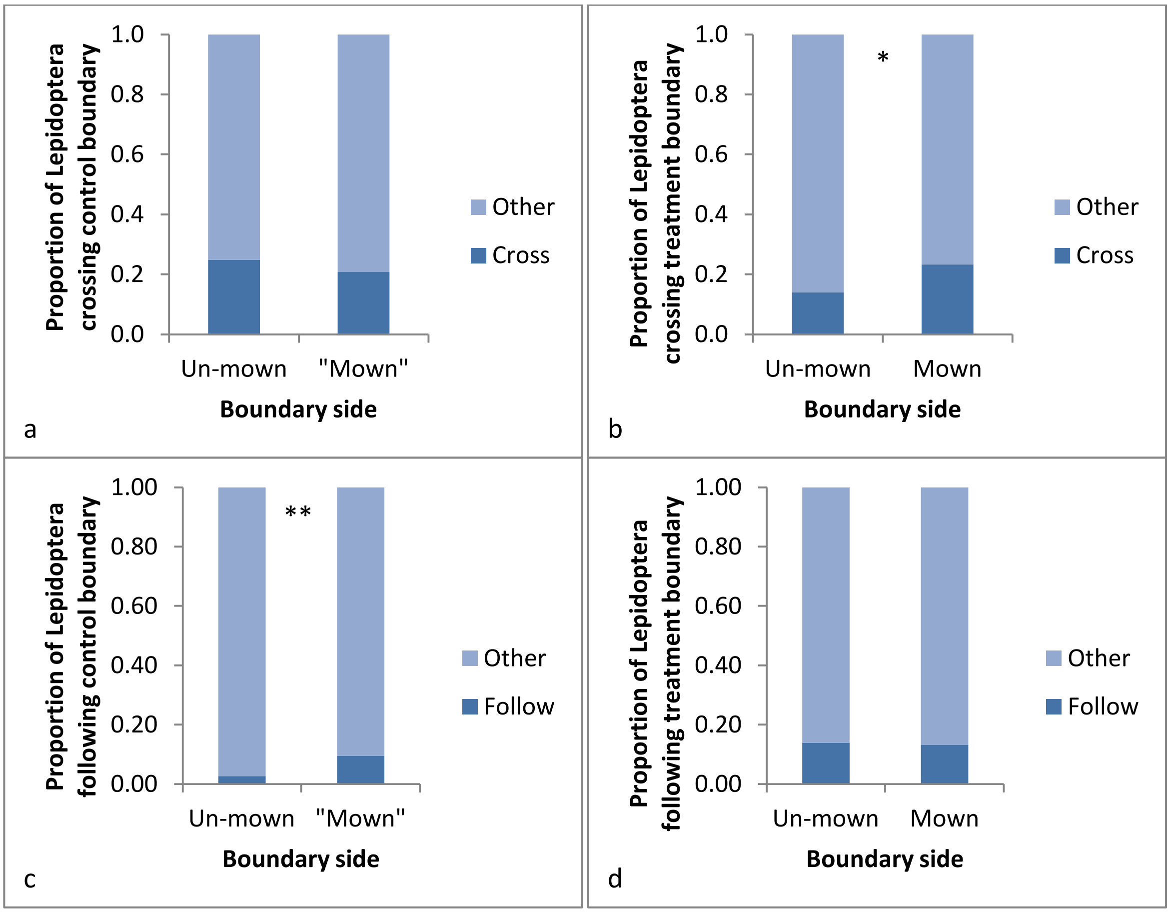


Figure 5-13. Proportion of Lepidoptera in the un-mown or mown ('Mown' for control as this was the corresponding side to the treatment boundary) side of the boundary, a) crossing at control and, b) treatment boundaries p=0.0251 and, c) following at control p=0.0069 and, d) treatment boundaries. Significance p<0.001 ***, p<0.01 **, p<0.05 *.

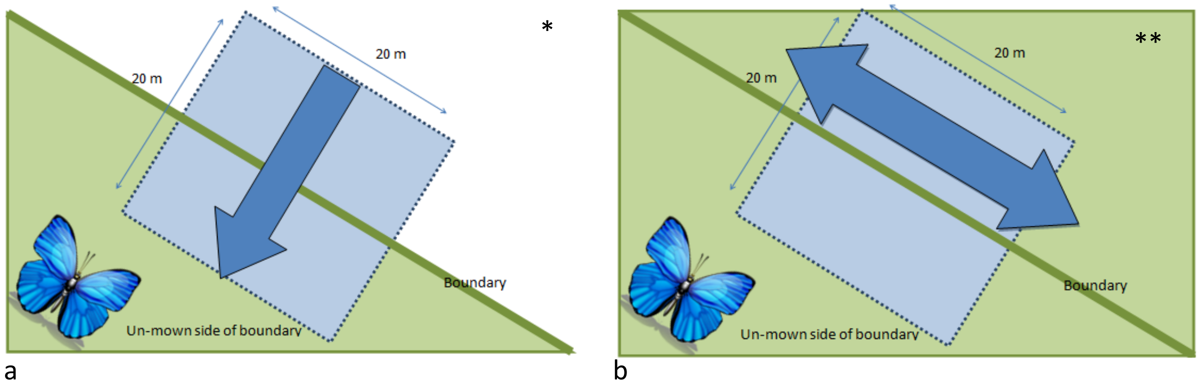


Figure 5-14. Results showed that there was more Lepidoptera in total crossing the treatment boundary from the mown side (a, p=0.0251), and more following the dummy 'boundary' from the "mown" side (b, p=0.0069).

5.4.4 Behaviour probability and boundary permeability measures

When comparing the behaviour probabilities, there were no significant differences between the proportions of Lepidoptera exiting the survey area by crossing the dummy 'boundary' in controls compared to the expected proportion if survey area exiting behaviour was random (Figure 5-15, Appendix D for full results). This was based on Lepidoptera flight paths that originated in the un-mown side of the treatment boundary (with the adjacent mown area) or the corresponding side of the control boundary. Following the boundary as a survey area exiting behaviour was significantly lower than expected if behaviour was random at the control boundaries (Figure 5-15) with less than 7% exiting the control survey area by following the dummy 'boundary' in controls (p<0.001).

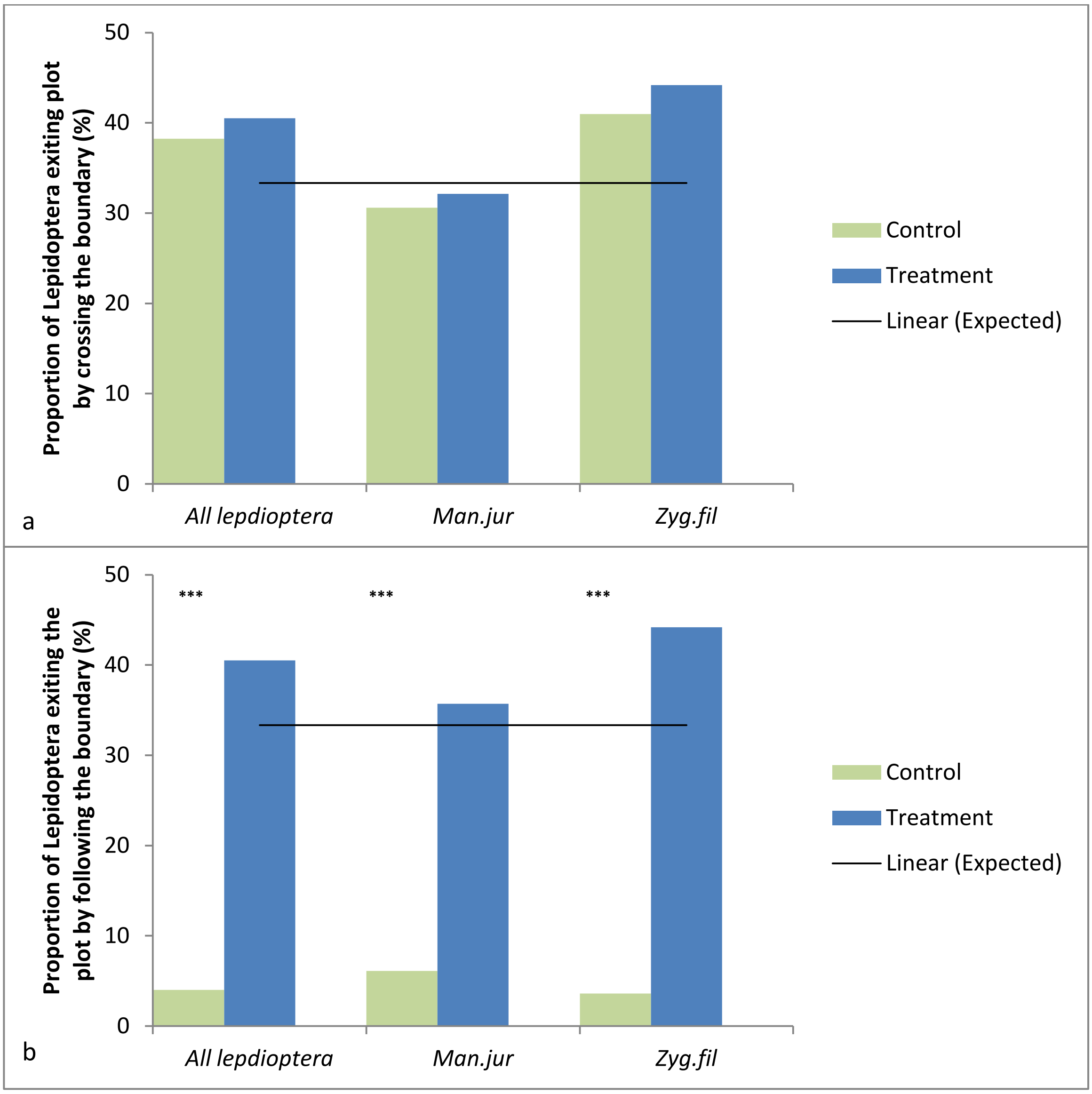


Figure 5-15. The proportion of Lepidoptera (%) exiting the survey area by, a) crossing the boundary and, b) following the boundary. Results of Chi-squared test comparing this proportion to the 33% that would be expected if survey area exit behaviour was random (for example, 33% would exit by crossing, 33% by avoiding and 33% by following the boundary). For all Lepidoptera and for *Maniola jurtin*a and *Zygaena filipendulae* separately (*Man.jur* and *Zyg.fil* respectively). Significance p<0.001 ***, p<0.01 **, p<0.05 *.

Results from the boundary permeability measure showed that for all Lepidoptera, the proportion that approached the boundary and then crossed it was similar between treatment and control boundaries and similar in total for *Maniola jurtina. Maniola jurtina*, had lower permeability value at the mown boundaries than the control. *Zygaena filipendulae* had a higher edge permeability of 70% (Table 5-3). Overall exiting the survey area through edges perpendicular to the boundary had a lower permeability but was higher at mown boundaries than controls (Table 5-3).

Table 5-3. Mean and 1 Standard Error (SE) for edge permeability estimates for treatment boundaries adjacent to a mown area and in control boundaries that were not mown for all Lepidoptera and for *Maniola jurtina (Man.jur)* and *Zygaena filipendulae(Zyg.fil)*. Flight path originating on the un-mown or corresponding control side of the boundary.

		Control	**Treatment**	**Total**	**Control**	**Treatment**	**Total**
Species		**Crossing (%)**			**Following(%)**		
All Lepidoptera	mean	55.14	44.79	49.96	24.92	51.35	38.14
	SE	6.83	8.90	±5.55	13.09	4.39	8.11
Man.jur	mean	57.58	37.86	47.72	22.92	47.92	35.42
	SE	8.11	16.76	9.39	15.73	8.59	9.55
Zyg.fil	mean	68.70	77.84	73.27	18.75	76.61	47.68
	SE	3.56	9.39	4.96	18.75	8.43	14.50

5.4.5 Generalized Linear Mixed Models

5.4.5.1 Lepidoptera behaviour on both sides of the boundary

This model investigated the factors influencing the response of Lepidoptera whose flight paths started on either side of the boundary in terms of boundary crossing or following behaviour. The environmental variables tested included treatment (mown or control boundary), survey period, block and species density as well as interaction between these. Overall results are illustrated in Figure 5-16. The proportion of Lepidoptera crossing boundaries was significantly lower for all Lepidoptera at treatment boundaries that were adjacent to the mown areas and significantly higher in the sheltered block, when there were high Lepidoptera densities and when there was an interaction of treatment boundaries and survey periods 2 and 3 (surveys done between 10th-24th August, Table 5-4, Model iteration 3 compared to the Null model $p<0.0001$, see Appendix D for all model iterations). No environmental variables that were included in the model had a significant effect on the proportion of *Maniola jurtina* crossing boundaries and there were significantly lower proportions of *Zygaena filipendulae* crossing boundaries at the treatment boundary but the model was borderline significant (Table 5-4, Model iteration 6 compared to the Null model $p=0.0679$, see Appendix D for all model iterations).

The proportion of Lepidoptera following boundaries when flight paths started on either side of the boundary was significantly higher for all Lepidoptera at treatment boundaries which were adjacent to the mown area and lower when there was high species density (Table 5-5, Model 5 iteration compared to the Null model $p=0.0001$, see Appendix D for all model iterations). No environmental variables in the model were significant for *Maniola jurtina* and there were higher proportions of *Zygaena filipendulae* following at treatment boundaries (Table 5-5, Model 6 iteration compared to the Null model p=0.0195, see Appendix D for all model iterations).

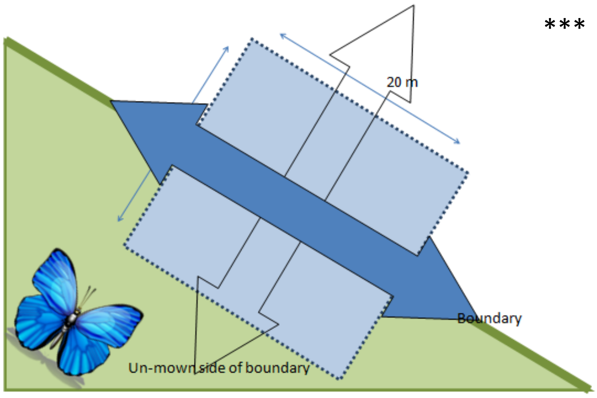


Figure 5-16. Significantly and borderline significantly lower proportions of all Lepidoptera and *Zygaena filipendulae* were crossing (p<0.0001 and p=0.0679, respectively) and significantly higher proportions following (p=0.0001 and p=0.0195, respectively) at treatment boundaries. There were significantly higher proportions of Lepidoptera crossing in the sheltered block and when there was a high species density and an interaction of treatment/control boundary and survey period. There were significantly higher proportions of Lepidoptera following boundaries when there were lower densities of Lepidoptera.

Table 5-4. Minimum Adequate Model of GLMM for all Lepidoptera, *Maniola jurtina* (*Man. jur*) and *Zygaena filipendulae* (*Zyg. fil*) crossing at boundary surveys. Variable estimate (Estimate), Standard error (Std.Error), z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). See Appendix D for all model iterations. Variables here are treatment or control boundaries, sheltered or exposed block, species density and survey periods 1,2 or 3.

Crossing	**Variables**	**Estimate**	**Std.Error**	**z**	**p**	
All Lepidoptera	Model iteration 3 compared to Null				**<0.0001**	***
	(Intercept)	-1.48	0.77	-1.92	0.0553	(*)
	Treatment	-1.52	0.42	-3.64	**0.0003**	***
	Sheltered block	0.57	0.29	1.98	**0.0475**	*
	Total sp. density	0.09	0.02	3.73	**0.0002**	***
	Control: Survey period 2	-0.48	0.47	-1.03	0.3044	

	Treatment: Survey period 2	1.73	0.52	3.36	**0.0008**	***
	Control: Survey period 3	1.36	0.86	1.58	0.1140	
	Treatment: Survey period 3	1.29	0.62	2.06	**0.0390**	*
Man.jur	Null					
Zyg.fil	Model iteration 6 compared to Null				0.0679	(*)
	(Intercept)	1.15	0.37	3.09	**0.0020**	**
	Treatment	-1.02	0.50	-2.03	**0.0428**	*

Table 5-5. Minimum Adequate Models of GLMM for all Lepidoptera, *Maniola jurtina* (*Man. jur*) and *Zygaena filipendulae* (*Zyg. fil*) following at boundary surveys. Variable estimate (Estimate), Standard error (Std.Error), z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). See Appendix D for all model iterations. Variables here are treatment or control boundaries and species density.

Follow	**Variables**	**Estimate**	**Std.Error**	**z**	**p**	
All Lepidoptera	Model iteration 5 compared to null				**0.0001**	
	(Intercept)	-0.33	0.42	-0.77	0.4413	
	Treatment	1.02	0.30	3.36	**0.0008**	***
	Total sp. density	-0.06	0.02	-3.54	**0.0004**	***
Man.jur	Null					
Zyg.fil	Model iteration 6 compared to Null				**0.0195**	*
	(Intercept)	-1.92	0.42	-4.59	**<0.0001**	***
	Treatment	1.44	0.53	2.70	**0.0069**	**

5.4.5.2 Lepidoptera behaviour on the un-mown side of the boundary

This model investigated the response of Lepidoptera whose flight paths started on the un-mown side of the treatment boundary or the corresponding control boundary. The behavioural response of crossing or following behaviour to environmental variables relating to the treatment (mown or control boundary), survey period, block and species density, wind speed and wind direction as well as interaction between these. Overall results are illustrated in Figure 5-17. The proportion of Lepidoptera crossing boundaries was significantly lower for all Lepidoptera for the treatment boundary which was adjacent to the mown area and significantly higher in the sheltered block (Table 5-6, Model iteration 8 compared to Null model p=0.0003, see Appendix D for all model iterations).

There were significantly higher proportions of *Maniola jurtina* crossing the control boundaries when there was high species density and significantly lower proportions of *Zygaena filipendulae* at treatment boundaries and significantly higher proportions when species density was high and in the sheltered block (Table 5-6, Model 10 iteration compared to Null model p=0.0099 and model iteration 7 compared to Null model p=0.0021 respectively, see Appendix D for all model iterations).

The proportion of Lepidoptera following boundaries when flight paths originated from the un-mown side of the boundary was significantly higher for all Lepidoptera at treatment boundaries and lower in the sheltered block (Table 5-7, Model 8 iteration compared to Null p=0.0029, see Appendix D for all model iterations). Increased species density potentially reduced boundary following in Model iteration 7 which was borderline significantly different in residual deviance to the Minimum Adequate Model 8 iteration (Table 5-7, Model 7 iteration compared to Null model p=0.0015, X^2 Model 7 and Model 8 p=0.0527, see Appendix D for all model iterations). There were significantly higher proportions of *Maniola jurtina* following at treatment boundaries and with high wind speed and lower proportions in survey period 3 (Table 5-7, Model 7 iteration compared to Null model p=0.0047). There were significantly higher proportions of *Zygaena filipendulae* following at treatment boundaries and lower proportions in the sheltered block and when species density was high (Table 5-7, Model 5 iteration compared to Null model p=0.0002, see Appendix D for all model iterations).

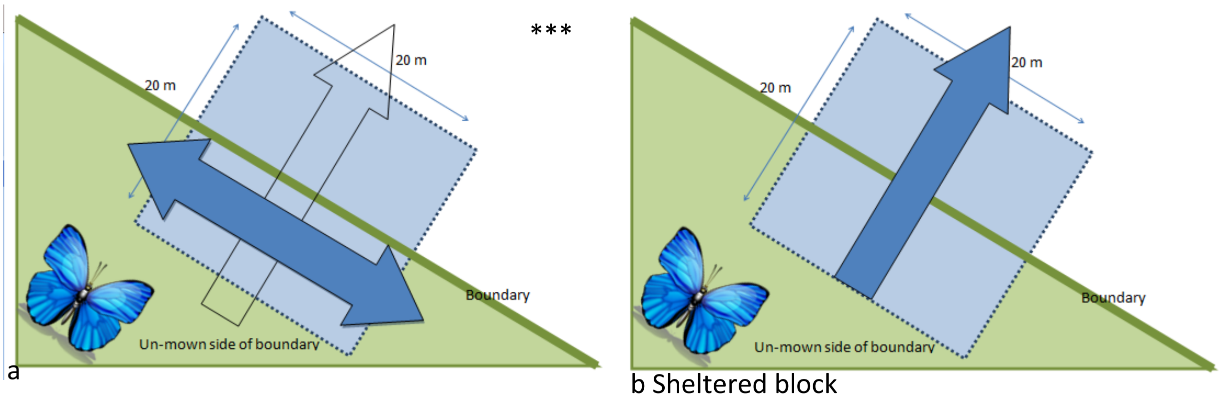


Figure 5-17. When Lepidoptera flight paths started from the un-mown side of the boundary, there were significantly lower proportions of all Lepidoptera crossing at treatment boundaries (a, p=0.0004) and higher proportions crossing in the sheltered block (b, p=0.0137). There was significantly higher proportions of Lepidoptera following at treatment boundaries (a, p=0.0015) and less in sheltered block and when species density was low.

Table 5-6. Minimum Adequate Model for GLMM for all Lepidoptera, *Maniola jurtina* (*Man.jur*) and *Zygaena filipendulae* (*Zyg.fil*) crossing the survey boundaries. Variable estimate (Estimate), Standard error (Std.Error), z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). See Appendix D for all model iterations. Variables here are treatment or control boundaries, sheltered or exposed block and species density.

Crossing	**Variables**	**Estimate**	**Std.Error**	**z**	**p**	
All Lepidoptera	Model iteration 8 compared to Null				**0.0004**	***
	(Intercept)	1.11	0.33	3.33	**0.0009**	***
	Treatment	-1.94	0.40	-4.89	**<0.0001**	***
	Sheltered block	0.95	0.39	2.47	**0.0137**	*
Man.jur	Model iteration 10 compared to Null				**0.0099**	**
	(Intercept)	-1.68	0.92	-1.82	0.0690	(*)
	Control: *Man.jur* density	0.63	0.26	2.45	**0.0145**	*
	Treatment: *Man.jur* density	0.14	0.12	1.17	0.2421	
Zyg.fil	Model iteration 7 compared to Null				**0.0021**	**
	(Intercept)	-1.09	0.81	-1.35	0.1782	
	Sheltered block	1.66	0.58	2.87	**0.0042**	**
	Zyg.fil density	0.28	0.10	2.69	**0.0071**	**
	Zyg.fil density: Treatment	-0.27	0.07	-3.73	**0.0002**	***

Table 5-7. Minimum Adequate Model for GLMM for all Lepidoptera, *Maniola jurtina* (*Man.jur*) and *Zygaena filipendulae* (*Zyg.fil*) following the survey boundaries. Variable estimate (Estimate), Standard error (Std.Error), z and p value. Significance p<0.001 ***, p<0.01 **, p<0.05 *, 0.1<p>0.05 (*). See Appendix D for all model iterations. Variables here are treatment or control boundaries, sheltered or exposed block, wind speed and species density.

Following	**Variables**	**Estimate**	**Std.Error**	**z**	**p**	
All Lepidoptera	Model iteration 7 compared to Null				**0.0015**	**
	(Intercept)	-1.227	0.61	-2.01	**0.0441**	*
	Treatment	2.14	0.50	4.27	**<0.0001**	***
	Sheltered block	-0.93	0.44	-2.13	**0.0334**	*
	Total sp density	-0.06	0.03	-1.93	0.0542	(*)
	Model iteration 8 compared to Null				**0.0029**	**
	(Intercept)	-2.05	0.45	-4.59	**<0.0001**	***
	Treatment	2.02	0.49	4.12	**<0.0001**	***
	Sheltered block	-0.84	0.43	-1.98	**0.0482**	*
Man.jur	Model iteration 7 compared to Null				**0.0047**	**
	(Intercept)	-7.73	3.02	-2.56	**0.0106**	*
	Treatment	2.67	1.33	2.02	**0.0439**	*
	Survey period 2	1.89	1.14	1.66	0.0964	(*)
	Survey period 3	-5.24	2.84	-1.84	0.0653	(*)
	Wind speed	0.70	0.34	2.04	**0.0417**	*
Zyg.fil	Model iteration 5 compared to Null				**0.0015**	**
	(Intercept)	0.02	0.96	0.02	0.9807	
	Treatment	2.64	0.76	3.50	**0.0005**	***
	Sheltered block	-1.47	0.65	-2.24	**0.0249**	*
	Zyg.fil density	-0.27	0.11	-2.62	**0.0089**	**

Overall, the significance of the Minimum Adequate Model when survey period was a random effect was higher or no different from when survey period was a fixed effect (Appendix D), these results are in the Appendix D. The environmental variables of treatment boundaries, sheltered block and species density remained significant in the Minimum Adequate Models when survey period was as a fixed effect and when it was a random effect.

5.4.6 Measures of micro-climate, weather, nectar resources and vegetation characteristics

There was no significant difference in weather or microclimate conditions between the treatment and control survey areas or between the sheltered and exposed block (p>0.05, Appendix D for table of results).

As a result of mowing half the survey area, nectar flowers were removed and vegetation density decreased. Statistical analyses quantified this effect; when comparing the nectar resources and vegetation characteristics between the treatment and control survey areas, (both sides of the boundary), there were significantly lower nectar flower numbers (average number of flowering units, T=5.1069, p<0.0001), in the Fabaceae family (T=3.62, p=0.0015, Figure 5-18) and species richness (T=2.41, p=0.0254, Figure 5-19) in treatments boundary survey areas. There were also significantly lower mean and variation in vegetation density (T=6.35, df=12, p<0.0001, Figure 5-19) at treatment survey area. There were no significant differences between sheltered or exposed blocks.

When comparing nectar resources and vegetation characteristics between the un-mown side of the boundary and the corresponding control dummy 'boundary' there were borderline significantly higher species richness (T=1.9504, p=0.0639) but no other differences. There were significantly higher nectar flowers (average number of nectar flowers T=3.10, p=0.0063), of Yellow Rattle (*Rhinanthus minor,* T=2.2664, p=0.0349) and vegetation density (T=4.53, p=0.0002) in the exposed block (Appendix D for results).

When comparing nectar resources and vegetation characteristics within the treatment survey areas by comparing between the un-mown and mown sides of the boundary, there were significantly higher nectar flowers (total number of nectar flowers, T=8.25, p<0,0001, Figure 5-18), Fabaceae (W=0, df=12, p<0.0001, Figure 5-18) and species richness (W=16, df=12, p=0.0012, Figure 5-19) at the un-mown side of the boundary. The mown side still provided some nectar flower resources of low growing and flowering Bird's-foot Trefoil (*Lotus corniculatus*), Daisy (*Bellis perennis*) and Black Medick (*Medicago lupulina)*, whereas the un-mown side had taller flowering plants such as Greater Knapweed (*Centaurea scabiosa)*, Sainfoin (*Onobrychis viciifolia*) and Field Scabious (*Knautia arvensis*). There were also significantly higher vegetation density and height as measured by the Drop Disc method Stewart *et al.* (2001) (T=0.72, df=12, p<0.0001, Figure 5-19) at the un-mown side of the boundary (There was no significant difference between the un-mown and 'mown' side for controls, see Appendix D for results).

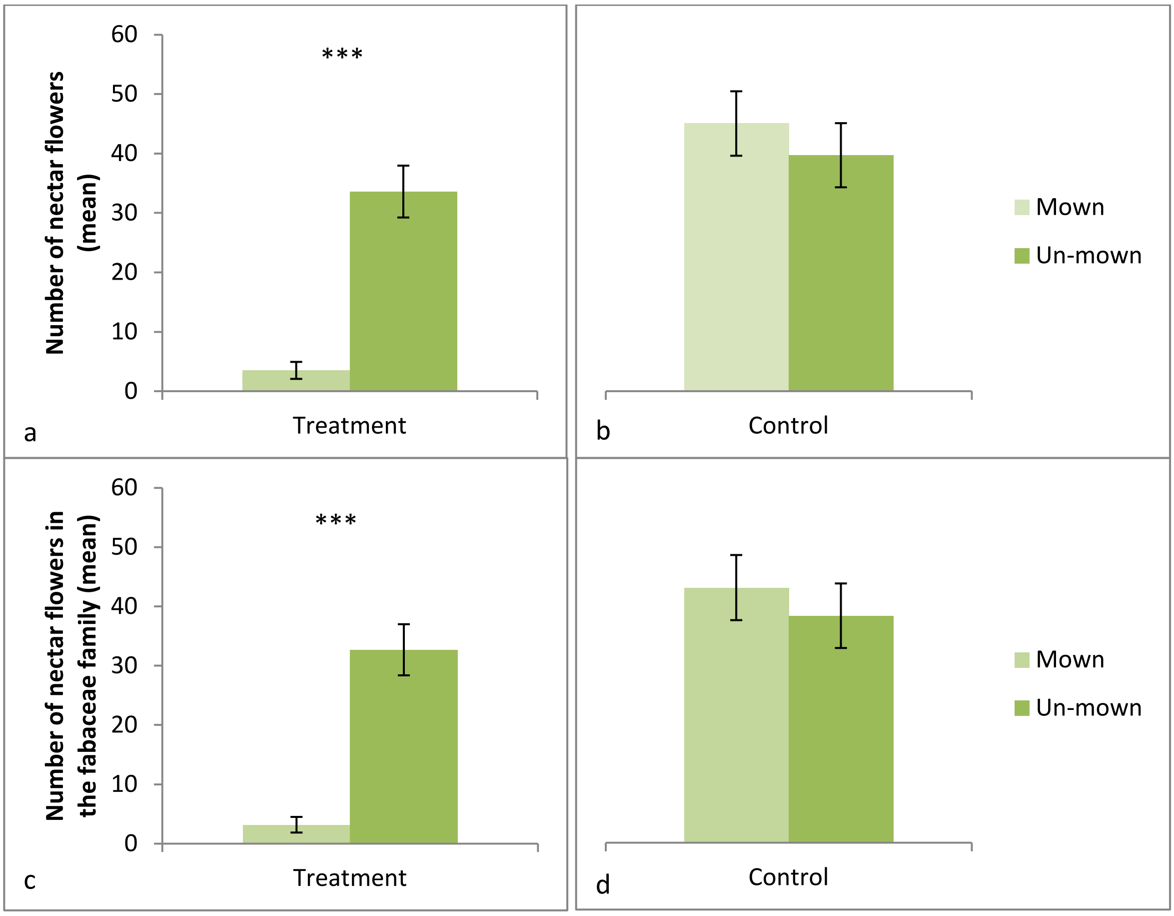


Figure 5-18. Number of nectar flowers in, a) mown and un-mown sides of the boundary in treatment survey areas, b) 'mown' and un-mown sides of the boundary in control survey areas, difference between the treatment and control survey area and within the treatment survey area, p<0.0001. Number of nectar flowers in the Fabaceae family in, c) mown and un-mown sides of the boundary in treatment survey areas, d) 'mown' and un-mown sides of the boundary in control survey areas, difference between the treatment and control survey area p=0.0015 and within the treatment survey area p<0.0001. Error bars show 1 Standard Error. Significance p<0.001 ***, p<0.01 **, p<0.05 *.

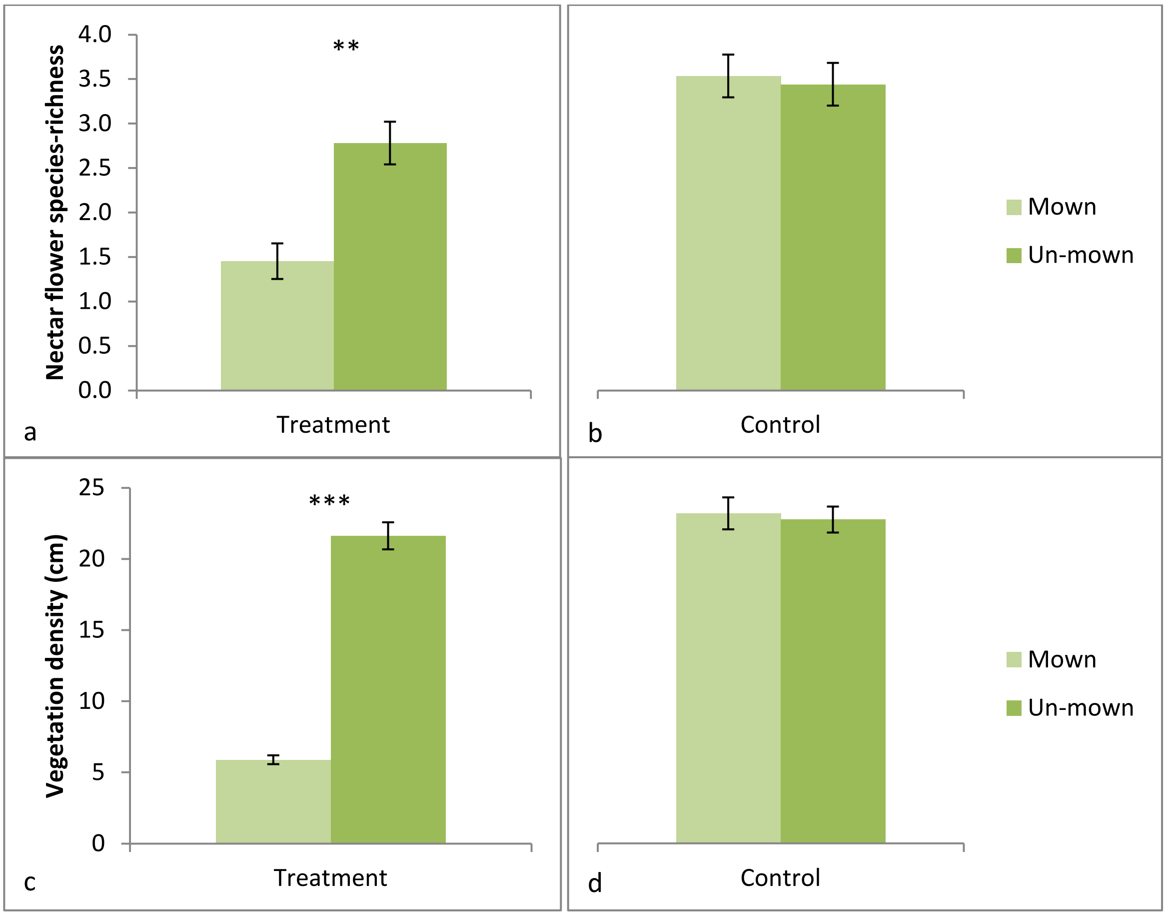


Figure 5-19. Nectar flower species richness in, a) mown and un-mown sides of the boundary in treatment survey areas, b) 'mown' and un-mown sides of the boundary in control survey areas, difference between the treatment and control survey area p= 0.0254 and within the treatment survey area, p=0.0012. Mean vegetation density (Drop disc method) in, c) mown and un-mown sides of the boundary in treatment survey areas, d) 'mown' and un-mown sides of the boundary in control survey areas, difference between the treatment and control survey area and within the treatment survey area, p<0.0001. Error bars show 1 Standard Error. Significance p<0.001 ***, p<0.01 **, p<0.05 *.

There were a total of 91 Lepidoptera/nectar flower feeding interactions, the majority being from *Zygaena filipendulae* and then *Maniola jurtina*, (52 and 25, respectively). There were a similar number of *Maniola jurtina*/nectar flower interactions between the control and treatment survey areas (13 and 12, respectively) for but more at control than treatment survey areas for *Zygaena filipendulae* (40 and 12, respectively). At both controls and treatment survey areas the majority of Lepidoptera/nectar flower plant interactions were with Greater Knapweed (*Centaurea scabiosa*, 36 and 12, respectively) then with Field Scabious (*Knautia arvensis*, 19 and 9, respectively). Lepidoptera feeding on Red Clover (*Trifolium pratense*) and Bird's-foot Trefoil (*lotus corniculatus*) were only recorded at treatment survey areas. The species which had the highest numbers of Lepidoptera/nectar flower interactions were *Zygaena filipendulae* on *Centaurea scabiosa*, *Maniola* *jurtina* on *Centaurea scabiosa* and *Zygaena filipendulae* on *Knautia arvensis* (Figure 5-20) which were not the most abundant nectar flowers within the plots but do produce abundant nectar.

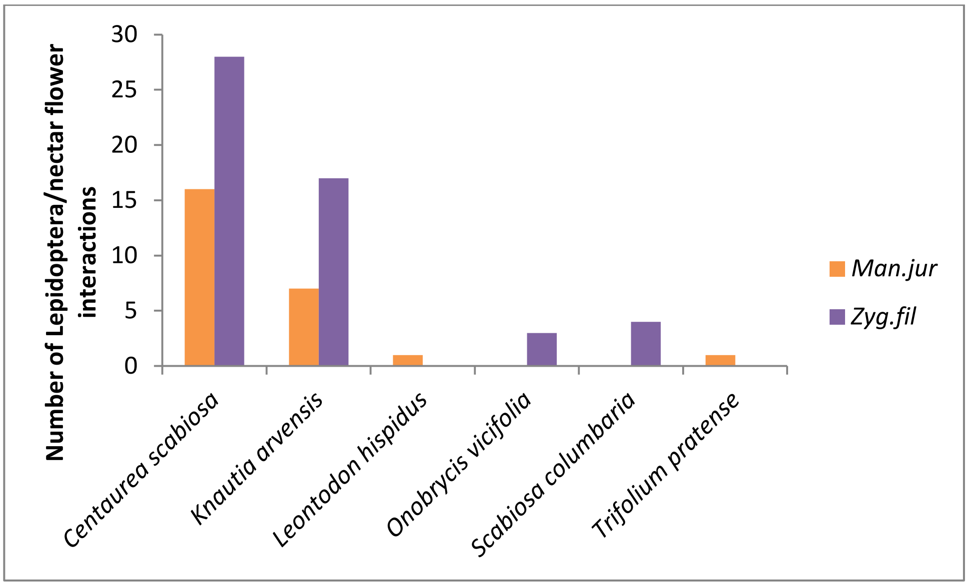


Figure 5-20. The number of Lepidoptera/nectar flower interactions for *Maniola jurtina* and *Zygaena filipendulae* (*Man.jur* and *Zyg. fil* respectively). The majority of Lepidoptera/nectar flower interactions being with Greater Knapweed (*Centaurea scabiosa*) and Field Scabious (*Knautia arvensis*).

5.5 Discussion

5.5.1 Lepidoptera response to small scale alterations in habitat structure

Overall, mowing had a weak effect on boundary crossing behaviour as there was no significant difference between the number of Lepidoptera at survey boundaries or the proportion crossing boundaries between those survey boundaries adjacent to the mown area and controls (and compared to expected). However, there were significantly higher proportions of Lepidoptera crossing from the mown side of the boundary to the un-mown side and vice-versa at treatment boundaries. Additionally, mowing did affect the proportion of Lepidoptera displaying boundary following behaviour which was significantly higher for all Lepidoptera and *Zygaena filipendulae* as treatment (mowing or control boundary) was a significant variable or interaction term in all Minimum Adequate Models (except where the Minimum Adequate Model was the null model). This result is consistent with results in Chapter 4, where a higher proportion of Lepidoptera were recorded following boundaries at chalk grassland fragments than expected. Boundary following is a behaviour associated with Lepidoptera in fragmented landscapes (Ovaskainen *et al.* 2008) and indicates that uncut areas connected to habitat patches could be utilised by Lepidoptera for dispersal and are also important refuges for insects that rely on grassland habitat for some part of their life cycle (Humbert *et al.* 2012). Boundaries are utilised for navigation during foraging and host-plant searching to an extent where butterflies will even follow artificial experimental boundaries of tape and plastic windbreak (Dover & Fry 2001). In fragmented landscapes, some species of butterflies have increased activity and dispersal but lowered fecundity rates as a trade off (Gibbs & Van Dyck 2009; Gibbs & Van Dyck 2010) by following habitat edges individuals are increasing the distance they have to travel to find a more permeable path and this may decrease their fecundity rates.

This following behaviour indicates that habitat patches that are connected to linear features (for example, hedgerows, verges and field margins) may be effective to encourage dispersal and increase landscape connectivity. This management option is supported by studies of *Maniola jurtina* in agricultural landscapes where grassy linear features are utilised by many grassland butterfly species and are important for connectivity and different resources (Delattre *et al.* 2010b; Ouin *et al.* 2008).

A habitat patch boundary with an adjacent matrix similar in structure to the habitat increases edge crossing and dispersal (reviews by Eycott *et al.* 2012; Prevedello & Vieira 2010). In this study, despite survey boundaries being within the same grassland re-creation field, the change in vegetation structure (and the subsequent loss of resources) significantly altered Lepidoptera boundary behaviour. This is a result similar to an experiment with grasshoppers, in which mown edges were avoided by grasshoppers even when if they were only mown to half the height of the un-mown areas (Berggren *et al.* 2002).

In addition to the mowing treatment, the variables that affected edge crossing behaviour were block, species density and an interaction of treatment with survey period when flight paths originated on both sides of the boundary. When considering the boundary behaviour where flight paths originated on the un-mown side of the boundary, interaction of species density and treatment was also apparent with lower proportions crossing with high densities at the treatment boundaries (mown area adjacent) and the opposite for the control boundaries. Species density was a significant variable explaining both crossing and following behaviours and affects Lepidoptera behaviour in this study, whereby a high co-specific density can either increase (Ouin *et al.* 2008) or decrease (Menendez *et al.* 2002; Ries & Debinski 2001; Roland *et al.* 2000) dispersal from habitat patches depending on the species, sex and habitat characteristics.

Lepidoptera boundary behaviour and the significant environmental variables in Minimum Adequate Models differed between blocks in sheltered and exposed locations indicating that there may be an effect of exposure on these behaviours. However, the microclimate conditions that were recorded did not differ significantly between theses blocks. Block was the significant variable explaining crossing and following behaviours with a lower proportion following and a higher crossing in the more sheltered block where the habitat to boundary direction was westerly. Wind speed and direction are likely to interact with shelter by reducing their effects on behaviour, especially when winds are in a prevailing west and south-westerly direction at the experiment site (as the small woodland was to the west of the survey boundaries). However, wind direction data was obtained from the nearest Meteorological station which was located 6 km from the site and so may have not been accurate. Wind speed and direction can affect the boundary behaviour of Lepidoptera, increasing boundary crossing when the wind is in that flight direction (Ries & Debinski 2001). However, the mean microclimate and weather variables did not differ between blocks and a high wind speed was only significant for *Maniola jurtina* following boundaries. The effect of shelter and wind speed on Lepidoptera behaviour is however complex, species specific (Clausen *et al.* 2001; Ries & Debinski 2001) and does not always affect butterfly activity (Ovaskainen *et al.* 2008).

The inclusion of survey period as a fixed or random effect in the models did not affect the overall variables retained in the Minimum Adequate Models except for when an interaction with treatment was retained in the Model for all Lepidoptera when flight paths originated from both sides of the boundary. It may be important to include time as a fixed effect in models due to different emergent times of butterflies and behaviours that can be affected by interacting temporal, environmental and intrinsic factors (for example, behaviours relating to mating, feeding or ovipositing). Additionally, some nectar flower species came into flower soon after they had been mown such as *Lotus corniculatus* for example and were then providing some nectar resources in the mown area (Twiston-Davies, *Personal observation*). The probability of Lepidoptera crossing habitat patch boundaries into the matrix can increase over time (Ries & Debinski 2001) as males and females disperse to locate new mates and to obtain nectar and host plants respectively. However, in this study the inclusion of survey period as a fixed effect in the Minimum Adequate Model is debatable given the relatively short survey period in unequal days per survey period.

It is likely that the differences in Lepidoptera responses between treatment and control boundaries were due to the reduction of nectar resources and vegetation density as a result of the mowing adjacent to treatment boundaries rather than the physical boundary. This is supported by the results that showed no significant differences between the numbers or proportions of different behaviours exhibited in the mown side of the treatment boundary compared to the un-mown side, although there were lower numbers (5.4.3).

Interpretation of these results is limited by the experimental set up which was restricted by the size of the experimental area and as a result, survey transects were in relatively close proximity to each other and with low replication. This low replication of experimental blocks as well as their close proximity to woodland may confound the results and makes disentangling the effect of shelter on butterfly behaviour difficult as woodland can provide many sources for butterflies that may have not been measured within the survey areas. However, regarding the microclimate conditions, there were no significant difference in wind speed, humidity or temperature which may have been as a result of proximity to shelter. An experiment with more replicated blocks would be recommended but was not feasible in this study due to the restricted area allocated to setting up the experimental blocks. Despite this, the high significance values Chi-squared tests and Minimum Adequate Models especially relating to boundary following behaviour indicate that this experimental set up was adequate in detecting a behavioural change of Lepidoptera in response to the mowing treatment. Additionally even though control boundaries were in close proximity to the fence and the woodland, following behaviour was still significantly higher at the treatment boundaries. *Maniola jurtina* is often used as a dispersal indicator species in fragmentation agricultural landscapes and therefore these results can be transferable to other species especially for those associated with grasslands (Conradt & Roper 2006; Delattre *et al.* 2010b) such as Marbled White (*Melanargia galathea*) and Ringlet (*Aphantopus hyperantus*) butterflies for example. However, the low numbers of Lepidoptera which were dominated by the two focal species may restrict the transferability of these findings due to species specific responses to and the use of boundaries, habitat patches and habitat structure (Clausen *et al.* 2001; Ouin *et al.* 2004; Ricketts 2001). Total Lepidoptera were comprised predominantly of *Zygaena filipendulae* and then *Maniola jurtina,* although other species responses were included in the analyses they would have had a low impact on the results. The conservation of butterfly communities is complex as they are affected by a range of variables (Rosin *et al.* 2012). Managing for landscape and habitat patch heterogeneity in vegetation structure, nectar and host-plant resource and habitat type is advocated (Shreeve & Dennis 2011) as it caters for both the general and the species specific requirements and behavioural responses.

5.5.1.1 Summary

Mowing has a significant effect on Lepidoptera boundary following behaviour within the same grassland field by changing the structure and availability of resources and is therefore be an important management consideration when aiming to increase landscape connectivity. Mowing has a significant impact on Lepidoptera behaviour, mainly by increasing boundary following behaviour indicating that more permeable areas and corridors may be an appropriate management option. The response of Lepidoptera communities is complex, not all species are affected by mowing for example, *Maniola jurtina* was not significantly affected and may respond to different management options so this means that managing for a range of species through habitat heterogeneity (type and vegetation structure) is important. Boundaries are important sources of resource including dispersal corridors, nectar sources, oviposition and shelter (Delattre *et al.* 2010b; Driscoll & Weir 2005; Ouin *et al.* 2008), this study investigates the role of boundaries for nectar resources and dispersal and further studies on the other resources would be recommended.

5.5.2 Differences in boundary behaviour between Lepidoptera species

Maniola jurtina did not respond significantly to mown boundaries (for example, Minimum Adequate Models when flight paths originated on both sides of the boundary) and had lower significance of Minimum Adequate Models in contrast to *Zygaena filipendulae*. Additionally, there were differences in the measures of boundary permeability between species, *Zygaena filipendulae* had higher permeability than *Maniola jurtina* as measured by survey area exiting behaviour compared to random (44.2% compared to 32.1% respectively) and as the proportion crossing boundaries which had approached them (at mown boundaries 77.8% and 37.9% respectively). These values for *Maniola jurtina* are similar to those reported in (Conradt & Roper 2006) where 25-30% of *Maniola jurtina* and Gatekeeper (*Pyronia tithonus*) crossed boundaries from tall grassland habitat into a mown short grass matrix. This result suggests that once *Zygaena filipendulae* are in close proximity to the boundary they are more likely to cross it and this could be because individuals are responding to the boundary (following or avoiding) outside of the 20 m by 20 m survey area. This has been reported in Ries & Debinski (2001) where the more specialist grassland Lepidoptera species Regal fritillary (*Speyeria idalia*) avoided edges at 0-20 m whereas the more generalist widespread Monarch (*Danaus plexippus)* at 0-9 metres. A lower percentage of *Maniola jurtina* crossed at boundaries than controls which reflects results from Chapter 4 where less crossing occurred at chalk grassland fragments and *Maniola jurtina* also had a higher proportion avoiding the boundary than *Zygaena filipendulae* (Appendix D). These results highlight that even when species utilise the same habitat they may differ in their response to boundaries and resources (Clausen *et al.* 2001; Ricketts 2001) and that a range of boundary behaviours need to be considered to fully understand Lepidoptera response to habitat boundaries.

Once *Zygaena filipendulae* reached within 20 m of the edge of the survey area, a higher percentage crossed than *Maniola jurtina* at mown boundaries and when compared to controls, and may be explained by differences in edge sensitivity and dispersal ability of these species. *Maniola jurtina* has a higher dispersal ability than *Zygaena filipendulae* which may related to its edge sensitivity as it will move on average 50 m-170 m out of habitat patches compared to less than 40 m (with very few over 100 m) for *Zygaena filipendulae*(Menendez *et al.* 2002), but is dependent on landscape characteristics (Ouin *et al.* 2008). Populations in fragmented landscapes can differ from those from more continuous landscapes with decreased edge sensitivity and increased activity and flight distances (Ockinger & Van Dyck 2012; Ovaskainen *et al.* 2008). Although both species are common in grasslands, *Maniola jurtina* is a common species in agricultural landscapes and may therefore be more adapted to a fragmented landscape of contrasting habitat types and structures.. Additionally, mowing can harm larvae and pupa (for example, *Zygaena filipendulae* pupate on long grass stems which may be damaged if mown early) and therefore a varied mowing and grazing regime throughout the season and within the field may be important to create refuges as demonstrated for orthoptera in Humbert *et al.* (2012).

Although there were significant differences in boundary behaviours exhibited by the two study species, both are associated with grassland habitats. *Maniola jurtina* is a open-grass associated species (Shreeve *et al.* 2001) with larval host plants of Meadow, Bent and Fescue grasses (*Poa.* sp, *Agrostis*. sp and *Festuca.* sp, respectively) and *Zygaena filipendulae* is most likely a herb-rich associated species (Chapter 3) with *Lotus corniculatus* as its larval host plant, both of which were present in the grassland recreation field. However, both species are likely to be affected by the availability of different resources at different scales due to differences in the abundance and distributions of host plants. For example, *Zygaena filipendulae* stayed in patches and moved to those with more host-plants (Menendez *et al.* 2002) and the presence of a closely related Carniolan burnet (*Zygaena carniolica)* was most dependent on nectar plants and the amount of adjacent grassland habitat (Binzenhofer *et al.* 2005). This was in contrast to a grass larval host plant species Pearly Heath (*Coenonympha arcania)* where larger areas of grassland within 100 m and shrubs and bushes were important (Binzenhofer *et al.* 2005).

Limitations of the experimental set up occur from the small study area which can only measure a section of the entire butterfly flight path and differences in the perceptual ranges of butterflies may affect the behaviour and the number of individuals entering the survey area. However, as long as the limitations on interpreting results from this type of experiment are understood, this method provides the opportunity to investigate these behaviours in a controlled environment setting which can measure boundary behaviour and edge permeability. Additionally, relatively small experimental areas have been used to investigate Lepidoptera behaviour to boundaries in other studies for example, grassland habitat patches 10-40 m wide, survey areas of 40 m by 40 m and grassy field margins of 10 m and 5 m across (Conradt & Roper 2006; Korpela *et al.* 2013; Ries & Debinski 2001).

5.5.2.1 Summary

Overall mowing had a significant effect of Lepidoptera boundary behaviours with following behaviour showing the most significant response. Species-specific responses to boundaries, variables in the Minimum Adequate Models and in boundary permeability, indicate that conservation measures designed for more generalist species or for a focal species may not be appropriate and that these species specific responses need to be considered. *Maniola jurtina* is abundant in fragmented agricultural landscapes and potentially not as sensitive to mowing as *Zygaena filipendulae*. However, these species may represent other grassland herb rich species that may significantly alter their behaviour due to mowing and therefore would require management to mitigate the effect this has on dispersal.

Again, these results highlight how boundaries are important sources of dispersal and nectar sources, however, as well at theses, boundaries are also important for other resources such as providing suitable microclimate for oviposition and thermoregulation. This study does not investigate these and therefore further studies on the other resources would be recommended.

5.6 Conclusion

Mowing has a significant effect on Lepidoptera behaviour by increasing boundary following behaviour, this could be at the cost of other important processes such as fecundity but this result also suggests that corridors and more permeable areas next to grassland fragments and un-mown areas may be an effective management options. Species respond differently depending on species-specific traits relating to foraging and dispersal behaviour and therefore, overall heterogeneous management at the within field (or habitat patch) and landscape scale is advocated to increase variation in habitat structure and the resources that are available. Understanding species behavioural response to grassland management may help to spatially target management and restoration.

Chapter 6 Increased landscape connectivity from a grassland re-creation scheme at the Stonehenge World Heritage Site, UK

6.1 Introduction

landscape connectivity is important for species in fragmented landscapes (Baguette *et al.* 2013; Ouin *et al.* 2008; Wagner *et al.* 2013), increasing species viability (Van Teeffelen *et al.* 2012) and potentially enhancing ecosystem services (Mitchell *et al.* 2013).

Evidence-based conservation is essential (Sutherland *et al.* 2004), however, there is a lack of studies that translate evidence-based research into policy and explicit management recommendations for landscape scale projects (Brudvig 2011; Menz *et al.* 2013; Young *et al.* 2005). Although it is essential to recognise that a range of scales are essential for the conservation and restoration of biological diversity from species and habitats through to landscapes and ecosystems (Lindenmayer *et al.* 2008). Landscape connectivity can be enhanced through restoration and conservation focussed actions that increase the overall size and connectivity of a network of specific habitat patches (Van Teeffelen *et al.* 2012). These include a series of measures comprising of the protection of high quality areas, restoring sites with the most potential, improving the permeability of the matrix between habitat patches and creating new patches (McIntyre & Hobbs 1999) which form the components of ecological networks and provide management targets to restore landscape connectivity (Lawton *et al.* 2010).

The size of habitat patches in a network and their distance from one another are important considerations for conservation (Hodgson *et al.* 2011; Prevedello & Vieira 2010) and the basis for much of the conservation work based on island biogeography and meta-population theory (Hanski *et al.* 1994; MacArthur & Wilson 1967; Moilanen & Hanski 1998). The landscape context and the matrix land cover between habitat patches can be just as important as they can decrease the functional distance between habitat patches, thereby increasing functional connectivity (Doerr *et al.* 2011; Prugh *et al.* 2008; Ricketts 2001). There are differences between structural and functional connectivity in ecology; structural connectivity refers to a network of similar habitat types or vegetation structure whereas, functional connectivity takes into account the dispersal distances of the target species or group and the landscape including the intervening matrix between habitat patches (Tischendorf & Fahrig 2000). Landscape composition is important as it influences the movement of invertebrates (Delattre *et al.* 2010b), enhances biodiversity (Vergnes *et al.* 2012), affects patch characteristics (Ockinger *et al.* 2012) and supports populations in fragmented landscapes (Oliver *et al.* 2010; Steffan-Dewenter & Tscharntke 2002).

In order to provide targeted conservation and evaluate different management, land use and climatic scenarios, analyses that utilise both habitat patch and matrix characteristics are one of the most robust methods to measure landscape connectivity. A commonly used method known as cost-distance analysis is used where the permeability of the intervening matrix between habitat patches and the dispersal distances of target organisms is included in landscape connectivity evaluation (for examples see Li *et al.* 2010; Watts *et al.* 2010; Watts & Handley 2010). Lepidoptera can be used as indictors to measure short term changes in restored and re-created grassland, especially chalk grasslands (Rakosy & Schmitt 2011), and their occurrence in a landscape (indicating biodiversity improvements as a result of restoration) is likely to result from a combination of patch and landscape characteristics such as landscape connectivity (Haaland & Bersier 2011; Heer *et al.* 2013; Ouin *et al.* 2008; Thomas *et al.* 2001b) and an interaction of landscape and habitat quality (Kleijn & van Langevelde 2006).

The distribution and density of butterflies is affected by their mobility, whereby, more mobile species are more widely distributed but less densely aggregated (Cowley et al) and they are often used as a proxy to measure metapopulation dynamics and landscape connectivity for mobile invertebrates (e.g. Brueckmann *et al.* 2010; Hanski & Ovaskainen 2000; Ricketts 2001; Severns *et al.* 2013) . A variety of metrics have been calculated to measure different dispersal abilities, many of these are estimated using mark and recapture studies and represent emigration rates and colonisation distances to put butterflies into mobility categories such as Pollard & Yates (1993) and Bink (1992), others are continuous index value based on questionnaires to experts such as in Cowley *et al.* (2001) and Komonen *et al.* (2004).

Some species with low mobility and specialist larval host plants may not travel over 100 m on average, for example, the 6-spot Burnet moth (*Zygaena filipendulae*) and Adonis blue (*Lysandra bellargus*) (Menendez *et al.* 2002; Thomas 1983). However, some specialist species are likely to travel up to 1000 m and a low number of individuals may even travel 13 km which can maintain metapopulation dynamics (Baguette 2003). Average dispersal is useful for evaluating landscape connectivity however, it is important to recognise that these long distance but rare events, can maintain metapopulation dynamics in fragmented landscapes. The dispersal abilities of a range of grassland associated but not single host-plant specific butterfly species is potentially between 1-2.5 km including Common Blue (*Polyommatus icarus*) and Meadow Brown (*Maniola jurtina*)(Baguette *et al.* 2011; Schneider *et al.* 2003). *Maniola jurtina,* Ringlet (*Aphantopus hyperantus*) *and* Small Heath (*Coenonympha pamphilus*) can reach grassy linear features 1 km away from grasslands (Ockinger & Smith 2007a).

The scale at which butterflies are affected by their landscape is also dependent upon mobility and ecological associations where more specialist butterflies are affected by the landscape composition a smaller scale (1km buffer) compared to generalist/wider countryside species (5km buffer) Oliver 2010.

The effects of habitat fragmentation on insect interactions are dependent on species and landscape characteristics (for a review see Tscharntke & Brandl 2004). Therefore, it is important to consider landscape connectivity for individuals of different taxa and functional groups, with varying species traits and different habitat associations. This means that the strength and direction of the response to landscape features and conservation measures can be dependent on these traits, characteristics and associations and vary between and within species (Keller *et al.* 2013; Prevedello & Vieira 2010; Ricketts 2001).

Some semi-natural grasslands have a high biodiversity value (WallisDeVries *et al.* 2002). However, species-rich lowland semi-natural grasslands have declined in the UK by 97% since the Second World War (Fuller 1987) as most improved and semi-natural lowland grasslands were replaced with arable land during and after the 1940s resulting in high local extinction rates and few grassland conservation sites remain (Hodgson *et al.* 2005). A landscape scale grassland restoration and re-creation project was implemented at the Stonehenge World Heritage Site landscape in Wiltshire, UK, from 2000-2012. This is situated between large expanses of lowland calcareous grassland and Sites of Special Scientific Interest (SSSI) across Salisbury Plain, Parsonage Down and Porton Down (Figure 6-1). The site provides an opportunity to investigate the effects of grassland restoration and re-creation on the connectivity of the landscape scale grassland habitat network.

6.2 Aims and Hypotheses

Aims;

- To map and compare the networks of chalk grassland and chalk and neutral grassland patches before grassland re-creation at the Stonehenge Landscape began in the year 2000 and after the last re-creation field was sown in 2012.
- To measure habitat patch and landscape connectivity metrics at two landscape scales; of the landscape within the World Heritage Site and a 1 km buffer from its boundary and the wider landscape around the World Heritage Site within an 8 km buffer of its boundary.
- To use cost-distance analysis to visualise and evaluate landscape connectivity depending on the matrix land cover types between grassland patches and the different dispersal abilities of butterflies.

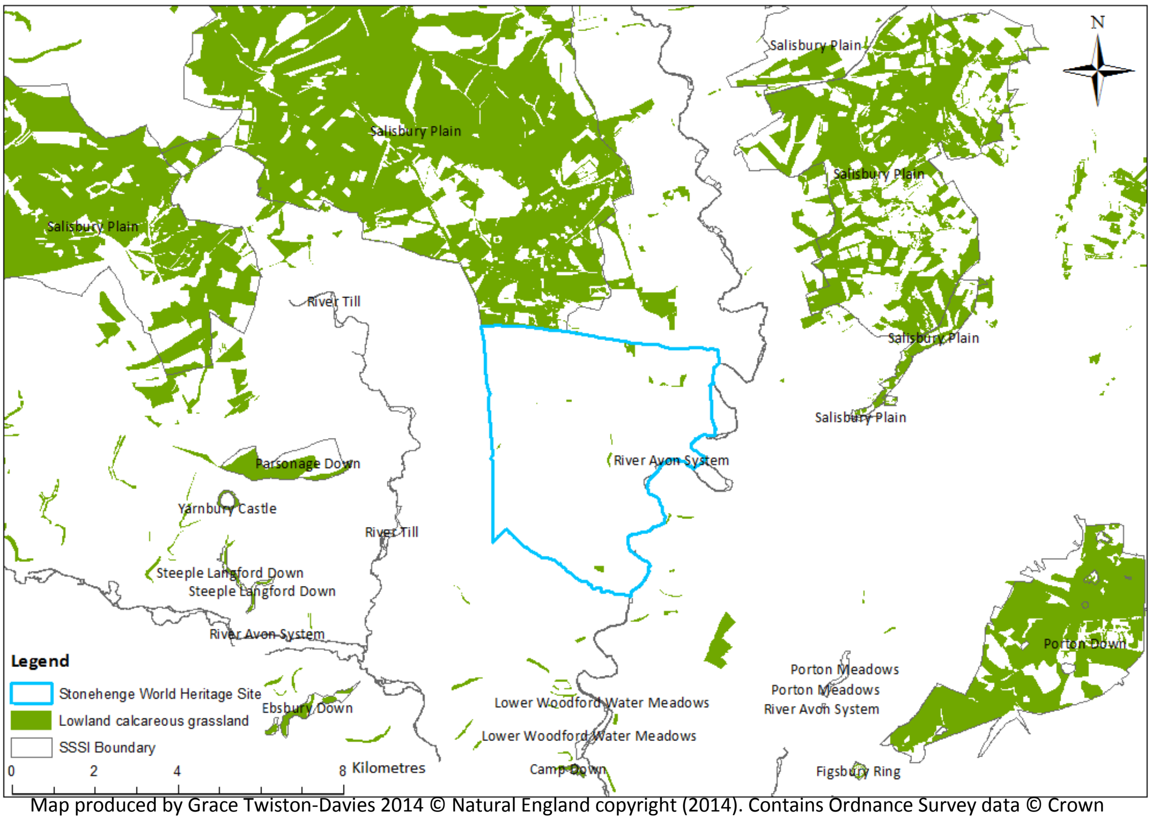
Hypotheses;

i. Landscape scale habitat restoration will increase the area, mean patch size and connectivity of the grassland network.
ii. The permeability of the matrix land cover will be important in measuring connectivity.
iii. Lepidoptera species with higher mobility will potentially be able to utilise more of the grassland network compared to those with lower mobility.
iv. Effects of grassland re-creation will be higher at the landscape scale compared to the wider landscape scale but wider landscape scale effects will be evident.
v. Grassland re-creation will increase the habitat heterogeneity of the landscape.

6.3 Methods and materials

6.3.1 Study Site

The study site was the Stonehenge World Heritage Site (WHS) landscape scale grassland re-creation project situated between large expanses of lowland calcareous grassland in Wiltshire, UK. Here, over 500 hectares of arable land has been sown with species-rich grassland seed originally sourced from Salisbury Plain SSSI (Young *et al.* 2009, Chapter 2, Section 2.1.5, Figure 6-1). This landscape consists of a grassland network of chalk, neutral, rough and improved grassland types and one of the main aims of the grassland re-creation scheme was to increase the area of permanent species-rich grasslands (Young *et al.* 2009).



Map produced by Grace Twiston-Davies 2014 © Natural England copyright (2014). Contains Ordnance Survey data © Crown copyright and database right 2014. English Heritage National Monuments Record

Figure 6-1. The Stonehenge World Heritage Site and surrounding Sites of Special Scientific Interest (SSSI). Salisbury Plain, Parsonage Down and Porton Down all large expanses of lowland calcareous grassland.

6.3.2 Land cover mapping

Four separate maps were created to reflect the landscape prior to grassland re-creation in 2000 and after the last field was sown in 2012. Grassland re-creation was classified into two grassland types, neutral grassland or chalk grassland, in order to adhere to the broad habitat classification of Land Cover Maps (Land Cover Map 2007, Morton *et al.* 2011). Maps were created of: a) the chalk grassland network in 2000, b) grassland re-creation contributing to the chalk grassland network in 2012, c) chalk and neutral grassland network in 2000 and, d) grassland re-creation contributing to the chalk and neutral grassland network in 2012.

Land Cover Maps for Wiltshire and Hampshire were sourced from the Centre for Ecology and Hydrology (Morton *et al.* 2011). These consisted of broad habitat types at 25 m by 25 m raster grid square resolution (Land Cover Map 2007). These data were edited in ArcMap (version 10.1 ESRI©) to reflect the habitat types in 2012 and prior to grassland re-creation in 2000 of the World Heritage Site based on Stonehenge World Heritage Site management Plans (Young *et al.* 2009) and personal observations. Polygons of grassland re-creation in arable fields were classified as either chalk grassland (maps a and b) or neutral grassland (maps c and d) to investigate the effect of the grassland re-creation on both the chalk grassland network and the chalk and neutral grassland network (no acid grassland was in the landscape).

Maps of the Lowland Calcareous Grasslands were obtained from Natural England (MAGIC 2014) in polygon format (data from 1998-2001) and edited to include the additional fragments at the Stonehenge Landscape on slopes and burial mounds (Winterbourne Stoke Group, Fargo Barrow, Full-moon Bank and Luxenborough Bank, See Chapter 2, section 2.1). The edited Lowland Calcareous Grassland map (layer) was combined with the edited Land Cover Maps (layer) for a more accurate chalk grassland network, as the Land Cover Map classed a larger area as chalk grassland than the lowland calcareous grassland survey (Natural England, MAGIC 2014) and had excluded small pockets of chalk grassland. Polygons of Land Cover Map that had been classified as chalk grassland but not confirmed by the Lowland Calcareous Grassland survey were reclassified as neutral grassland. This new map was converted to raster at 25 m by 25 m grid square resolution for analysis. The World Heritage Site boundary was obtained from English Heritage (MAGIC 2014).

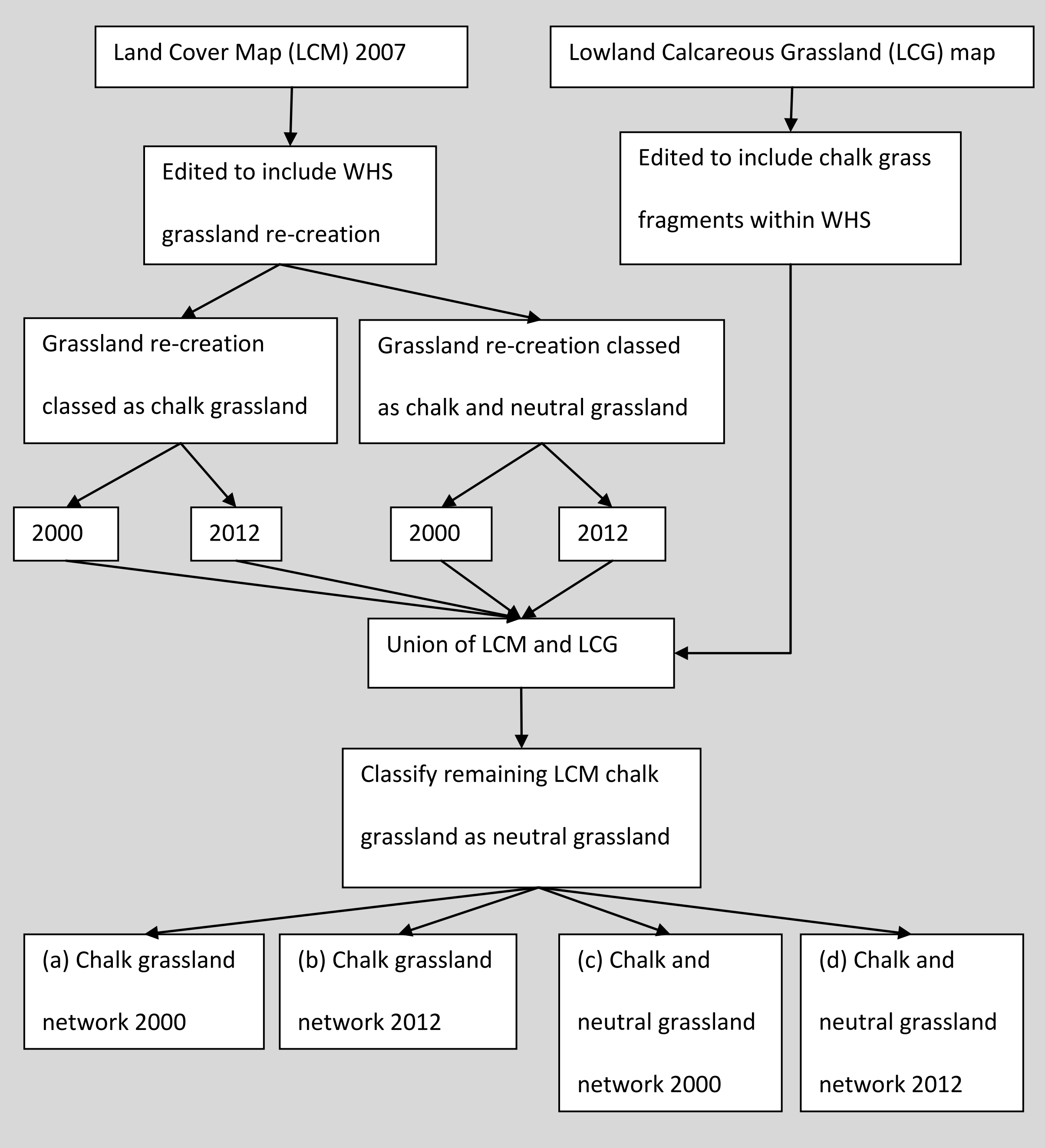


Figure 6-2. Method for creating grassland habitat network maps using Land Cover Map 2007 and Lowland Calcareous Grassland map (1998-2001), edited to represent the Stonehenge World Heritage Site (WHS) in 2000 and 2012.

All maps were clipped for editing and analysis using buffers around the Stonehenge World Heritage Site boundary at 1 km and at 8 km for the Stonehenge Site and the wider landscape habitat networks, respectively. These scales were chosen as 1km buffer from the WHS boundary included the chalk grassland on Salisbury plain to the North of the WHS and represented the landscape context that some specialist species are affect by (Oliver *et al.* 2010) and the maximum dispersal distances of some specialist butterfly species e.g. approximately 1km (Baguette 2003; Gutierrez 2005; Pe'er *et al.* 2014). The 8km buffer was selected to include the large expanses of chalk grassland and SSSIs that surround the WHS an encompass the 5km buffer that wider countryside/generalist butterflies may be affected by (Oliver *et al.* 2010) and the scale at which some long distance dispersal events which maintains metapopulation dynamics e.g. 13km (Baguette 2003). This created a new map to edit without changing the properties of the raw data.

This method only considers land cover changes within the WHS, controlling for land use changes that may have occurred across the wider landscape (8 km buffer of WHS boundary) between 2000-2012 and enables the landscape-scale effect of the Stonehenge landscape grassland restoration and re-creation project to be measured and evaluated. This method was used to control for other land-use changes that may have occurred between 2000 and 2012 in order to evaluate just the grassland restorations contribution to landscape connectivity and associated habitat patch and landscape metrics.

6.3.3 Cost-distance analysis

Landscape connectivity was investigated using cost-distance analysis in ArcMap (version 10 ESRI©) based on the permeability values of different matrix land cover types to a generic focal species associated with a neutral grassland habitat. These permeability values were calculated using iterative rounds of expert opinion in a Delphi analysis and displayed as a proportion of relative permeability for each matrix land cover type with a proportion of 1 being full permeability and 0 being a complete barrier (Eycott *et al.* 2011, Table 6-1). These values were used on the assumption that the permeability scores of different matrix land cover types to a neutral grassland associated species would be similar to that of a chalk grassland associated species. This may overestimate the connectivity of the landscape as a chalk grassland species may be more sensitive to other land cover types due to its specialism for short-turf and herb-rich habitats, however, this method provides a quantitative measure of matrix permeability that can be a basis for evaluating landscape connectivity. The functional distance between habitat patches can be calculated as the Euclidean distance between patches divided by the matrix permeability value of the intervening land cover. For example, if two chalk grassland patches are 50 m apart (Euclidean distance) and are separated by a matrix of arable land, the permeability of this matrix land cover is 0.05 (Eycott *et al.* 2011)and therefore the functional distance between these habitat patches is 1,000 m (50 divided by 0.05, Figure 6-3). In this example a butterfly in one habitat patch would need to have a dispersal ability of 1,000 m rather than 50 m to reach the other patch due to the low permeability of the intervening arable land matrix and therefore these two patches would be functionally isolated for those butterflies with dispersal abilities under 1,000 m.

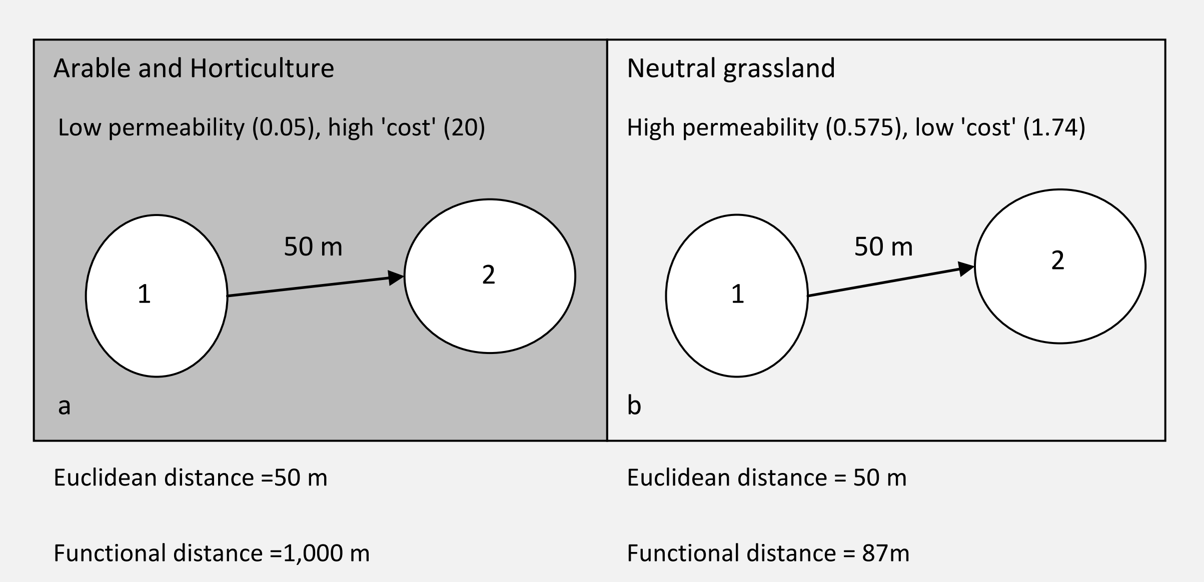


Figure 6-3. Diagram of two chalk grassland habitat patches (1 and 2) separated by a matrix of, a) arable and horticultural land and, b) Neutral grassland. Permeability value from (Eycott *et al.* 2011), cost is calculated as 1 divided by the permeability value and functional distance is Euclidean distance divided by the permeability value or Euclidean distance multiplied by cost. The Euclidean distance between habitat patches 1 and 2 is 50 m but as the matrix type has either, a) a low permeability value of 0.05 and therefore, the cost of travelling 1m in the matrix is 20 m and therefore the functional distance is 1,000 m or, b) a high permeability value of 0.575 and therefore, the cost of travelling 1m is 1.74 and the functional distance is 87m.

For cost-distance analysis the permeability value is converted into a 'cost' which is assigned for each land cover type in the attribute table (ArcMap version 10.1 ESRI©). This is the 'cost' in metres of travelling 1 metre in the matrix land cover and calculated as 1 divided by the matrix permeability value (Figure 6-3, Table 6-1). For example, a grassland associated butterfly species may be able to travel 1,000 m in grassland habitat but will only be able to travel 50 m through a matrix of coniferous woodland where the permeability value is 0.05 as every 1 metre travelled in this matrix will 'cost' 20 metres (1 divided by 0.05).

From the 'cost' value a separate map (layer) was created (25 m by 25 m grid square resolution) and this was done for networks of chalk grassland prior to grassland re-creation in 2000, after the last re-creation field was sown in 2012 and for networks of chalk and neutral grassland in the same years (maps a-d, Figure 6-5). For the habitat network of chalk grassland all cost values were as described in (Eycott *et al.* 2011) except for the cost for a matrix of neutral grassland, which was 1.74 (Table 6-1, taken from the cost for neutral grassland generic focal species travelling in a matrix of chalk grassland),the assumption here us that the cost of a chalk grassland matrix to a neutral grassland species is the same as the cost of a neutral grassland matrix to a chalk grassland species. Additionally, this method assumes that arable and horticultural land cover have the same cost when in reality the difference in permeability and resource available in oil-seed rape and winter wheat for example can be great oil-seed rape can provide early flowering sources of nectar for many nectar feeding insects (Bartomeus *et al.* 2014; Riedinger *et al.* 2014; Woodcock *et al.* 2013) as well as microclimate an larval host plants for *Pieris.* sp. of butterfly (Langmaid *et al.* 1989).

Table 6-1. Edge impact (metres), permeability value (proportion) and 'cost' of moving 1 metre (1 divided by permeability value) through different matrix land cover types for a generic focal species associated with neutral grasslands from (Eycott *et al.* 2011).

Land cover type	**Edge impact (m)**	**Permeability value**	**Cost per metre**
Broadleaved and Yew Woodland	5.0	0.100	10.00
Coniferous Woodland	15.0	0.050	20.00
Arable and Horticulture	10.0	0.050	20.00
Improved Grassland	8.0	0.150	6.67
Neutral Grassland	0.0	0.000	0.00
Calcareous Grassland	0.0	0.575	1.74
Rivers and Streams	4.5	0.050	20.00
Urban/Suburban	10.0	0.075	13.33

Cost-distance is calculated (Spatial Analyst in ArcMap 10.1 ESRI©) as the cumulative Euclidean distance from a habitat patch multiplied by the cost of each cell it passes (each cell was 25 m by 25 m). The output map represents the habitat network (cost-distance of 0) and the matrix classified by the functional distance of each part of the matrix and can be interpreted as the dispersal distance an individual would need to be capable of to reach that matrix patch (Figure 6-4, Figure 6-5).

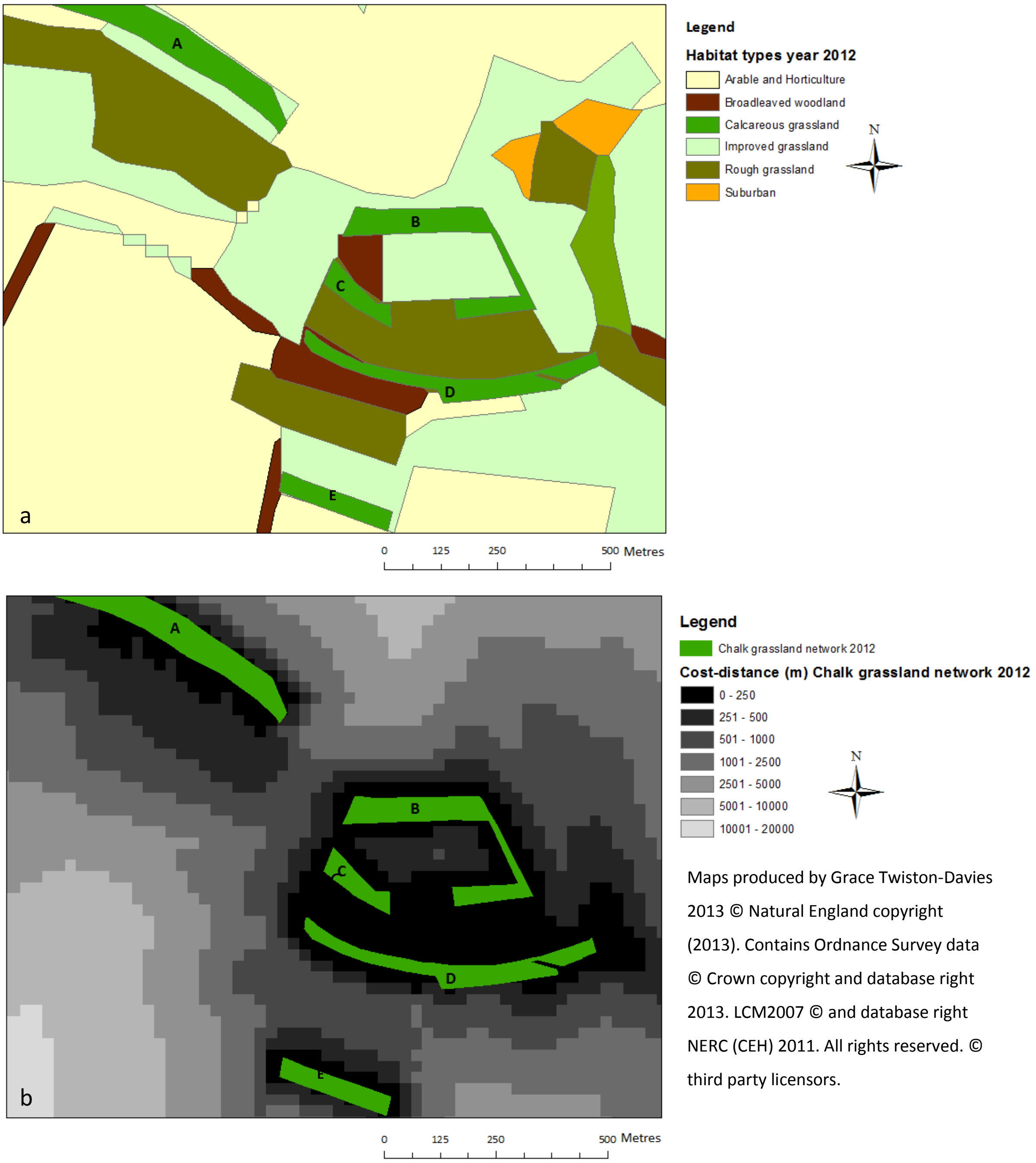


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Figure 6-4. Example of focal habitat patch of calcareous grassland and (a) surrounding matrix land cover types and (b) cost-distance analysis results (calcareous grassland has been overlaid onto the cost-distance map to highlight patches). Cost-distance is the dispersal distance an individual would need to capable of to reach that area. For example, all patches are functionally connected to each other for butterflies with dispersal abilities of up to 1,000 m as they are all within the 0-1,000 m cost-distance categories. Patches B, C and D are all functionally connected for dispersal abilities up to 250 m as they are separated by high permeability and low 'cost' rough grassland matrix land cover. A butterfly in D would need a dispersal ability of 500-1,000 m to reach E even though these patches are 260 m away due to the low permeability, high 'cost' Woodland and Improved pasture matrix.

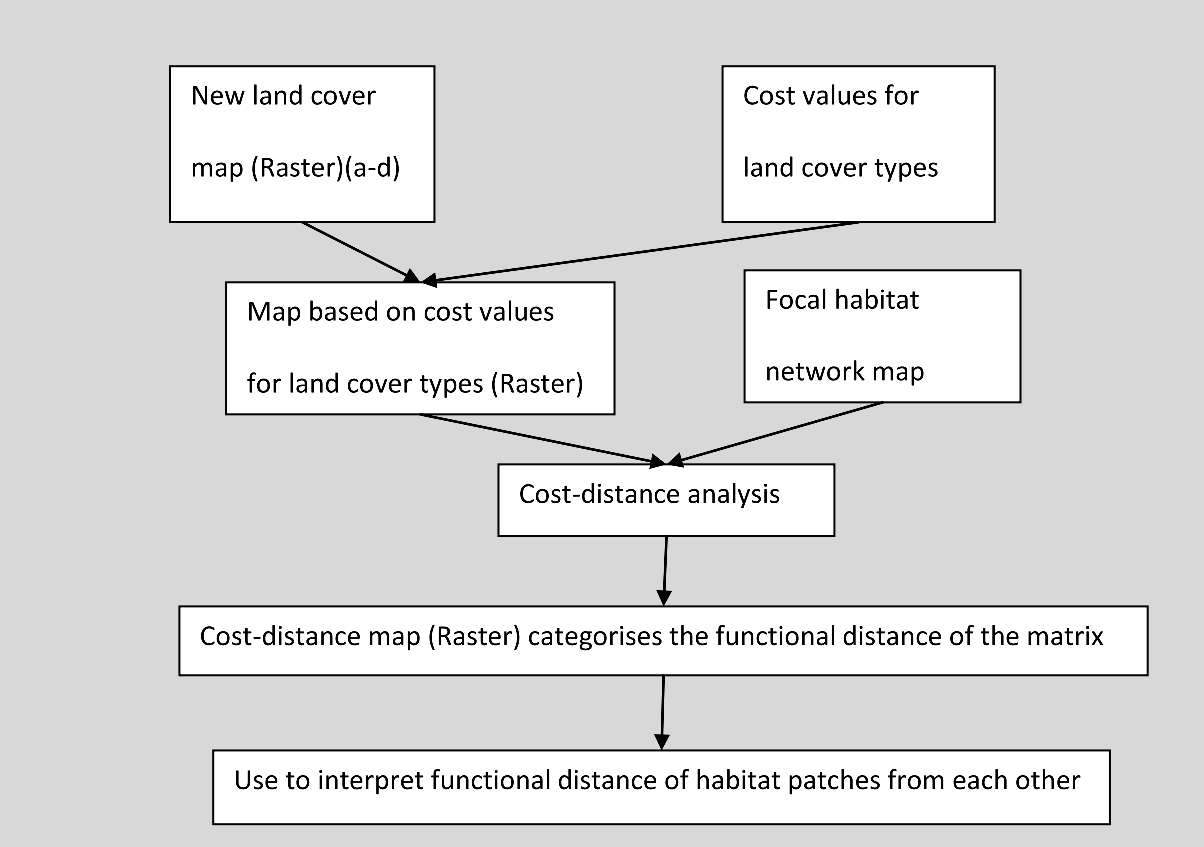

Figure 6-5. Outline of method for Cost-distance analysis in ArcMap (version 10) and interpretation of the output map.

The assumption of Cost-distance analysis is that travel is linear, however, many studies show that butterflies may use non-direct but less cost routes such as grassy linear features and tracks (Delattre *et al.* 2010b; Ouin *et al.* 2008) additionally supported in Chapters 4 and 5 in this Thesis. This method can encompass some of this as it creates a network of last cost areas that are not necessarily direct. The 25 m by 25 m does means that many linear features are not included. Higher resolution landscapes can accommodate the inclusion of linear features but this LCM resolution doesn't.

6.3.4 Distribution of focal Lepidoptera species

Distribution data of focal Lepidoptera species from 2000-2012 were obtained from the Butterflies for the New Millennium Recording Scheme, courtesy for Butterfly Conservation UK and the Wiltshire and Swindon Biological Records Centre used to investigate the potential role of the grassland re-creation in linking previously isolated populations. These were presence records of focal species of conservation concern: Adonis Blue (*Lysandra bellargus*), Chalkhill Blue (*Polyommatus coridon*), Small Blue (*Cupido minimus*) and the Marsh Fritillary (*Euphydryas aurina*) which are host plant specialists mainly dependent on herb-rich grasslands. Theses presence data were collected by volunteers reporting random sightings and from surveying regular fixed Butterfly Monitoring Scheme Transects, there may have been bias in these recordings and areas under represent in survey effort, especially in the "matrix" land cover where people are unlikely to survey these areas. These data are used to represent the potential area here these species occur in this landscape but are used with caution. These species distribution maps were overlaid onto focal grassland networks and the cost-distance analysis maps for interpretation with the assumption that the distribution across the landscape may represent populations although most of these presence sights are likely to represent the dispersal of individuals.

6.3.5 Landscape connectivity measures

Landscape connectivity as a result of the grassland re-creation project was evaluated by calculating focal habitat patch, network connectivity and landscape-scale measures using Fragstats (version 4.2, McGarigal *et al.* 2012). Re-creation grasslands were either classified as adding to the focal chalk grassland network or adding to the focal chalk and neutral grassland network. The assumption here is that dispersal is linear rather than indirect but least cost and this data with 25m by 25m resolution does not accommodate a least cost path using linear features to be measured.

Focal habitat patch characteristic measures were total area of focal habitat (hectares), mean patch area (hectares) and percentage of the landscape that was focal habitat. The effect of the adjacent matrix land cover on the focal habitat patch was analysed by measuring the 'core' area and this is the area of habitat that is left once the edge impacts of the adjacent matrix type have reduced the habitat area (Figure 6-6). These values were adapted from (Eycott *et al.* 2011, Table 6-1) to adhere to the 25 m by 25 m grid square resolution of the data and as a result, adjacent matrix types that had the highest edge effects of arable land, coniferous woodland and urban/suburban areas were included as having an edge impact of 25 m (lowest impact that could be used given the resolution of the data, see Appendix E for this update). The total area of 'core ' focal habitat (hectares), mean patch core area (hectares) and the percentage of the landscape that was core area were then also measured (Figure 6-6). Shape index was also calculated, which is based on the perimeter-area ratio and is a measure of shape complexity, a shape index of 1 is a square patch and the metric value increases as the patch shape becomes more irregular. Shape index is the simplest measure of shape complexity and is a good predictor of dispersal success (Calabrese & Fagan 2004; Schumaker 1996).

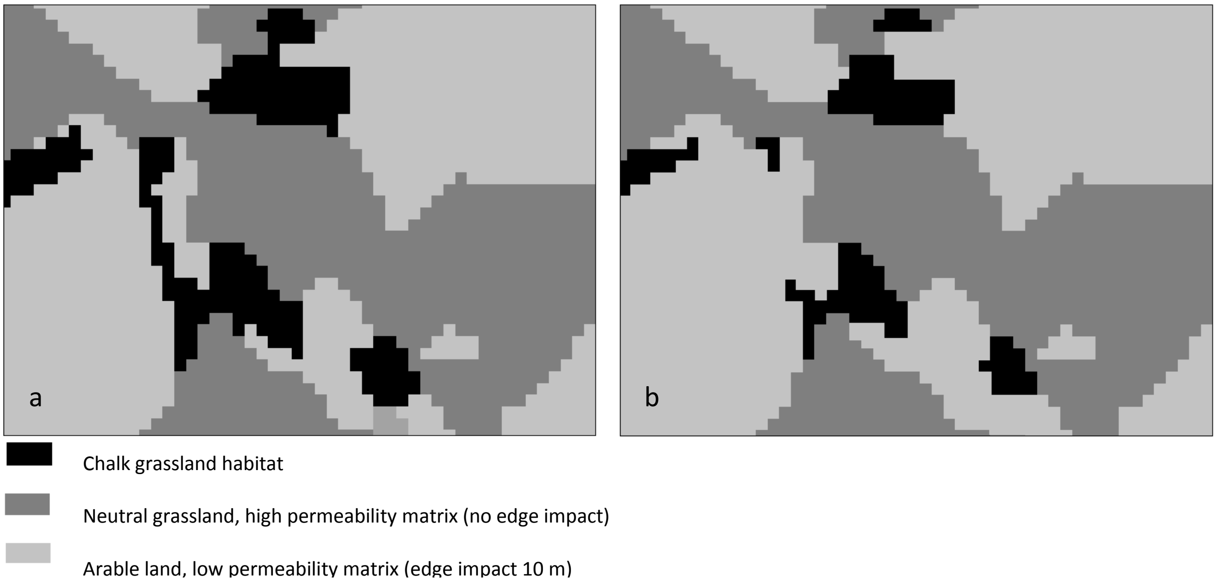

Figure 6-6. Example of how adjacent land cover can reduce the core area of habitat depending on its edge impact. Here the habitat fragments of chalk grassland are reduced by the edge effect of adjacent land cover of arable and matrix by 10 m but not affected when the adjacent land cover is neutral grassland. The core area is reduced. Here four larger patches of chalk grassland in, a) are reduced to six small patches, b) due to the edge effect of the adjacent matrix.

Connectivity was measured as the Nearest Neighbour Distance and Proximity Index. Nearest Neighbour Distance is the Euclidean distance to the nearest patch of the same habitat type, this measures structural connectivity and is used to assess distance to next habitat patch which maybe important for some low mobility species, this is a widely used and simple measure but does not necessarily explain patch occupancy as well as some more complex measures (Calabrese & Fagan 2004; Moilanen & Nieminen 2002). Proximity Index, considers the size and proximity of habitat patches within a specified search radius (based on Gustafson & Parker 1994), these two variables are important for species conservation (Hodgson *et al.* 2009; Prevedello & Vieira 2010). The Proximity Index is zero if there are no other habitat patches of the same type within the search radius. Proximity Index measures potential connectivity for organisms with the same dispersal abilities of the search radius and can represent different focal or example species.

Proximity Index measures were based on specific search radiuses of 300 m and 2,500 m to represent example Lepidoptera with grassland ecological associations based on the dispersal abilities of the 6-spot Burnet moth (*Zygaena filipendulae*) and Common Blue (*Polyommatus icarus*), respectively (Baguette 2003; Menendez *et al.* 2002) which are used as examples of focal species by the Forest Research (Smith *et al.* 2012). These two species were used as example species as they are in high abundance in the landscape and colonised older grassland re-creation fields as detailed in Chapter 3, therefore the connectivity of the landscape may be important for these species. The 6-spot Burnet moth (*Zygaena filipendulae*) is a sedentary Lepidoptera associated with herb-rich grasslands which contain its larval host plant *Lotus corniculatus* in abundance and has a dispersal threshold of 300-500 m ((Heath & Emmet 1985; Menendez *et al.* 2002). *Polyommatus icarus* is an intermediate mobility open-grass associated species with a dispersal distance of approximately 2500 m (Binzenhofer *et al.* 2005; Pollard & Yates 1993; Shreeve *et al.* 2001).

Landscape metrics that included all land cover types were calculated as the number of patches and the total 'core' area, which included the edge impacts of different land cover types to chalk and neutral grassland as well as coniferous and yew woodland as described in (Eycott *et al.* 2011) (coniferous and yew woodland was the other habitat type in the landscape that would have high edge impact scores from adjacent land cover type and have been calculated by (Eycott *et al.* 2011), see Appendix E). Landscape heterogeneity was also measured as Shannon diversity and evenness, widely used measure of land-use change (e.g. Antwi *et al.* 2008; Benini *et al.* 2010) and landscape indicators utilised by the European Commission (2014) .

These analyses were conducted for the wider landscape scale (8 km from the WHS boundary) and the Stonehenge landscape scale (within the WHS and 1 km boundary) for the chalk grassland network prior to grassland re-creation in 2000 and after the last field was sown in 2012 and similarly for the chalk and neutral grassland network (relating to maps a-d previously).

6.4 Results

6.4.1 Grassland habitat network and cost distance analysis

Results showed that between 2000-2012, 493 hectares of arable land was converted into grassland, this is less than the actual recorded amount (Young *et al.* 2009) due to the 25m by 25m resolution of the land cover map which has underestimated the area of new re-created grassland. In 2000 chalk and neutral grassland accounted for 8.8% of the land cover within the WHS and 1km of its boundary, this was increased by 2013 to 18.27%. In 2000 the majority of land-cover was arable and horticulture in 2000 at 54.8% followed by improved pasture 18.1%, in 2012 this had been reduced by 9.5% and chalk and neutral grassland accounted for (Table 6-2).

Table 6-2. Percentage of land cover types in the year 2000 and 2012

Land-cover Type	**Percentage of land cover**	
	2000	**2012**
Arable and Horticulture	54.84	45.41
Improved Grassland	18.11	18.07
Rough Grassland	7.07	7.07
Broadleaved Woodland	5.33	5.33
Suburban	5.02	5.02
Neutral Grassland	4.5	4.5
Chalk Grassland	4.3	4.3
Urban	0.56	0.56
Coniferous Woodland	0.18	0.18
Inland Rock	0.07	0.07
Freshwater	0.02	0.02
Re-created Grassland	0	9.46

The re-creation grasslands at the Stonehenge World Heritage Site are potentially extending the chalk grassland and the chalk and neutral grassland network in a southerly direction from Salisbury Plain (Figure 6-8, label a), connecting the small fragments of chalk grassland within the landscape and creating a corridor through the landscape towards the medium size isolated patch to the southeast of the World Heritage Site (Figure 6-8, label b). Small fragments of chalk grassland have been buffered and potentially connected to the re-creation grasslands and the matrix that surrounds them has a higher permeability and lower cost of dispersal.

The cost-distance of the matrix between grassland patches are illustrated in grey-scale in Figure 6-7, Figure 6-8, Figure 6-9 and 6-10 with darker areas indicating matrix land cover types with low dispersal cost and lighter areas with a higher cost (cost in metres). Darker patches have a low dispersal cost and could be functional corridors through the landscape, increasing the connectivity between the patches they separate for butterfly species with dispersal abilities under 1 km. Medium-grey patches show medium dispersal cost and could be reached for those with dispersal abilities of 1-5 km. Lighter patches have a very high dispersal cost that would only be permeable to a few species of high mobility or migrants.

This has also potentially halved the cost of dispersal in areas adjacent to urban and suburban land cover that are within the 1 km buffer of the WHS boundary to the East of the World Heritage Site (Amesbury) that had a very high dispersal cost prior to the grassland re-creation (<20 km dispersal, Figure 6-8).

The largest expanses of matrix land cover with very high cost are to the east and south-east of the World Heritage Site. These are urban and suburban areas around the towns of Winterbourne Stoke and Amesbury/Bulford connected by the A303 road (Figure 6-7 and Figure 6-8, to the West and East of the WHS respectively). There is also matrix land cover with very high dispersal cost between the WHS and Porton Down along the A338 road due to these areas being dominated by urban and arable land cover types (Figure 6-8, Label e).

Within 1 km of the boundary of the WHS, the majority of grassland patches in 2012 (after the grassland re-creation) are functionally connected for dispersal distances of 1 km-2.5 km except for the small fragments to the South West of the WHS 1 km buffer. The maximum Lepidoptera dispersal distance required for patches to be functionally connected has reduced since the grassland re-creation from 5-10 km in 2000 to 2.5-5 km post re-creation in 2012.

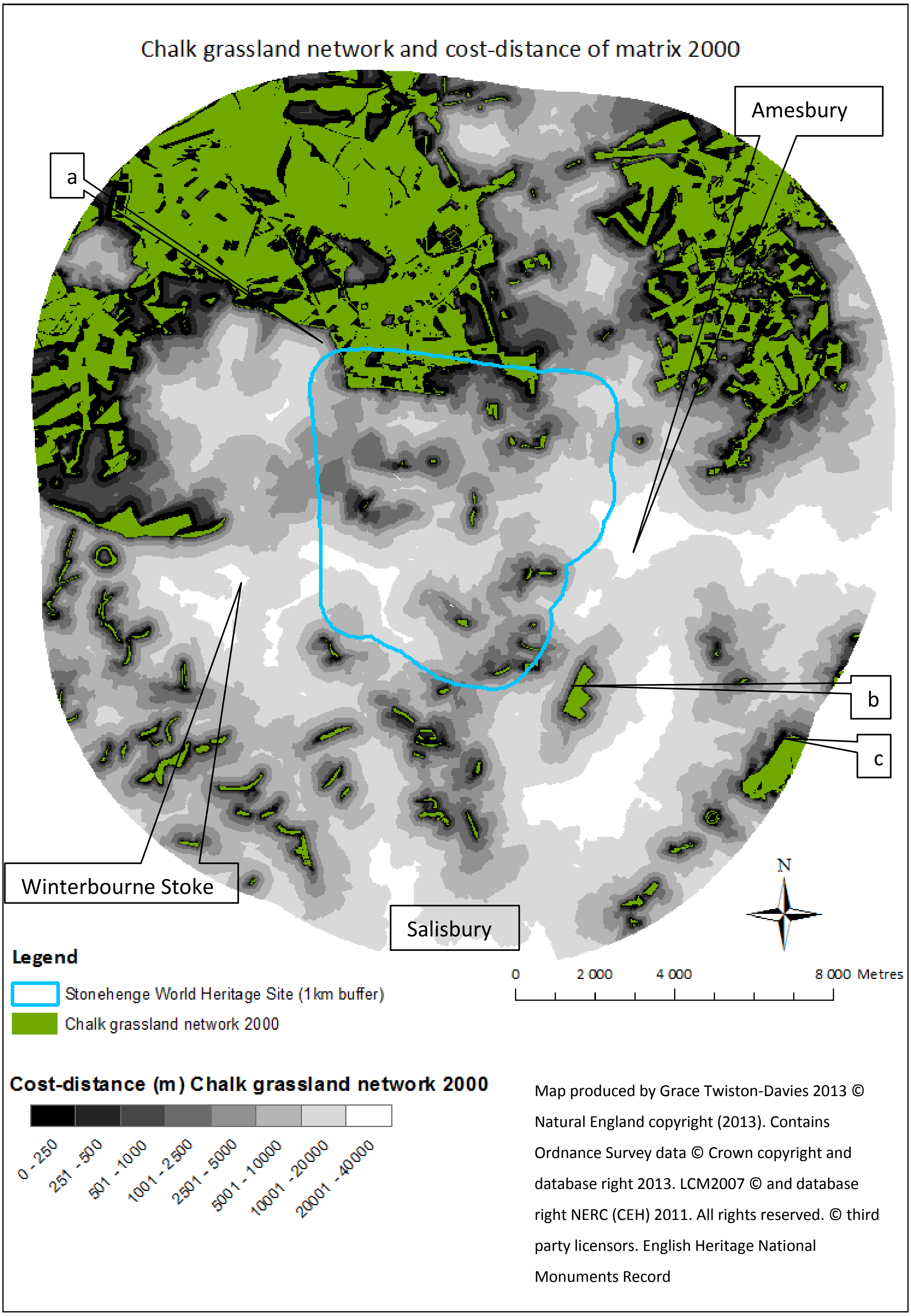

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Figure 6-7. Map a of the Stonehenge World Heritage Site and the surrounding landscape. Chalk grassland network and cost-distance matrix in 2000. Cost-distance in metres represents the distance that an individual would need to be capable of dispersing to reach that area of matrix. Labels, a) Salisbury Plain, b) chalk grassland patch south-east of the World Heritage Site and, c) Porton Down.

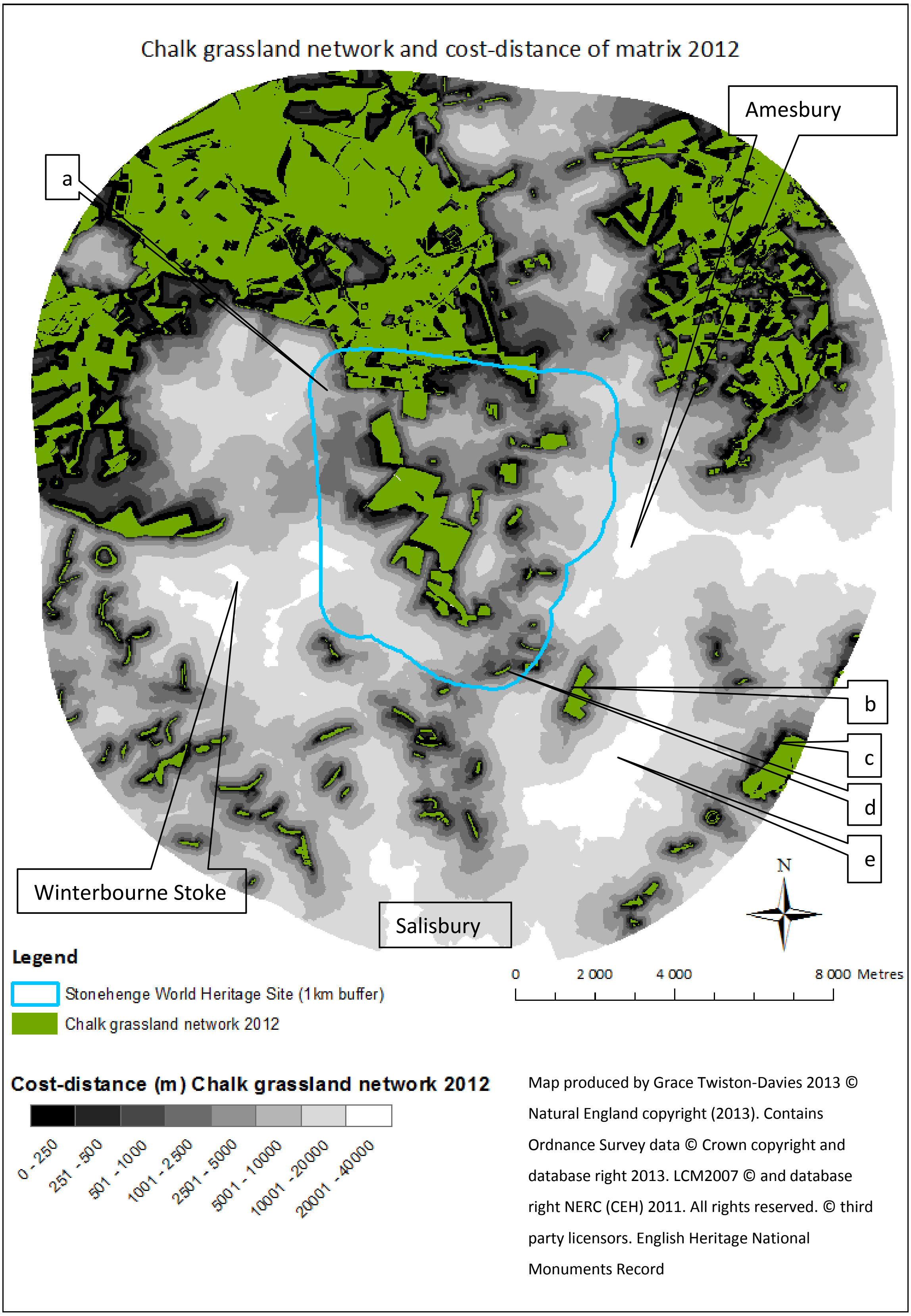

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Figure 6-8. Map b of the Stonehenge World Heritage Site and the surrounding landscape. Chalk grassland network and cost-distance matrix in 2012. Cost-distance in metres represents the distance that an individual would need to be capable of dispersing to reach that area of matrix. Labels, a) Sailsbury Plain, b) chalk grassland patch south-east of the World Heritage Site and, c) Porton Down and, d) isolated fragments.

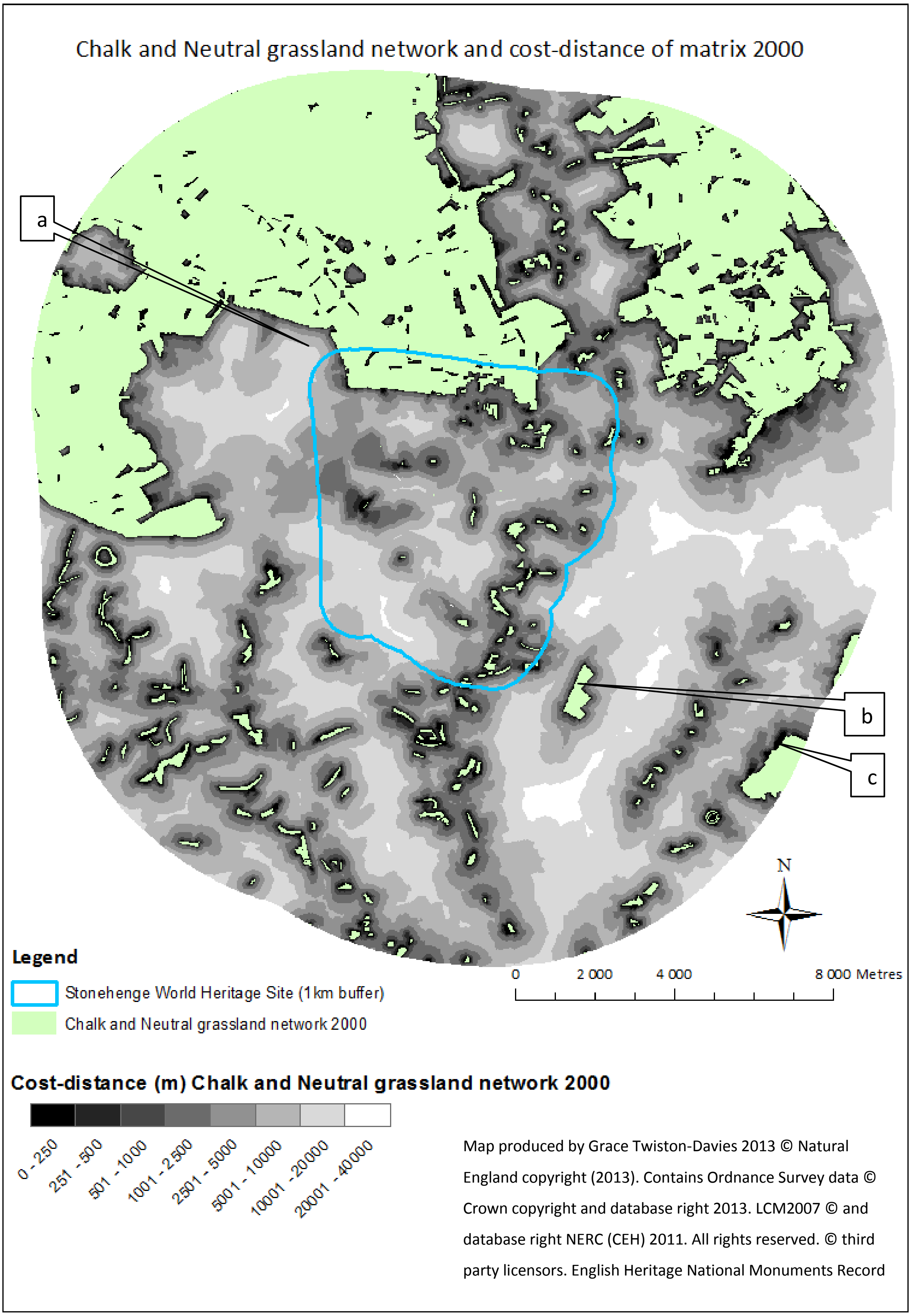
Chalk and Neutral grassland network and cost-distance of matrix 2000

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Figure 6-9. Map c of the Stonehenge World Heritage Site and the surrounding landscape. Chalk and neutral grassland network and cost-distance matrix in 2000. Cost distance in metres represents the distance that an individual would need to be capable of dispersing to reach that area of matrix. Labels, a) Sailsbury Plain, b) chalk grassland patch south-east of the World Heritage Site and, c) Porton Down.

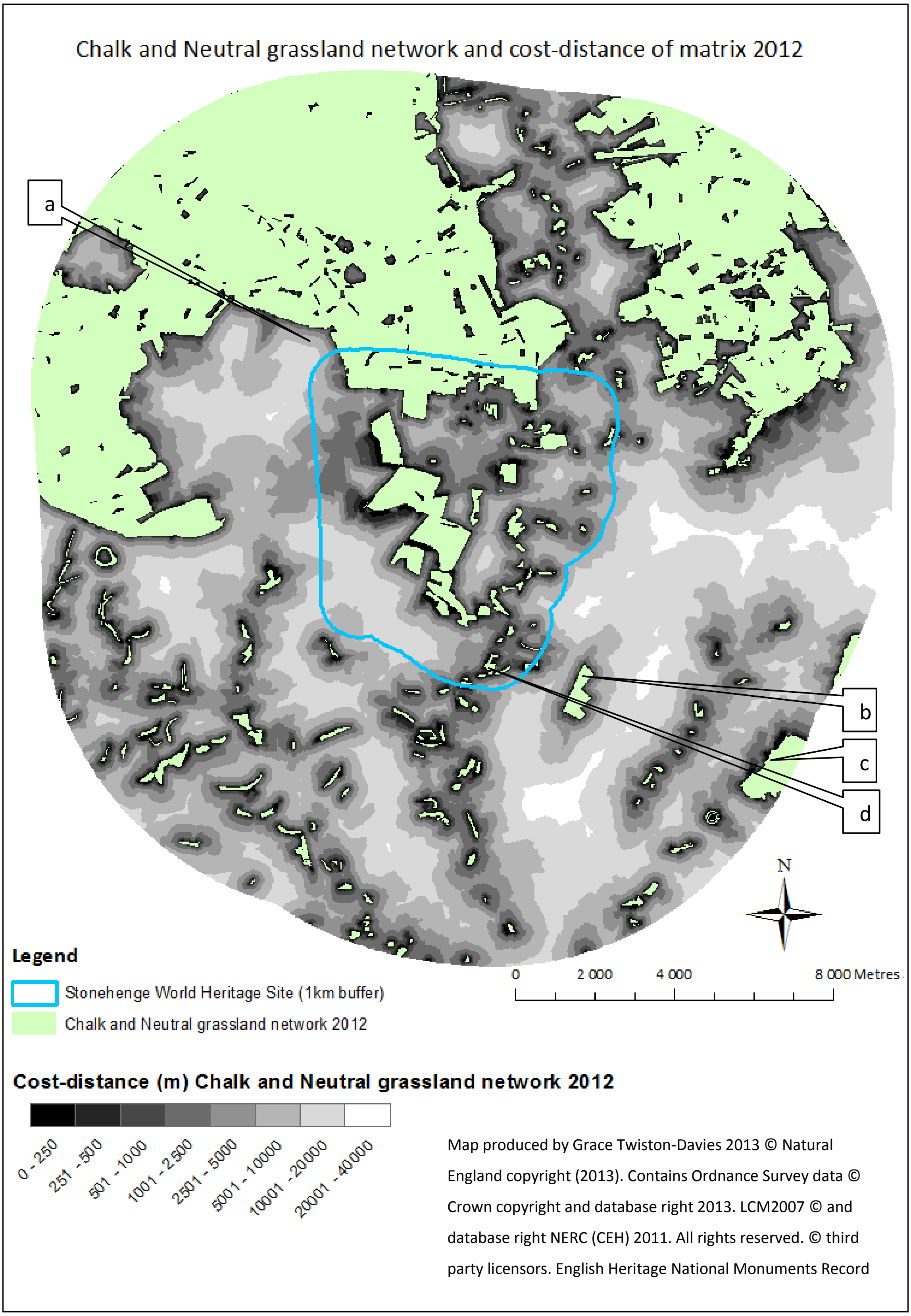

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Figure 6-10. Map d of the Stonehenge World Heritage Site and the surrounding landscape. Chalk grassland network and cost-distance matrix in 2012. Cost distance in metres represents the distance that an individual would need to be capable of dispersing to reach that area of matrix. Labels, a) Sailsbury Plain, b) chalk grassland patch south-east of the World Heritage Site and, (c) Porton Down and (d) isolated fragments.

6.4.2 Distribution of focal Lepidoptera species

Distribution maps of focal Lepidoptera species from the Butterflies for the New Millennium Recording Scheme along with the recording of Lepidoptera from this study (Chapters 3, 4 and 5 not shown in the Figure) indicate that the Stonehenge grassland re-creation has the potential to connect populations of *Lysandra bellargus* and *Cupido minimus* within the Stonehenge Landscape to each other and to link these populations to those in Salisbury Plain to the north of the site (Figure 6-10). *Euphydryas aurinia* have been recorded across Salisbury Plain but not at the Stonehenge WHS and therefore the grassland re-creation may only enhance the connectivity of the landscape by decreasing the dispersal 'cost' and not necessarily link potentially isolated populations (see Appendix E for map with *Euphydryas aurinia* distributions). There have been many recordings of *Lysandra bellargus* and *Cupido minimus* in the low permeability, high 'cost' suburban matrix area of Amesbury to the East of the WHS boundary (Figure 6-10), from 2000-2012; these are from the Boscombe Down Butterfly Monitoring Transect on an area that is classed as improved grassland.

Table 6-3. Adonis Blue (*Lysandra bellargus*) and Small Blue (*Cupido minimus*) and Chalkhill Blue (*Polyommatus coridon*) sightings in the Stonehenge World Heritage Site and 1 km buffer. Map location on Figure 6-11. Appendix E for all species distributions of interest.

Species	**No. seen**	**Month**	**Year**	**Location**	**Map location**	**Fixed transect**
Adonis Blue	4	May, June	2010	Salisbury Plain	a	
Adonis Blue	1	June	2010	Salisbury Plain	a	
Adonis Blue	11	September	2011	Salisbury Plain	a	
Adonis Blue	1	None	2011	Salisbury Plain	a	
Adonis Blue	4	June, September	2010	Larkhill Garrison	b	
Adonis Blue	4	None	2011	Larkhill Garrison	b	
Adonis Blue	3	August	2004	Fargo Barrow	c	
Adonis Blue	3	June	2012	Cursus Barrows	d	
Adonis Blue	3	June	2006	Great Durnford, Little Down East	f	
Small Blue	1	June	2009	Salisbury Plain	a	
Small Blue	1	June	2009	Salisbury Plain	a	
Small Blue	1	July	2010	Salisbury Plain	a	
Small Blue	>100	May, June, July, August	2010	Larkhill Garrison	b	
Small Blue	39	None	2011	Larkhill Garrison	b	
Small Blue	4	None	2010	Normanton Down	e	
Small Blue	4	None	2010	Normanton Down	e	RSPB transect
Chalkhill Blue	1	None	2006	Normanton Down	e	RSPB transect
Chalkhill Blue	1	None	2007	Normanton Down	e	RSPB transect

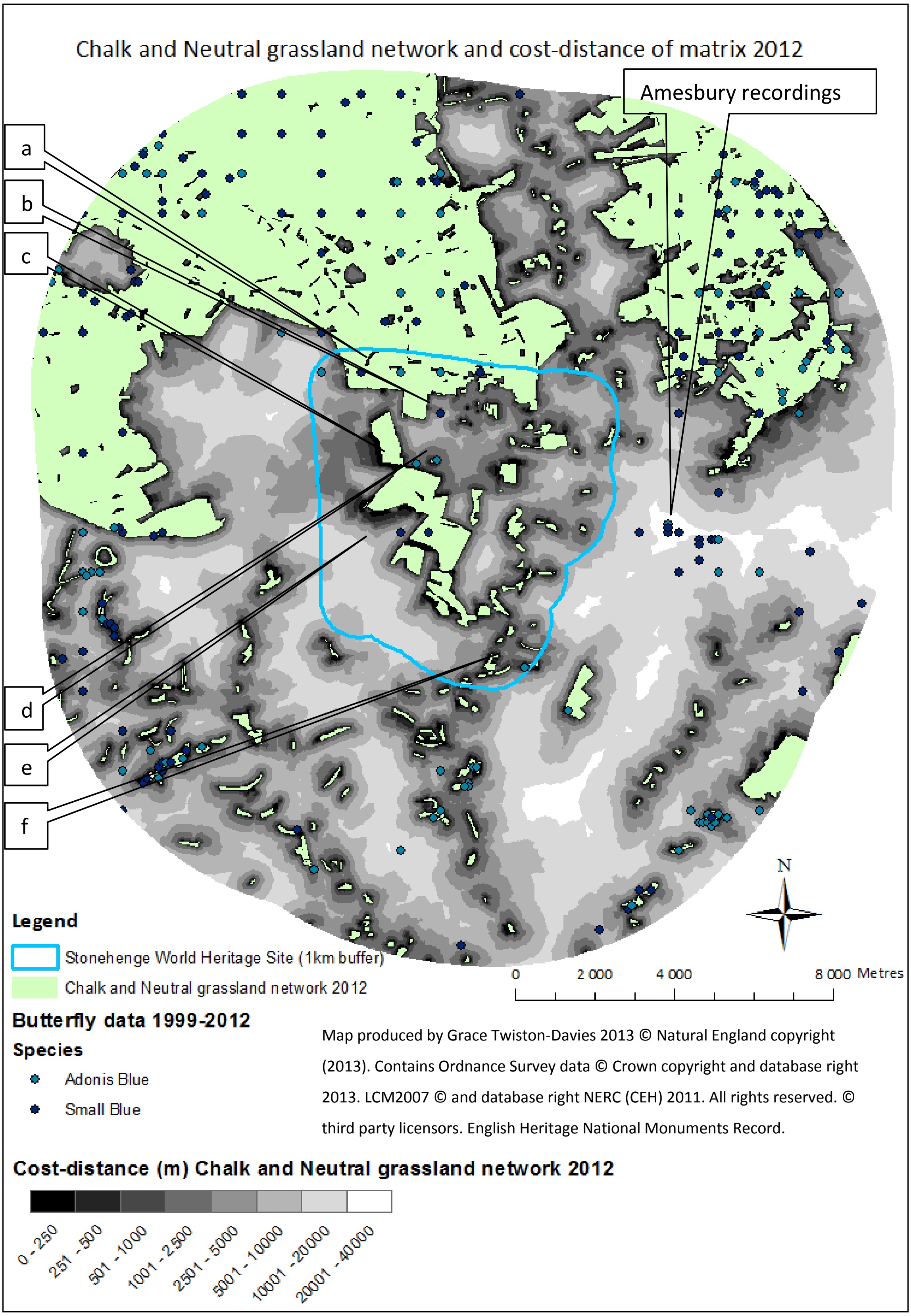

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Figure 6-11. Map of the Stonehenge World Heritage Site and the surrounding landscape with locations of sightings of Adonis Blue (*Lysandra bellargus*) and Chalkhill Blue (*Polyommatus coridon*) from 1999-2012. Chalk and neutral grassland network and cost-distance matrix in 2012. Cost-distance in metres represents the distance that an individual would need to be capable of dispersing to reach that area of matrix. Labels refer to sightings at, a) Salisbury Plain, b) Larkhill Garrison, c) Fargo Barrow, d) Cursus Barrows, e) Great Durnford, Little Down East and, f) Normanton Down RSPB reserve. Recordings in the town of Amsbury area are also highlighted. Lepidoptera distribution data were provided from the Butterflies for the New Millennium Recording Scheme, courtesy of Butterfly Conservation.

6.4.3 Landscape connectivity measures

At the wider landscape scale, the grassland re-creation at the Stonehenge WHS has had a small but measurable effect by increasing the number of chalk and neutral grassland patches over4 hectares from 30 to 38 patches which is the Minimum Area Requirement (MAR) for habitat for the minimum viable population size of many grassland associated butterfly species such as *Aphantopus hyperantus*, *Coenonympha pamphilus*, *Polyommatus icarus*, *Cupido minimus* (MAR 1 ha), *Arica agestis*, *Lycaena phlaeas* and *Melanargia galathea* (MAR 4 ha) (Bink 1992). The grassland re-creation has also increased the mean area of a grassland patch by over 1.5 hectares (see Appendix E for full table of results). Within the WHS and a 1 km boundary as a result of the grassland re-creation project, the total number of habitat patches and number of patches over 2 hectares in area (Figure 6-12) have increased. This is true also of the total area of grassland and mean area of a patch of grassland (Figure 6-14) which has increased to 19 and 23 ha for chalk and neutral and for chalk grassland respectively, now potentially encompassing the MAR of *Maniola jurtina* and *Lysandra bellargus* (16 ha) for example and the percentage of the landscape that are grassland patches that have increased (Figure 6-13).

The total area, mean patch area and percentage of the landscape of core grassland also increased after re-creation across the wider landscape and within the WHS (Figure 6-13), this is the amount of grassland patch that remains once the edge impact (metres) of the adjacent matrix type has been removed (refer to section 6.3.5 for details on how core area was calculated). This was lower than the total amount of grassland that was re-created due to the edge impacts of the surrounding matrix land cover types within the World Heritage Site of predominantly arable land.

The complexity of grassland patches as measured by the Shape index, (similar to perimeter area ratio) increased due to the irregular shape of the grassland re-creation.

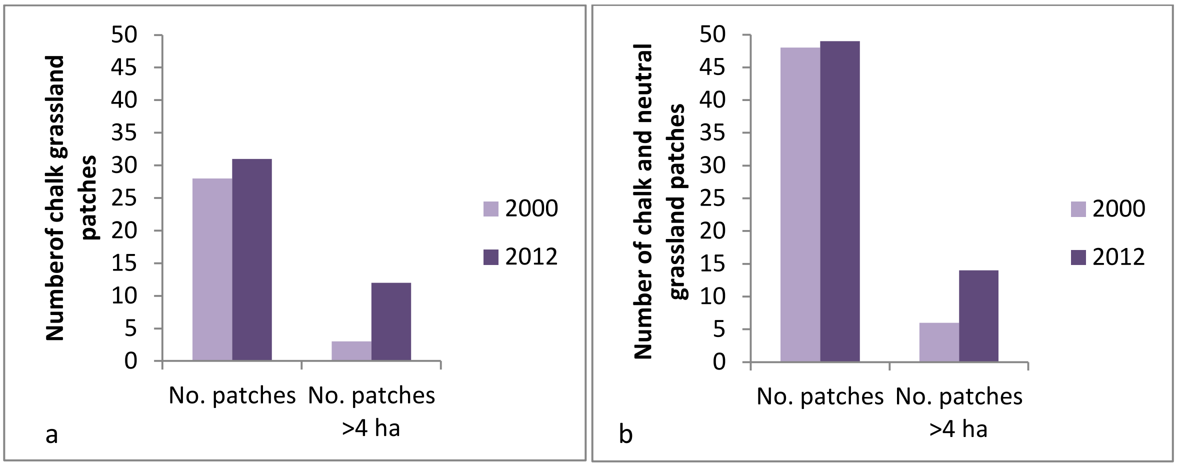


Figure 6-12. Number of a), chalk grassland and, b) chalk and neutral grassland within the Stonehenge World Heritage Site and 1 km buffer patches and patches more than 4 hectares in area in 2000 and 2012.

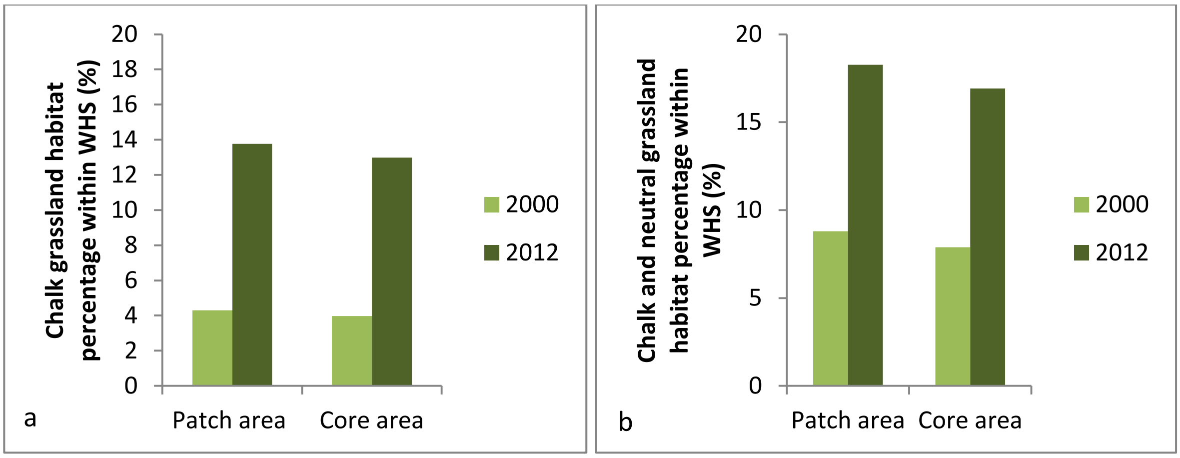


Figure 6-13. Percentage of the landscape that is habitat and core area in 2000 and 2012 for habitat types as , a) chalk grassland and, b) chalk and neutral grassland within the Stonehenge World Heritage Site (WHS) and 1 km buffer.

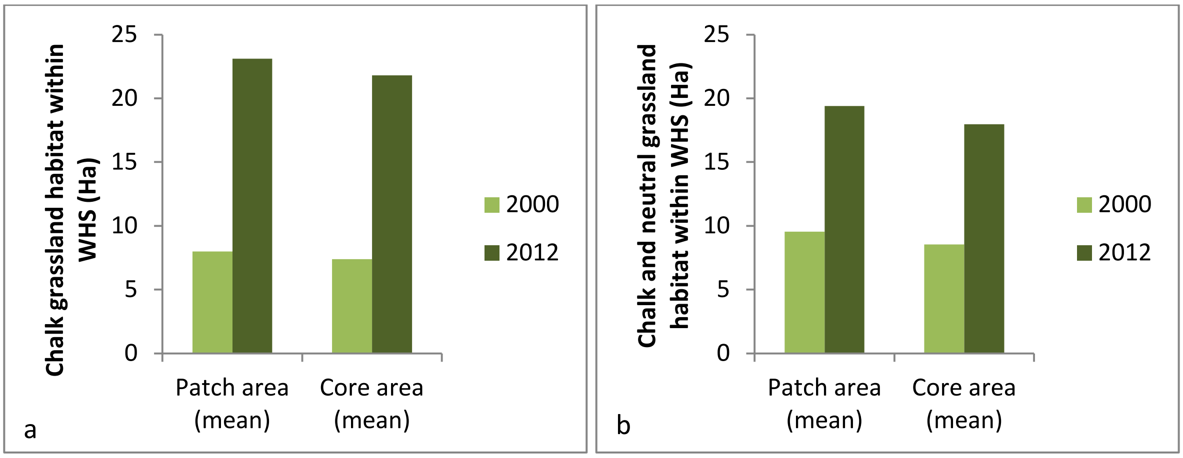


Figure 6-14. Area (hectares) of, a) Chalk grassland and, b) Chalk and neutral grassland within the Stonehenge World Heritage Site (WHS) and 1 km buffer and percentage of core chalk grassland/chalk and neutral grassland once the edge effects of the adjacent matrix were considered in 2000 and 2012.

Measures of network connectivity included the distance in metres to the nearest habitat patch using Nearest Neighbour Distance, which decreased across the wider landscape by 10 m and within the WHS by 100 m (Figure 6-15). The Proximity Index increased for both dispersal distances and wider landscape and within the WHS and 1 km buffer (Figure 6-16).

Results from landscape metrics that consider all types of land cover and not just focal habitats of chalk and neutral grassland showed that the number of patches of different land-cover types increased across the wider landscape and within the WHS and its 1 km buffer as large expanses of arable land were broken up by grassland re-creation. Grassland re-creation also increased the total amount of 'core' area by 18.9 and 19.5 hectares (for wider landscape and WHS scales, respectively see Table 6-4) as grassland has a much lower edge impact on coniferous and yew woodlands compared to arable land. There were small but measurable increases in landscape heterogeneity calculated by diversity and evenness that were more pronounced within the WHS and its 1 km boundary (Table 6-4, see Appendix E for full results table).

Table 6-4. Results from landscape metric calculations considering all habitat patch types of re-creation grasslands contributing to the chalk grassland network and to the chalk and neutral grassland network. Measured at the scale of the surrounding landscape in N 8 km buffer from the World Heritage Site boundary (Surrounding landscape 8 km buffer) that encompasses the many other large expanses of chalk grassland and within the 1 km buffer of the World Heritage Site (Stonehenge landscape 1 km buffer). Values in 2000 before the re-creation project started, after 2012 when it was finished and the difference.

	Surrounding landscape (8km buffer)			**Stonehenge Landscape (1km buffer)**		
Metric	**2000**	**2012**	**Change**	**2000**	**2012**	**Change**
<u>Landscape</u>						
Total core area (Ha)	36672.50	36691.38	18.88	4679.94	4699.44	19.50
Re-creation grasslands adding to chalk grassland network						
Number of patches	3398.00	3404.00	6.00	444.00	451.00	7.00
Shannon diversity	1.67	1.68	0.01	1.46	1.62	0.17
Shannon evenness	0.65	0.65	0.00	0.61	0.68	0.07
Re-creation grasslands adding to chalk and neutral grassland network						
Number of patches	2605.00	2610.00	5.00	387.00	392.00	5.00
Shannon diversity	1.49	1.49	0.01	1.39	1.52	0.13
Shannon evenness	0.60	0.60	0.00	0.61	0.66	0.05

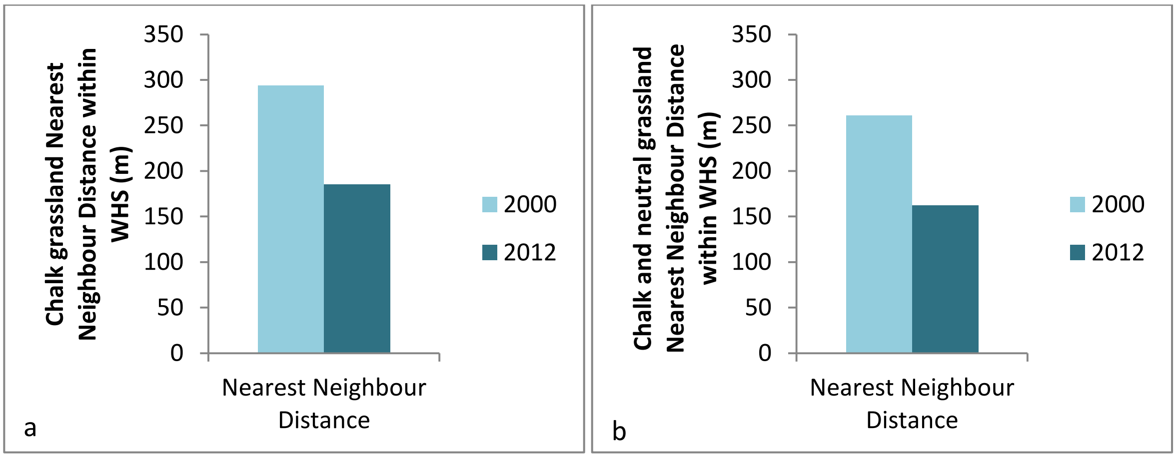


Figure 6-15. Nearest Neighbour Distance (Euclidean distance in metres) for habitat patches of, a) chalk grassland and, b) chalk and neutral grassland within the Stonehenge World Heritage Site (WHS) and 1 km buffer in 2000 and 2012.

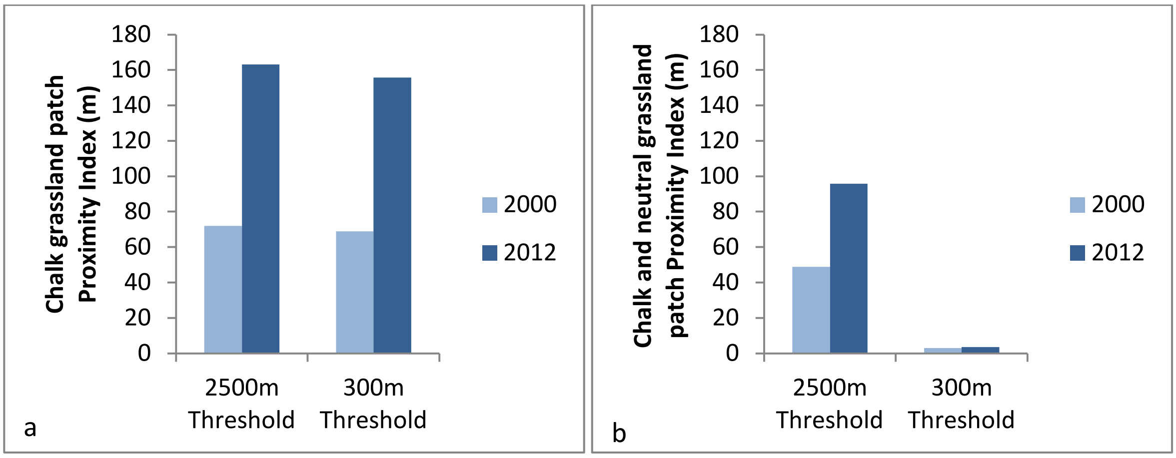


Figure 6-16. Proximity Index of 2,500 m and 300 m threshold to represent potential dispersal distance for *Zygaena filipendulae* and *Polyommatus icarus* as example species for habitat networks of, a) chalk grassland and, b) chalk and neutral grassland within the Stonehenge World Heritage Site and its 1 km buffer in 2000 and 2012.

6.5 Discussion

6.5.1 Habitat network and cost-distance analysis

Focal habitat networks and cost-distance analysis show that the grassland re-creation project within the Stonehenge World Heritage Site has increased the area and extent of species-rich grassland South from Salisbury Plain, into an area that was predominantly arable land and semi-improved pasture (Figure 6-8, 6-10). This has also potentially halved the cost of dispersal (Section 6.4.1) in areas adjacent to urban and suburban land cover that are within the 1 km buffer of the WHS boundary to the East of the World Heritage Site (Amesbury) that had a very high dispersal cost prior to the grassland re-creation (<20 km dispersal, Figure 6-8). The grassland re-creation has potentially reduced the Lepidoptera dispersal ability required for functional connectivity between the majority of grassland patches within the WHS from 5 to 10 km (Figure 6-7, Figure 6-9) to 1 to 2.5 km. Functional connectivity for the majority of grassland fragments for species with dispersal abilities of 1-2.5 km reflects the upper range of mean dispersal abilities of a range of grassland associated butterfly species including Common Blue (*Polyommatus icarus*) and Meadow Brown (*Maniola jurtina*)(Baguette *et al.* 2011; Schneider *et al.* 2003). *Maniola jurtina,* Ringlet (*Aphantopus hyperantus*) *and* Small Heath (*Coenonympha pamphilus*) can reach grassy linear features 1 km away from grasslands (Ockinger & Smith 2007a). *Maniola jurtina* will move on average up to 350 m in short grassland (Conradt & Roper 2006), indicating a dispersal ability of approximately 2333m if the permeability of this matrix land-cover types is 0.15 (350 divided by 0.15, Eycott *et al.* 2011).

Limitations to the enhancement of landscape connectivity as a result of the grassland re-creation are due to the small fragments of chalk grassland South of the World Heritage Site (Figure 6-8, label d) that may still remain functionally isolated in the absence of targeted conservation actions and these are isolated from the re-creation grasslands for species with dispersal abilities under 2.5 km. Additionally, the grassland network between Salisbury Plain to the North, Parsonage Down to the West and Porton Down to the east of the WHS may still remain mainly functionally isolated from one another for all but very high distance dispersers (10-20 km dispersal distances only likely for migrant species such as the Painted Lady (*Vanessa atalanta)* or a very few individuals of widespread species) due to low permeability and high dispersal cost of the arable land between Parsonage Down and Stonehenge WHS and between Stonehenge WHS and Porton Down. This large landscape scale perspective is important when considering meta-population dynamics and the future persistence of populations in the landscape (Hanski 1998; Hanski *et al.* 1994). However, large landscape scale projects to increase connectivity of habitat networks can be difficult due to complications and conflicts arising from the need to reconcile different land owner objectives and arable, residential and conservation priorities.

Although the majority of fragments are functionally connected for Lepidoptera with dispersal abilities of 1-2.5 km, many grassland specialist species may still be functionally isolated due to the high 'cost' of travelling through the matrix and low dispersal abilities. For example *Lysandra bellargus* butterflies may not travel any more than 100 m from their residential patch (Thomas 1983) which means that if habitat patches in close proximity but are separated by a high cost matrix, individuals may be potentially isolated. In addition to this the fact that male and female dispersal can differ as dispersal can be affected by different environmental and population factors and can differ in dispersal distances (Matter & Roland 2002; Rusterholz & Erhardt 2000; Schultz *et al.* 2012) which then skews the sex ratio within populations and the differences between sexes have not been investigated.

In urban and suburban areas, which have very low permeability and high dispersal 'cost' other policies may need to be considered. However, in landscapes dominated by agricultural land, gardens can enhance the abundance and richness of pollinators for example by providing floral resources not otherwise found in the landscape (Samnegard *et al.* 2011) and therefore, not all urban and suburban areas necessarily have a high "cost". These could include targeting for urban biodiversity or Agri-environment schemes that prioritise species-rich grasslands to increase connectivity through these landscapes for example, Amesbury, arable land west of the Stonehenge Landscape and the Salisbury City area (Figure 6-8).

The assumption of the grassland re-creation adding to the chalk grassland network is made on the transitional mesotrophic and chalk botanical characteristics of re-creation grasslands over 7 years old (Campbell 2009; Pemberton 2011; Twiston-Davies *et al. in press*) and assumes that Lepidoptera with chalk grassland habitat associations would be able to fully utilise this new network. This time threshold is supported by studies for other grasslands sown with locally sourced seed mixtures (Prach *et al.* 2013), for butterfly communities in re-creation grasslands (Woodcock *et al.* 2012a) and for mobile invertebrate species that are characteristic of the target habitat which can re-colonise grasslands in as little as 2 years (Deri *et al.* 2011). This however, may not be the case if the larval host plants of Lepidoptera are not well established across the landscape, for example, Horseshoe Vetch (*Hippocrepis comosa)* for *Lysandra bellargus*. However, given that 7-10 years after first sowing, the grasslands are approaching the botanical conditions of the target chalk grassland on Salisbury Plain (Chapter 3 and (Twiston-Davies *et al. in press*), the assumption that the grassland re-creation can contribute to the chalk grassland network may be true in the future given time and specific management. Results from Chapter 3 suggest that re-created grasslands that are over 7 years since sowing contribute to the chalk grassland network and those that are younger, which have transitional grassland characteristics contribute to the chalk and neutral grassland network, this means that this grassland network represents the future potential of the landscape to support chalk grassland and its associated Lepidoptera species.

The contribution of re-creation grasslands to the chalk and neutral grassland network may be more realistic given the transitioned botanical conditions and therefore less specialised grassland species may utilise this new habitat such as Marbled White (*Melanargia galathea*), *Polyommatus icarus* and 6-spot Burnet moth (*Zygaena filipendulae*) with larval host plants highly abundant in the re-creation grasslands (Campbell 2009; Pemberton 2011)*.* Many species associated with chalk grassland in Europe are also found in other types of species-rich grasslands and are abundant across the Stonehenge landscape such as *Polyommatus icarus, Melanargia galathea* and *Coenonympha pamphilus* (Chapter 3) and these are most likely to benefit from the grassland re-creation (van Swaay 2002). Most species surveyed in the re-creation fields were associated with open-grass grasslands such as *Melanargia galathea, Maniola jurtina* and *Coenonympha pamphilus*, (Shreeve *et al.* 2001) and therefore the contribution of the re-creation grasslands to the chalk and neutral network is more realistic at present.

Habitat network and cost-distance maps can inform strategic conservation and management but do have limitations. Habitat can be defined in many ways; butterflies have overall habitat associations but these may be wide and flexible depending on species, location (range) climatic and population factors. Habitat preferences are based only on a single habitat type, and many butterflies have supplementary and complementary resources or require particular habitat types for shelter in the matrix (Clausen *et al.* 2001; Rosin *et al.* 2012) and habitat affinity can better explain biodiversity as this considers a multiple habitat types rather than just one habitat type (Proença & Pereira 2013).

Additionally, the effects of different matrix types are species specific with even closely related species responding differently (Prevedello & Vieira 2010; Ricketts 2001; Ries & Debinski 2001).

Linear features in the landscape such as hedgerows, lanes, verges and grassy field margins are important for invertebrate colonisation, dispersal, growth, survival and species-richness and abundance (Berggren *et al.* 2001; Clausen *et al.* 2001; Delattre *et al.* 2013; Driscoll & Weir 2005; Duelli & Obrist 2003; Ockinger & Smith 2007b). The 25 m by 25 m grid square resolution however does not accommodate these features.

6.5.1.1 Summary

Habitat network properties such as the total area of habitat and connectivity are important for species persistence (review see Van Teeffelen *et al.* 2012) and overall the grassland re-creation project has increased the area of permanent species-rich grassland and reduced the dispersal 'cost' of the matrix within the 1 km buffer of the WHS. However, this network may be only functionally connected for species with dispersal abilities of over 1 km, meaning that those of lower dispersal abilities may be functionally isolated in some patches and therefore will require targeted conservation action. These types of analysis are useful for targeting area which are most suited for restoration such as through opportunity mapping, and this is recommended for future projects.

6.5.2 Lepidoptera distribution

Focal Lepidoptera species distribution maps indicate that the grassland network has the potential to link populations of Lepidoptera that may have previously been functionally isolated due to the low permeability, high dispersal 'cost' land cover types, between habitat patches within the Stonehenge World Heritage Site of arable land and semi-improved pasture. Within the landscape, *Lysandra bellargus* butterflies were surveyed at a few of the chalk grassland fragments (Chapter 3) and *Cupido minimus* at one chalk grassland fragment. These species have specific host plant requirements and very low mobility so are likely to benefit from grassland re-creation through the effect of buffering of their chalk grassland fragments, which increases the availability of resources and potentially increases connectivity.

Limitations of classifying the re-creation grasslands as either chalk or neutral grassland occur due to the transitional habitat type of the grassland re-creation. Even though older re-creation shares many similar species with the chalk grassland target habitat patch from where the seed was sourced (Chapter 3), it can take decades for grassland re-creation to reach the precise botanical conditions of the target habitat (Fagan *et al.* 2008). This leaves the classification of grassland re-creation and interaction networks difficult and potentially designated as sub-optimal habitat or matrix enhancement depending on the age and floristic composition. Despite these limitations, even a matrix of similar structure increases dispersal (see for reviews (Eycott *et al.* 2012; Prevedello & Vieira

2010). For the purposes of this study the grassland re-creation was classified as either adding to the chalk grassland network due to its species-rich characteristics and dominant plant species associated with chalk grassland (for example, Upright Brome, *Bromopsis erecta* and Quaking Grass, *Brizia media*), or as adding to the more general chalk grassland and neutral grassland network. However, grassland re-creation would be more beneficial for grassland Lepidoptera species than arable land or improved pastures as it is less intensively managed and more species-rich, thereby providing additional resources such as, nectar flower abundance and diversity, which are important for supporting Lepidoptera abundance and species-richness (Binzenhofer *et al.* 2005; Clausen *et al.* 2001; Haaland & Bersier 2011; Matter & Roland 2002). Grassland re-creation can protect and buffer species-rich grassland fragments that are sources of more specialised butterfly species such as *Lysandra bellargus* and *Cupido minimus* and provide low dispersal 'cost' links through the landscape to aid dispersal. Additionally, the recordings of *Lysandra bellargus* and *Cupido minimus* in improved grassland at Boscombe Down indicate that an area not classified as 'habitat' using LCM classifications may be important for supporting these populations.

6.5.2.1 Summary

Grassland re-creation can protect and buffer fragmented patches of chalk grassland, providing nectar resources and a more permeable matrix land cover for more specialist species even if their larval host plant require chalk grassland preferences for. However, some species of conservation concern may still remain functionally isolated if the dispersal 'cost' of travelling through the matrix is beyond their abilities and re-creation grasslands do not reach the required ecological conditions to become suitable habitats for these species.

6.5.3 Patch indices and connectivity measures

The main objective of the grassland restoration and re-creation project as set out in the Stonehenge World Heritage Site Management Plan (Young *et al.* 2009) was to extend the area of permanent pasture in the World Heritage Site and this has been fulfilled, as the number of patches and the total area of grassland has increased due to the grassland re-creation. The effects of the re-creation has wider landscape effects that are small but measurable and has increased landscape heterogeneity and size and area of habitat across the landscape, which are important for supporting biodiversity (Hendrickx *et al.* 2007; Hodgson *et al.* 2011). The distance between patches of the same habitat type measured as Nearest Neighbour Distance has decreased by 100 m within the WHS. This may be especially important for species with low dispersal abilities such as *Lysandra bellargus* and *Cupido minimus* which may only travel a hundred metres (Thomas 1983) .

Landscape heterogeneity measured by the Shannon Diversity of land cover types increased by 0.17 within the WHS and 1 km of its boundary, although this value is limited by the fact that only arable land was converted to grassland with no other Land cover changes. There is no set criteria as to what levels of heterogeneity should be the target at a landscape scale, but an increase is nonetheless a positive indicator and these values can be compared to other studies that investigated landscape diversity after land-cove changes. Antwi *et al.* (2008) showed Shannon Diversity increased by 0.4 (1.7 to 2.1) in 5 years after the restoration of dry grassland (511 ha) and afforestation of deciduous trees (629 ha) after mining and Benini *et al.* (2010) showed a decrease of 0.03 in 9 years due to agricultural intensification of the landscape where there was a 1500 ha increase in crop land and the subsequent decrease of grassland.

The number of patches over 4 and 16 ha have increased, potentially representing the Minimum Area Requirements for many grassland associated Lepidoptera. However, these MAR measures are approximations based on expert opinion and the wing span of Lepidoptera (Bink 1992) and therefore may underestimate the MAR. For example the Marsh Fritillary (*Euphydryas aurinia*) may have a MAR of over 80 ha for metapopulation persistence (Bulman *et al.* 2007), far greater than the 4 ha estimated from its wingspan in Bink (1992). Over the entire landscape there were 9 patches of chalk and neutral grassland increased by 1 as a result of the grassland re-creation that could accommodate.

Shape complexity has increased by a small amount due to the irregular shape of the re-created grassland: a more irregular habitat patch shape can be an indication or more species-rich habitats (Mitchley & Xofis 2005) or potentially decrease the area of core habitat due to negative edge effects (Ewers *et al.* 2007). Proximity index increased due to the grassland re-creation (measured as the distance to a patch and the size of patches within a search radius). This was higher for a search radius threshold of 2.5 km as individuals with this dispersal ability could reach more patches, but not as high for those with low mobility (search radius 300 m).

Network properties such as patch characteristics and connectivity are important for species persistence (for review see Van Teeffelen *et al.* 2012). This study has illustrated that due to the re-creation project the connectivity was increased as measured by Nearest Neighbour Distance and Proximity Index. Patch area and the Euclidean distance between patches are the main components driving metapopulation stability (Hanski 1998; Hanski *et al.* 1994). Due to the grassland re-creation, patch area has been increased and distance between patches has been decreased and this may be more important than patch quality or landscape structure (Moilanen & Hanski 1998). Many studies stress that the size and quality of habitat patches and the distance between them are the most important components for landscape connectivity and conservation (for example, Hodgson *et al.* 2011; Prevedello & Vieira 2010) and for Lepidoptera in chalk grasslands (Rosin *et al.* 2012).

Much evidence also suggests that the characteristics of the intervening habitat type can be just as important such as the permeability of the matrix or the resources it has (Doerr *et al.* 2011; Ouin *et* *al.* 2004; Prugh *et al.* 2008). The occurrence and distribution of Lepidoptera in a landscape is likely to be from a combination of patch and landscape characteristics which can be measured as functional connectivity (Haaland & Bersier 2011; Heer *et al.* 2013; Thomas *et al.* 2001b). This means that the effect of habitat restoration and re-creation on enhancing landscape connectivity will require a focus on both habitat quality and landscape aspects (Kleijn & van Langevelde 2006). Measures that considered the adjacent matrix were limited to including the edge effects when the core area of the focal habitat was calculated in Fragstats (version 4.2) as a quantitative measure and the cost-distance analysis (ArcMap 10.1 ESRI©) as a qualitative measure. However, no measure was used that combined the two and further investigation would benefit from these two methods they combined as they can provide a robust analysis of landscape connectivity (Watts & Handley 2010).

Limitations of the interpretation of these results are that increased landscape connectivity is assumed due to increased number of patches and patch size and overall area of habitat type, however, if the matrix is not managed to increase permeability this may not be the case. this means that management to increase patch quality, connectivity through matrix permeability and reduce negative edge effects should be implemented. The coarse scale of the landscape at which analyses were done also means that edge effects can be overestimated; land cover types of coniferous, arable and urban/suburban were given the same edge effects of 25 m when they have been shown in Eycott *et al.* (2011) to differ greatly. This does however give some indication using the core area measure and considers the land cover types of the adjacent matrix, a component that other landscape metrics such as Nearest Neighbour and Proximity Index do not account for.

6.5.3.1 Summary

The grassland re-creation project has increased the area of species-rich grassland, number of patches, and the area of patch, and decreased the distance to the nearest habitat patch by 100 m within the Stonehenge WHS. Limitations of the grassland restoration and re-creation project are evident when considering the dispersal ability of species in the landscape. For species with intermediate dispersal ability, connectivity measures increased but for those more sedentary many grassland patches were still isolated from each other.

6.6 Conclusion

Overall, the grassland re-creation at the Stonehenge World Heritage Site has increased the area of permanent species-rich grassland, thus fulfilling one of the aims of the grassland restoration and re-creation project. As a result, patch area has increased and the distance from one patch to the nearest other patch has also reduced by up to 100 m. Both of these aspects important for the long term survival of Lepidoptera populations in fragmented landscapes (Hendrickx *et al.* 2007; Hodgson *et al.* 2011). The distribution of Lepidoptera across the landscape indicated that the grassland re-creation could potentially link up populations of Lepidoptera across Salisbury Plain to fragments in the south and additional investigation is needed to assess this. The grassland re-creation has limitations; patches within the landscape are still potentially functionally isolated for those species with low dispersal ability due to high 'cost' matrix types and the transport network and urban areas may need to be managed with schemes to increase biodiversity. The techniques used of cost-distance and landscape measures are widespread and can be valuable for monitoring and evaluating landscape scale conservation projects. However, evaluating the effect of landscape scale habitat restoration is complex as habitat quality, shape, size, matrix conditions and landscape heterogeneity must all be considered.

Chapter 7 Discussion, Recommendations and Conclusion

7.1 Context

This study explores the role of landscape connectivity for enhancing the conservation of species in fragmented landscapes and specifically aims to investigate landscape connectivity as a key to effective habitat restoration for butterflies in lowland agricultural landscapes. Landscape connectivity is defined as the degree to which features of the landscape facilitate or impede the movement of organisms amongst resource patches (Taylor *et al.* 1993) and is characterised by a combination of species ability to move through the landscape and landscape structure (see review in Tischendorf & Fahrig 2000). Many studies have investigated connectivity; either examining individual behaviour and dispersal in fragmented landscapes as a measure of functional connectivity (for example, Keller *et al.* 2013; Merckx & Van Dyck 2007; Pither & Taylor 1998; Ricketts 2001; Ries & Debinski 2001; Schultz *et al.* 2012) or the effect of landscape structure (Aviron *et al.* 2005; Diekotter *et al.* 2008; Hendrickx *et al.* 2007), but very few have looked at the structural and functional connectivity of the wider landscape alongside these factor (see Hobbs 2007).

Functional connectivity is important for the conservation and restoration of calcareous grasslands (Wagner *et al.* 2013). The majority of grassland restoration studies focus on restoring plant communities (Fagan *et al.* 2008; Kiehl & Pfadenhauer 2007; Prach & Walker 2011) and not on the subsequent colonisation by mobile taxa (but see Woodcock *et al.* 2012a), or their ecological interactions (Menz *et al.* 2011), or the effect of restoration on potential landscape connectivity. In this study, Lepidoptera species were used as indicators to evaluate the effect of restoration on enhancing Lepidoptera biodiversity and landscape connectivity. Both landscape and local factors affect butterfly communities (Batary *et al.* 2012; Clausen *et al.* 2001; Davis *et al.* 2007; Ockinger & Smith 2007a; Roland *et al.* 2000). A landscape approach is particularly important for the conservation of this group in fragmented landscapes, as responses to landscape features and the use of resources differ at different spatial scales and depending on ecological characteristics such as habitat and host-plant specificity (Batary *et al.* 2011; Dover & Settele 2009; Ockinger *et al.* 2009; Tscharntke & Brandl 2004). No studies have explored these different spatial scales in a single landscape restoration project and provided subsequent conservation management recommendations as a result.

Overall, results from this study indicate that an approach that considers and combines the habitat boundary, field (habitat patch) and landscape scales may be most appropriate to manage landscape-scale species-rich temperate grassland restoration projects for Lepidoptera and to monitor and evaluate their progress. Conclusions drawn from this study may be transferable to other mobile organisms but are by no means definitive and other studies are advocated to build on these results as described in section 7.5.

Limitations highlighted by this study mainly relate to the fact that the majority of grassland re-creation is yet to reach the botanical conditions of the reference or donor habitat patch and that there is limited colonisation by specialist species. This means that a long term vision and commitment to landscape restoration is required. New habitats can take decades to reach conditions similar to the target habitat given appropriate time and management and some restoration may never reach target habitat conditions (Fagan *et al.* 2008). However, these newly-created habitats can provide resources for a variety of species, increase matrix permeability and enhance landscape connectivity (Deri *et al.* 2011; Diepenbrock & Finke 2013; Donald & Evans 2006; Ockinger & Smith 2007b; Ouin *et al.* 2004).

Few habitat restoration studies outline transferable management recommendations except for those concerning the establishment of plant communities (Brudvig 2011; Menz *et al.* 2013; Young *et al.* 2005). Therefore, an objective of this study is to provide management recommendations for the Stonehenge World Heritage Site that are also applicable to other temperate grassland European landscape scale restoration projects. The main concepts that emerge from this study that have implications for landscape scale restoration and management recommendations are in consideration of habitat compositional similarity, structural heterogeneity and functional connectivity at a range of spatial scales, these are discussed further in sections 7.2, 7.3 and 7.4. In this study, habitat compositional similarity refers to the plant community assemblages and flowering plant nectar sources for Lepidoptera, structural heterogeneity refers to the variation in vegetation density and height and functional connectivity takes into account the dispersal distances of the target species or group and the landscape including the intervening matrix between habitat patches (Tischendorf & Fahrig 2000).

The objectives of this study are to evaluate landscape restoration project in terms of the application and ecological benefits of restoration techniques for species-rich grassland at a landscape scale. The aim of this was to distinguish landscape and Lepidoptera species characteristics that promote colonisation, the distribution across land cover types, behaviour at boundaries and the wider landscape connectivity. These were to be used to make transferable management recommendations for other temperate European species-rich grassland restoration projects and these are described below. Although there is no set quantitative criteria or thresholds that are used in this study to measure the effects of restoration, this observational study can provide an evidence base for what sorts of biodiversity and landscape connectivity changes may be expected when long-term, large-scale habitat restoration is implemented through Agri-environment schemes.

7.1.1 Which landscape, habitat patch and species characteristics facilitate or impede the colonisation of restored habitats by target insect species?

7.1.1.1 Landscape and habitat patch characteristics

This study highlights a range of habitat patch and landscape characteristics that facilitate the colonisation of habitats undergoing restoration management and include the number of years since the field or habitat patch has been sown, diversity and density of nectar resources, vegetation structure and proximity to reference habitat patches. Results from Chapter 3 illustrate that habitat conditions that can be influenced by management can be as important as the age of the restoration habitat patch in determining Lepidoptera community similarity to the reference habitat patch and encouraging dispersal from fragments.

During this discussion, landscape refers to the Stonehenge World Heritage Site (26,000 ha) and 1 km of its boundary or other landscapes of similar sizes unless the discussion is referring to the wider landscape which is beyond this scale (8 km of the WHS boundary as used in Chapter 6). Field specifically refers to the field which has been or will be sown with grassland seed for habitat re-creation (also habitat patch) and habitat boundary refers to the edge of the site where either two fields meet or where different habitat or land-cover types meet. In these contexts, a field or habitat patch is often but not always categorised as being under one land owner or Agri-environment scheme whereas at the landscape scale there may be many land owners and land management schemes.

This study shows that the age of grassland re-creation is significantly related to the enhancement of butterfly biodiversity as measured by community assemblages and species richness (section 3.4.2.1). Older grassland re-creation fields that are 7-10 years old have higher Lepidoptera density and species richness than newer re-creation fields and a community assemblage more similar to the reference habitat (section 3.4.1). This result is supported by other restoration studies for both grassland plant and Lepidoptera communities for example, (Piqueray *et al.* 2011; Prach *et al.* 2013; Woodcock *et al.* 2012a). However, age is not the only significant factor in determining communities assemblages that re approaching the target habitats, it is also apparent that variables relating to nectar plant species and vegetation characteristics are also significant (sections 3.4.2.1 and 3.4.2.2) and this is supported by many other studies (Binzenhofer *et al.* 2005; Clausen *et al.* 2001; Haaland & Bersier 2011; Matter & Roland 2002; Rosin *et al.* 2012). These variables such as high densities of particular nectar plants or families or varied grazing an mowing regimes can be managed to enhance the biodiversity outcomes of restoration projects and provide resources for colonising Lepidoptera.

These recommendations are outlined below at the boundary, field and landscape scales in sections 7.2, 7.3 and 7.4.

The structural heterogeneity of vegetation at grassland re-creation habitat patches is a significant factor explaining Lepidoptera colonisation (section 3.4.2.2.3), but increased variation in vegetation height and density is negatively associated with habitat boundary crossing (section 4.4.5.2) at the habitat patch scale. This occurs as individuals are less likely to cross if the matrix contrasts structurally from the habitat (see reviews in Eycott *et al.* 2012; Prevedello & Vieira 2010). A more variable vegetation density is associated with the ancient grassland reference habitat patches(Appendix B) and structural heterogeneity is important at the habitat patch or field scale to account for inter and intra species preferences (NCC 1986; Slamova *et al.* 2013).

Proximity (less than 100-150 m, Kohler *et al.* 2008) to reference habitat patches appears to be important and even though there are low Lepidoptera densities in the new grassland re-creation habitat patches (section 3.4.1), there are significantly higher proportions of Lepidoptera crossing chalk grassland fragment boundaries when the adjacent habitat is newer re-creation compared to arable than would be expected (section 4.4.1). Much of this crossing behaviour may be attributed to the foray loop behaviour described in Lepidoptera where individuals fly into the adjacent habitat and return as a first attempt at dispersal (Delattre *et al.* 2010a). Proximity to source habitat patches is especially important for pollinating insects in fragmented landscapes (Ockinger & Smith 2007b; Ouin *et al.* 2008; Roland *et al.* 2000). Additionally, species with low mobility (sedentary mobility group which may only travel a few hundred metres) were potentially isolated in chalk grassland fragments at the Stonehenge landscape and are more affected by habitat fragmentation than other groups (Ockinger *et al.* 2009; Woodcock *et al.* 2012b) as the landscape connectivity analysis in section 6.3 showed. Small chalk grassland fragments of under 2 hectares in size are still potentially isolated, indicating that targeted restoration in close proximity to these fragments would be beneficial.

The proportion of linear features in the proximity of sampled transects (section 3.4.2.1) did not significantly explain Lepidoptera community composition but did explain Lepidoptera density at all buffer scales examined (50-1000 m) (Appendix B). The importance of linear features for dispersal, abundance and community composition is supported in many studies of grassland associated Lepidoptera and other insects (Delattre *et al.* 2010b; Duelli & Obrist 2003; Ockinger & Smith 2007b). However, not all studies report a significant effect of the surrounding landscape, for example landscape factors were not found to be as important for Lepidoptera colonisation on restoration mining land (as measured by species richness and conservation value) as local factors of management and habitat heterogeneity (Tropek *et al.* 2013).

7.1.1.2 Species characteristics

The effect of species traits has been extensively studied in relation to habitat fragmentation (Davies *et al.* 2000; Driscoll & Weir 2005; Henle *et al.* 2004; Ockinger *et al.* 2009; Steffan-Dewenter & Tscharntke 2002; Tscharntke & Brandl 2004) and in relation to vegetation traits in habitat restoration (Pywell *et al.* 2003; Renton *et al.* 2012), but less for insects in habitat restoration (but see (Woodcock *et al.* 2012a). This study highlights the differences in the enhancement of biodiversity and landscape connectivity as a result of restoration for Lepidoptera with different ecological associations and dispersal abilities whereby those associated with open-grass habitats with medium to tall swards and who utilise grasses as larval host-plants colonised grassland re-creation earlier. Overall, older grassland re-creation is colonised by Lepidoptera associated with grassland habitats, with representative species from both open-grass and herb-rich ecological groups with some species from each group abundant, for example, Common Blue (*Polyommatus icarus)* and Meadow Brown (*Maniola jurtina)*, respectively (section 3.4.1). The herb-rich associated groups are those that utilise short-medium sward of warm grasslands , have legume larval host-plants and are likely to have a symbiotic relationship with ants. However, differences are evident between these ecological groups, with biodiversity enhancement from restoration measures most apparent for the open-grass ecological group associated with short-tall sward and open mesotrophic vegetation characteristics who use grasses as larval host pants (section 3.4.2) (Shreeve *et al.* 2001). Enhancement from the restoration project appears to be for Lepidoptera species that have grass larval host plants; *Maniola jurtina* and Marbled White (*Melanargia galathea*) which have colonised older and newer grassland re-creation habitat patches (section 3.4.1). However, those species associated with herb-rich warm grasslands are restricted to reference and older grassland re-creation habitat patches (sections 3.4.1 and 4.4.1). These differences are apparent when looking at boundary behaviour (sections 4.4.1 and 4.4.4) and when comparing *Maniola jurtina* and 6-spot Burnet moth (*Zygaena filipendulae)* responses to mown areas in older restoration fields (section 5.3). Despite being associated with grasslands, the resources that these two ecological groups utilise differ; larval host plants of open-grass associated species are grasses which appear to colonise grassland restoration such as Red Fescue (*Festuca rubra)* and Common Bent (*Agrostis capillaris)* for example (Pywell *et al.* 1999). However, some of the herb larval host plants of Lepidoptera, such as Horseshoe Vetch (*Hippocrepis comosa)* and Common Rock-rose (*Helianthemum nummularium*), do not establish as well even when they are in the seed mixtures (Pywell *et al.* 1999), restricting the colonisation of these associated Lepidoptera species.

These differences in biodiversity enhancement for specific ecological groups of Lepidoptera indicate that restoration projects will not result in biodiversity enhancement without the establishment of specific host plants, a result supported by (Woodcock *et al.* 2012a; Woodcock *et al.* 2012b). Target insect colonisation representative of the target habitat will inevitably lag behind vegetation in restoration projects, but the rate of this can be enhanced if the group and species specific requirements of the target taxa are understood and appropriate management is undertaken. Recommendations for these are made in section 7.2, 7.3 and 7.5.

Mobility appears to not be as significant as ecological group in explaining Lepidoptera colonisation of new habitats in this landscape (section 3.4.2). However, in Chapter 6 (section 6.3.1), the analysis of the functional connectivity of the landscape indicates that Lepidoptera with low mobility may be restricted to chalk grassland fragments and therefore these areas would need targeted management in the future. These species include *Cupido minimums* and *Lysandra bellargus* that would required management to establish their larval host plants Kidney Vetch (*Anthyllis vulneraria*) and Horseshoe Vetch (*Hippocrepis comosa*) respectively.

It is apparent that management needs to consider differences in the colonisation of re-creation grasslands for open-grass and herb-rich associated species. Management designed to enhance structural and habitat heterogeneity at both the habitat patch/field and landscape sales is advocated and includes varied vegetation height and density as well as a variety of microhabitats at the patch scale and land-cover types at the landscape scale (Kalarus *et al.* 2013; Kumar *et al.* 2009; Slamova *et al.* 2013; Steffan-Dewenter & Tscharntke 2002) but should not be at the expense of conservation for specialist species which may require targeted management. Management options that increase functional landscape connectivity for specialist species associated with chalk grassland with low mobility such as Adonis Blue (*Lysandra bellargus*) and Small Blue (*Cupido minimus*) are outlined in section 7.2-7.4 and should be implemented alongside management that increases heterogeneity (vegetation structure, available resources and habitat type) and landscape connectivity at a range of scales. Conservation priorities for the generalist species may conflict with those for specialist species and in these circumstances collaboration and consultation may be needed.

Other ecological associations will also need to be considered beyond the plant-insect interactions. For example, many Lycaena butterflies have symbiotic relationships with ants and this is a major contributor to the conservation and re-establishment of these populations (Thomas *et al.* 2009). *Lysandra bellargus* has a symbiotic relationship with (*Myrmica sabuleti* and *Lasius alienus* Forster) (Thomas 1983) and the colonisation by these in the grassland re-creation fields has not been studied.

7.1.2 Density, richness and community compositions of Lepidoptera

The density, diversity, distribution and community assemblages of Lepidoptera were investigated to evaluate the grassland re-creation project. Although these measures are not measures of functional connectivity (Tischendorf & Fahrig 2000) they are important for determining if restoration projects have resulted in biodiversity improvement (SER 2004), as the affect of restorative actions is mostly measured by comparing diversity, vegetation structure and ecological processes to the reference habitat patch (Ruiz-Jaen & Aide 2005).

The effect of restoration on biodiversity, as measured by the density, richness, distribution and community compositions of Lepidoptera approaching that of the reference habitat patch, is apparent within a decade for the Stonehenge WHS project, a time span supported by other studies of plant and Lepidoptera communities (Conrad & Tischew 2011; Piqueray *et al.* 2011; Woodcock *et al.* 2012a). Similarity of plant communities in re-created fields to a chalk grassland reference habitat patch (Rodwell 1992) was 57% after 10 years compared to the reference habitat patch at the landscape (Luxenborough bank) which was 66%. For Lepidoptera communities, the older grasslands (7-10 years) were 52% similar to reference patch at the landscape compared to the other two grassland fragments which were 67% similar. These results are similar to Piqueray *et al.* (2011) with 48% similarity of pant communities to reference habitat patches after 10 years (similarity between reference patches was 81%) but lower than Woodcock *et al.* (2012a) with 72% similarity between re-created grassland and target habitat patches for butterfly communities after 10 years. Lepidoptera density at re-creation was not significantly different from that of reference habitat patch. However, species richness and community compositions did differ (section 3.4.1), with older re-created grassland patches being closer in community composition to reference habitat patches than younger habitat patches, but still having distinct communities. Within this time span it is often apparent that the abundance of some target species is not as high as that in reference habitat patches (Conrad & Tischew 2011; Mitchley *et al.* 2012) and in this study the re-creation grasslands lacked the specialist species of plants (Pemberton 2011; Twiston-Davies *et al. in press*) and Lepidoptera (section 3.4.1) associated with chalk grasslands.

Overall, the aims of the grassland restoration project have been fulfilled which were outlined in the WHS Management Plan (Young *et al.* 2009) to increase the area of permanent pasture and increase the nature conservation value of the landscape. The Management Plan did not set out defined quantitative measures to evaluate the landscape restoration project and therefore improvements in species-richness and increases in similarity with local grassland community types are taken as fulfilling theses aims. The area of permanent grassland has been extended by over 500 ha and the ecological and nature conservation value has been increased as a consequence. This is illustrated by the higher Lepidoptera species richness and the colonisation of grassland associated species in older grassland re-creation fields . Two out of the three specific aims for the grassland have also been fulfilled and these were for it to be species-rich, based on local grassland community types and for natural regeneration and development to be possible. At present there are no management recommendations in place to encourage natural regeneration. These new grasslands are species-rich, and resemble local community types by being over 50% similar to the target habitat (reference habitat patches were over 66% similar to target habitat, Twiston-Davies *et al. in press*) and the new grassland re-creation (sown since 2009) also extend fragments of chalk grassland. The biodiversity value of these chalk fragments can be maintained and enhanced with appropriate management outlined in sections 7.2, 7.3 and 7.4. Limitations of the restoration project are that the chalk grassland fragments will only be enhanced if the grassland re-creation adjacent to the grassland supports and extends populations in the fragments thereby providing them with resources and corridors (Ockinger & Smith 2007b; Ouin *et al.* 2004). This is evident for nectar resources in this study, with abundant nectar flowers and evidence of butterflies feeding from nectar plants in re-creation fields (Twiston-Davies *et al. in press*, and Appendix B), but is not evident for the establishment of specialist larval host plants. Additionally, in order for the aim for natural regeneration and development to be fulfilled, enhancement may only occur if specific management to encourage these processes is put in place.

7.1.3 Behaviour of Lepidoptera at habitat and structural boundaries.

The behaviour of individuals is rarely considered as a method to understanding restoration actions despite being an important component in measuring landscape connectivity (Kuefler *et al.* 2010), assessing the viability of metapopulations (Heinz *et al.* 2006) and in assigning appropriate management recommendations (Pickens & Root 2009; Slamova *et al.* 2013). This method enables the understanding of the re-conisation mechanism but alone is not a measure of the effect of restoration actions on biodiversity enhancement or landscape connectivity, methods such as mark and recapture may be more appropriate for measuring connectivity if resources and time are available.

Lepidoptera behaviour at habitat and structural boundaries differs significantly between adjacent land cover types and between ecological and mobility groups in this study. Overall, behaviour at grassland re-creation boundaries with grassland re-creation which is only 1 or 2 years old is significantly different from that for arable for all grassland and intermediate to low mobility groups, indicating that this new habitat can encourage the dispersal of these groups (section 4.4.1 and 4.4.4). Newer grassland re-creation appears to be more beneficial to the open-grass ecological group and sedentary mobility group as evident by a doubling in boundary crossing behaviour (section 4.4.4). However, this is not evident for the herb-rich associated group which appear to be reluctant to leave chalk grassland fragments as lower proportions crossed habitat boundaries and higher proportions followed these boundaries than expected. This is consistent with much research showing that specialist species with low mobility are more sensitive to habitat fragmentation (Henle *et al.* 2004; Ockinger *et al.* 2009; Tscharntke *et al.* 2002) and therefore may potentially benefit from habitat restoration adjacent to habitat fragments.

Boundary crossing and following behaviour is influenced by a combination of nectar resource density and other vegetation characterises, as well as weather conditions and group density (Chapter 4). The occurrence of Lepidoptera in habitat patches is related to nectar and host plant resources (Binzenhofer *et al.* 2005; Clausen *et al.* 2001; Haaland & Bersier 2011; Heer *et al.* 2013; Rusterholz & Erhardt 2000) and some of these variables could be managed for and are discussed below in section (7.2, 7.3).

Mowing has a significant effect on Lepidoptera behaviour, with boundary following behaviour increasing at mown boundaries. This appears to be a result of the change in structure of the grassland, rather than the removal of floral resources, as there was no significant difference between densities of Lepidoptera either side of the mown boundary (section 5.3.3). Structural similarity is a key component in increasing matrix permeability (for reviews see (Eycott *et al.* 2012; Prevedello & Vieira 2010). This illustrates the effect that mowing can have on behaviour and the potential for this to inform management decisions in these types of grassland is discussed in relation to un-mown refuges and the utility of corridors and grassy field margins (7.3, 7.4) which are important for insects in agricultural landscapes (Buri *et al.* 2013; Delattre *et al.* 2013; Dover *et al.* 2010; Humbert *et al.* 2012; Ockinger & Smith 2007b).

7.1.4 Effect of the landscape scale restoration on connectivity of target habitat at the landscape and the wider landscape scales.

The Landscape scale here as defined as the landscape within the 1 km buffer of the boundary of the WHS and the wider landscape as 8 km from the WHS boundary (Chapter 6). The use of landscape metrics have been mainly utilised as indicators of ecosystem functions and land-use change (for example see review by Uuemaa *et al.* 2013) but none have specifically quantified the effect of landscape scale restoration on the biodiversity of the wider landscape. Connectivity between Lepidoptera populations can be measured as the distance between populations and as the permeability of the matrix between populations (Binzenhofer *et al.* 2005; Matter & Roland 2002; Ouin *et al.* 2008; Ricketts 2001; Roland *et al.* 2000). Chapter 6 aimed to calculate connectivity for habitat patches of chalk and neutral grassland using data on the cost-distance of land-cover types and the known Lepidoptera distributions.

There were measurable differences within the Stonehenge landscape and the wider landscape as a result of the landscape restoration project (Chapter 6). Overall the grassland re-creation at the Stonehenge World Heritage Site has increased the area of permanent species-rich grassland by over 500 ha, as well as the number of patches that are over 4 ha in area (section 6.3.3). The restoration project has increased the functional connectivity of the landscape as measured by a decrease in dispersal cost within a buffer of 1 km of the boundary of the WHS (section 6.3.1) and increased the structural connectivity with patches closer together as measured by a reduction in the Nearest

Neighbour Distance by up 100 m within the Landscape (section 6.3.3). Increasing both the functional and structural connectivity of the landscape are important, as the area of habitat patches and their distance from each other determine metapopulation stability (Hanski 1998; Hanski *et al.* 1994; Wiens 1997) and affect landscape scale species richness of arthropods (Hendrickx *et al.* 2007). Additionally, the permeability of the intervening matrix habitat is important for landscape connectivity (Donald & Evans 2006; Eycott *et al.* 2012; Prevedello & Vieira 2010; Ricketts 2001).

At a landscape level(landscape within 1km buffer of the WHS boundary and the wider landscape 8km buffer of the boundary), the restoration project has increased the richness in land cover types and potentially increased the quality of other land cover types by increasing the total core habitat area (6.3.3 and Appendix E). Landscape level heterogeneity Varied habitat types, resources and structure) is important for insect species richness, population stability (Hendrickx *et al.* 2007; Kumar *et al.* 2009; Oliver *et al.* 2010; Steffan-Dewenter & Tscharntke 2002) and the conservation of chalk grasslands (Diacon-Bolli *et al.* 2012). Results also illustrate that the grassland re-creation has limitations; patches within the landscape are still potentially functionally isolated for those species with low dispersal ability due to surrounding high 'cost' matrix types (section 6.3.1). Additionally the grassland network may not have reached the precise ecological conditions of the reference habitat patches required for chalk grassland specialist species to establish, but could still provide resources and enhance connectivity (Deri *et al.* 2011; Diepenbrock & Finke 2013; Donald & Evans 2006; Ockinger & Smith 2007b; Ouin *et al.* 2004).

7.1.5 Recommendations for landscape-scale restoration

The following management recommendations are made based on the findings of this study which have encompassed a range of spatial scales for measuring landscape connectivity and evaluating the effect of restoration on biodiversity and landscape connectivity. These recommendations may be transferable to other landscape-scale restoration projects of species-rich grassland and support existing management recommendations for grassland restoration and the for enhancing the conservation and biodiversity value of landscapes. These recommendations are made based on the overall response of Lepidoptera associated with grassland habitats but no species specific management recommendations are made. This study also highlighted methodological and interpretation limitations and therefore, recommendations for future research avenues are also discussed (section 7.5).

7.2 Habitat boundary management

The behavioural responses of Lepidoptera are examined in Chapters 4 and 5 where an overall significant increase in boundary following and decrease in boundary crossing behaviour is evident at habitat (Chapter 4) and structural boundaries (Chapter 5). This emphasises that conservation measures that take into account Lepidoptera boundary behaviour should be included in management plans, especially when grassland re-creation is located adjacent to reference habitat.

These conservation measures need to be implemented at the field and habitat boundary and should, a) prioritise land adjacent to source habitats for restoration where possible, b) have management designed to increase the botanical similarity of restoration habitat patches to adjacent source habitat, c) to increase the structural heterogeneity (for example, vegetation density) of restoration habitat patches and, d) include corridors buffer, stepping stones or refuges. Management recommendations are detailed below and many of these relate to both the habitat patch/field and the habitat boundary.

The field or habitat patch refers to the area that is under habitat re-creation management which is often categorised as a field and therefore the habitat boundary refers to the edge of and where either two fields meet or where different habitat or land-cover meet. In these contexts, a field or habitat patch is often but not always categorised as being under one land owner or Agri-environment scheme and many of the management recommendations at the habitat boundary are also advocated at the field or habitat patch scales.

7.2.1 a) Prioritise land adjacent to source habitats for restoration

The low permeability of chalk grassland fragments boundaries to all grassland associated Lepidoptera in the Stonehenge Landscape is illustrated in Chapter 4 and indicates that colonisation of new restoration and re-creation habitat patches may be slow if it is not located directly adjacent to source habitats. This is characteristic of re-creation grassland sites where colonisation occurs for species which can easily disperse and that are generalists (Poschlod *et al.* 1998; Pywell *et al.* 2002; Pywell *et al.* 2003; Woodcock *et al.* 2010). Grassland re-creation habitat patches should be located directly adjacent to existing reference habitat where possible, thereby increasing colonisation of less mobile species (Helsen *et al.* 2013; Woodcock *et al.* 2012a). Therefore, this would especially benefit the sedentary mobility species or those in both herb-rich grassland ecological and sedentary mobility groups. Proximity is also discussed in section 7.3.2 but in this section proximity refers to new grassland re-creation to be ideally under 150 m away from the reference is habitat patch (Kohler *et al.* 2008).

7.2.2 b) Management designed to increase botanical similarity of restoration habitat patches to adjacent source habitat

Lepidoptera boundary crossing behaviour increased when chalk grassland fragments were adjacent to grassland re-creation habitat patches which shared similar plant species and vegetation structure, even for re-creation grassland patches that are only 1-2 years old (Chapter 4). This management recommendation is beneficial at the boundary and the field/habitat path scales but here it focuses on the boundaries. Both plant species and vegetation structure could be manipulated through management; by selecting an appropriate seed source or seed mixture and by managing the restoration grassland in a way to reflect the vegetation characteristics of the adjacent chalk grassland fragment (described below and in section 7.3). The density of nectar producing flowers in the Asteraceae and Dipsacaceae families did not significantly affect boundary crossing behaviour (Chapter 4). However, these families are significant drivers of Lepidoptera community compositions, are characteristic of the chalk grassland fragments, abundant in the restoration grasslands and used frequently as sources of nectar (Chapter 3 and Appendix B) (the selection of these are discussed further in section 7.3) and supported by many studies for example, (Binzenhofer *et al.* 2005; Clausen *et al.* 2001).

7.2.3 c) Increase the structural heterogeneity of restoration habitat patches

A varied grazing and mowing regime is recommended at the boundary, patch and landscape scales and is discussed in detail in this section. Mowing and grazing is the main management technique for grasslands, enhancing biodiversity value and controlling ecological succession (Rook *et al.* 2004). Mowing has a significant effect on boundary behaviour for the majority of Lepidoptera observed in this study (Chapter 5) and vegetation height and density is a significant variable explaining Lepidoptera richness and occurrence in the landscape (Chapters 3, 4 and 5). This is because boundaries are more permeable when the adjacent land cover has little contrast in structure or resources when compared to the target habitat (Eycott *et al.* 2012; Prevedello & Vieira 2010) and therefore, grazing and mowing can affect the quality of the habitat and the permeability of the intervening matrix. Mowing is an alternative to grazing in maintaining species-rich calcareous grassland (Kahmen *et al.* 2002), however, combined cattle and sheep grazing increases vegetation heterogeneity and biodiversity (Rook *et al.* 2004) and therefore, varied grazing and mowing should be continued at the Stonehenge WHS. Currently each tenant manages their grassland with their own stock of cattle or sheep (Chapter 2), however, if stock were swapped between tenant farmers within the WHS it could potentially be beneficial to increase structural heterogeneity (varied vegetation height and density) of grassland sward and also increases the dispersal of seeds (Auffret *et al.* 2012; Mouissie *et al.* 2005; Poschlod *et al.* 1998). Late season mowing and grazing is also advocated to allow for the different flowering and seeding times of the different species in the grassland restoration and is recommended for insect conservation in semi natural pastures (Berg *et al.* 2013;

Lenoir & Lennartsson 2010). Additionally low intensity grazing is recommended in order to avoid the negative impacts that grazing can have on the larvae of insects (van Noordwijk *et al.* 2012b) and the loss of other important microhabitats such as plant seed heads and flowers.

7.2.4 d) Refuges and corridors

Leaving permanent and temporary refuges free from mowing and grazing in close proximity to source and restoration habitat edges is an important management strategy as these could connect source habitat to restoration habitat patches if they are not adjacent to one another, or link restoration grassland patches. This recommendation is made based on the results from behaviour studies in Chapters 4 and 5 and it is recommended that these refuges structurally connect to adjacent habitat boundaries. Mobile grassland species can utilise un-mown refuges (Berg *et al.* 2013; Berggren *et al.* 2002; Buri *et al.* 2013; Humbert *et al.* 2012) and therefore a grazing and mowing regime that leaves refuges is advocated. This may be especially vital during times of Lepidoptera life cycle where they may be more vulnerable to disturbance, for example, when Lepidoptera larvae of rare or specialist species are abundant (van Noordwijk *et al.* 2012b). Management options for the implementation of refuges are described in the following section (7.3).

Habitat boundary management summary

Restoration should:

- **a)** Be located adjacent to or in close proximity to existing species-rich grasslands
- **b)** Be managed for resource and structural similarity to adjacent source habitat
- **c)** Have low intensity grazing and mowing regimes designed to increase the structural heterogeneity of vegetation
- **d)** Have un-mown/un-grazed refuges connected to habitat edges

7.3 Field-level management

From this study there are four broad pre-restoration and post-restoration recommendations for field/patch-level management: a) the selection of an appropriate seed source and collection method, b) consideration of the landscape context, c) management objectives designed for heterogeneity and, d) the consideration of linear features.

Field specifically refers to the field which has been or will be sown with grassland seed for habitat re-creation (also habitat patch) In these contexts, a field is often but not always categorised as being under one land owner or Agri-environment scheme.

7.3.1 a) The selection of an appropriate seed source and collection method

Surveys of plants and Lepidoptera indicate that seed brush-harvested directly from the donor habitat patch or from restoration that is at least 3 years old with the appropriate vegetation characteristics is suitable for restoring species-rich grasslands and Lepidoptera communities (Pemberton 2011; Twiston-Davies *et al. in press*; Chapter 3). The effect of restoration on the enhancement of biodiversity and landscape connectivity is limited by the absence of late flowering or low growing plant species characteristic of chalk grasslands which are Lepidoptera larval host plants or nectar sources (Chapter 3; Twiston-Davies *et al. in press*). These include Devil's-bit Scabious (*Succisa pratensis)* and Horseshoe vetch (*Hippocrepis comosa*), the larval host-plants of Marsh Fritillary (*Euphydryas aurinia*) and Adonis blue (*Lysandra bellargus*), respectively as well as high quality nectar sources in the Dipsacaceae, Asteraceae families for example, Small Scabious (*Scabiosa columbaria*) and Greater Knapweed (*Centaurea scabiosa*). These may need to be harvested separately and later added to seed mixtures or planted as plugs.

Other seed collection methods could also be used in combination with brush harvesting which would provide other benefits, for example, the technique of hay spreading in which harvested hay from a target habitat is laid on a receptor site, thereby transferring some invertebrates and larvae to new grasslands (Mortimer *et al.* 2002; Woodcock *et al.* 2008). It is possible that some species may require assisted colonisation if their establishment in new habitats is an aim of the restoration project (for example, species characteristic of the target habitat and or with low dispersal ability).

7.3.2 b) Consideration of the landscape context

For restoration actions to result in improvements in biodiversity measures and landscape connectivity it is important to firstly target areas near existing habitat with high connectivity which would increase the colonisation potential of taxa with a range of mobility groups (specific landscape-scale management is described in section 7.4). Ideally new habitats should be under 150 m away from source or reference habitats (Kohler *et al.* 2008) or if chalk grassland specialist and low mobility species are the target then new habitat re-creation patches should be less than 100m away as *Lysandra bellargus* for example, are unlikely to travel further than this (Thomas 1983) . The opportunistic nature of this restoration project, in which ex-arable fields were brought into the restoration project as the tenant farmers' contracts came up for renewal, has meant that areas adjacent chalk grassland fragments were converted from arable to grassland re-creation later on. This is in contrast to restoration recommendations where firstly existing sites would be enhanced, buffered and expanded for an ecological network (Lawton *et al.* 2010; McIntyre & Hobbs 1999).

7.3.3 c) Management objectives designed for heterogeneity

The results of this study indicate that habitat conditions that could be manipulated through habitat patch management such as vegetation height, nectar flower richness and densities of nectar rich, late flowering species (Dipsacaceae family and *Centaurea scabiosa),* can be as important as the age of the habitat in explaining Lepidoptera occurrence in restoration grasslands (Chapter 3). Many of these are discussed in section 7.2.3 but are further expanded upon in this section with reference to the results in Chapter 3. Although seed source is a vital component, the restoration of plant communities can be limited by the species specific responses to management regimes (Maccherini & Santi 2012). Variation in vegetation density and in the coverage of bare ground significantly explained Lepidoptera community composition in habitat transects and there were-species and group-specific responses to environmental variables relating to nectar resources and vegetation characteristics (Chapter 3). The response of Lepidoptera to the environmental variables is species-specific (Chapter 3), illustrating the importance of managing habitat patches for heterogeneity to accommodate a range of species requirements by increasing the variation in vegetation structure and the available resources. Additionally, management designed for the restoration of plant communities may not have the same effect for insect communities (for example, Woodcock *et al.* 2010) further highlighting the need for heterogeneous management. These management objectives can be achieved through grazing and mowing regimes designed for habitat heterogeneity and the requirements of late flowering species (as also discussed in section 7.2).

7.3.4 d) The consideration of linear features

Grassy linear features are important for Lepidoptera dispersal in agricultural landscapes, increasing connectivity and providing food, roosting and oviposition resources (Delattre *et al.* 2013; Ockinger & Smith 2007b; Ouin *et al.* 2008; Powney *et al.* 2012). This study does not explicitly investigate the utility of linear features in the landscape such as corridors and grassy field margins. However, the boundary following behaviour observed at habitat edges (Chapter 4) implies that this type of management could be effectively used to direct Lepidoptera to functional corridors and uncut refuges (Section 7.2). Agri-environment scheme options at the Stonehenge landscape comprising grassy or forb-rich field margins or pollen and nectar rich for pollinators adjacent to source habitat patches and grassland restoration with varied cutting (not at the same time as the adjacent habitat) is advocated.

Field-scale management summary

Restoration should:

a) Have appropriate selection of seed source, seed collection method and timing
b) Have consideration of the landscape context of restoration habitat patches
c) Be managed to enhance structural heterogeneity of vegetation
d) Include refuges (for example, grassy field margins and linear features)

7.4 Landscape-scale management

At the larger landscape scale, the Stonehenge World Heritage Site (WHS) is situated between Salisbury Plain, Porton Down and Parsonage Down, Sites of Special Scientific Interest and Special Areas of Conservation. The Stonehenge WHS has the potential to contribute to the network of chalk grassland in Wiltshire connecting these important sites.

During this discussion, landscape refers to the Stonehenge World Heritage Site (26,000 ha) and 1 km of its boundary or other landscapes of similar sizes unless the discussion is referring to the wider landscape which is beyond this scale (8 km of the WHS boundary as used in Chapter 6). In this context landscape scale there may be many land owners and land management schemes.

It is vital that conservation actions take account of the wider landscape (Fahrig 2001) and based on the results of this study, a range of management recommendations can be made to increase landscape connectivity within the World Heritage Site and across the surrounding landscape. These recommendations may be transferable to other landscape scale projects such as Nature Improvement Areas, which are being implemented across the UK (Natural England 2014). Management recommendations include, a) increasing the area and quality of all grassland types, b) buffer existing chalk grassland fragments, c) enhancing overall landscape connectivity with targeted management and, d) for restoration to be implemented alongside the enhancement and management of all types of land-cover.

7.4.1 a) Increase the area and quality of all grassland types

The main aim of the grassland restoration project is to increase the area of permanent species-rich grassland across the landscape and this has been fulfilled (Chapter 6). Increasing the area of habitat and reducing the distance to other patches can have the biggest effect on population stability and persistence (Hanski 1998; Hanski *et al.* 1994; Wiens 1997) and affect landscape scale species richness of arthropods (Hendrickx *et al.* 2007), but the quality of the grassland also needs to be enhanced and maintained (Hodgson *et al.* 2011; Thomas *et al.* 2001b). Management to increase the species richness of grasslands in order to provide a variety of larval host plants and nectar sources for a range of insects would be beneficial, as would management that encourages the heterogeneity of these habitats, discussed in previous sections (7.2, 7.3). A large proportion of the Stonehenge landscape is semi-improved grassland which should be included in plans to increase the diversity of the sward using the management recommendation outlined for the grassland re-creation fields.

7.4.2 b) Buffer existing chalk grassland fragments

As discussed in section 7.2, restoration should be targeted adjacent to exiting habitat fragments to increase their size, quality and to enable colonisation. It is recommended that management priority be given to grassland restoration adjacent to existing fragments and that future restoration is located at other habitat fragments, many of these to the south-west of the World Heritage Site are potentially isolated.

7.4.3 c) Enhance overall landscape connectivity with targeted management

Connectivity at the habitat boundary scale and field/habitat patch scale has already been discussed (sections 7.2, 7.3) but as habitat patches need to be functionally connected to act as a network, this means that the adjacent and intervening land cover needs to be managed to increase functional connectivity (Donald & Evans 2006; Tischendorf & Fahrig 2000). The results from Chapter 6 on measuring the landscape connectivity of the Stonehenge WHS illustrates that targeted management based on landscape connectivity analysis would be beneficial. There are three potential targeting strategies; (i) target the matrix areas of highest permeability as they may further enhance connectivity, (ii) target the matrix areas of lowest permeability as they can create new connections, (iii) target areas with intermediate permeability, and (iv) target specific habitat fragments or parts of the network.

Matrix areas which have good functional connectively but could be enhanced include the areas between the chalk grassland expanses on Salisbury Plain to the north of the WHS (Figure 7-1). These areas are mostly arable land and could benefit from targeted Agri-environment and conservation schemes that increase landscape connectivity, such as grassy field margins sown with seed brush harvested from the grassland re-creation fields. Areas of lowest permeability could also be targeted for mitigation actions that reduce the functional isolation of habitat patches with lowest connectivity for example, urban/suburban areas. Finally, particular habitat patches and the adjacent land cover can be targeted for landscape connectivity management that are either most isolated, most connected, intermediate connectivity or have target, characteristic species. For example, the fragments to the south-west of the WHS or fragments such as Full-moon Bank and Luxenborough Bank that have herb-rich grassland associated species that are potential isolated such as *Lysandra bellargus* and *Cupido minimus*. The strategy or combination of strategies used would depend of the objectives and priorities of the stakeholders and what measures are ecologically, socially and financially acceptable.

The configuration of habitat patches are also important for landscape connectivity and can be enhanced and managed even with limited resources the potential configuration of re-creation patches could be carefully targeted to maximise colonisation and connectivity. A method for this is opportunity mapping (Catchpole 2006) which uses some of the methods used in Chapter 6 to explore the trade-offs between patch number, size, location and cost to achieve the best ecological and economic outcomes (e.g. Curran *et al.* 2012; Knight *et al.* 2010; Tambosi *et al.* 2014; Watts *et al.* 2010) and this is recommended for future studies.

7.4.4 d) The enhancement and management of all types of land-cover

The view of habitat as the sole location of the resources that a species requires for all parts of its lifecycle may limit conservation and management recommendations, especially as many resources can be found in the matrix (Dennis *et al.* 2003; Ouin *et al.* 2004). Lepidoptera use different parts of the landscape for different behaviours, activities and resources for example, *Maniola jurtina* used road verges, lanes, hedgerows and grazed and mown fields in the agricultural landscape with verges and lanes used for feeding and meadows for flying (Ouin *et al.* 2004). This makes species specific habitat restoration and habitat re-creation complex if a species requires both the restoration of the habitat and the resources in the matrix. Overall landscape richness and heterogeneity enhance biodiversity (Gossner *et al.* 2013; Hendrickx *et al.* 2007) and this means that restoration needs to consider all types of land-cover and not just target "habitat" land cover type. The management plan highlighted the importance of maintaining areas of arable land for birds and the arable plants (Young *et al.* 2009) and the recording and conservation of these should be implemented.

Landscape connectivity can be increased by grassy field margins in arable land, grassland corridors and temporary uncut refuges through targeted, landscape specific and strategic Agri-environmental schemes options that take account of the landscape configuration (discussed previously). The importance of linear features that connect to habitat boundaries has been discussed in the previous section (7.2) and there is much support for their ecological value for grassland associated butterflies (Delattre *et al.* 2013; Ockinger & Smith 2007b; Powney *et al.* 2012).

Landscape-scale management summary

Restoration should:

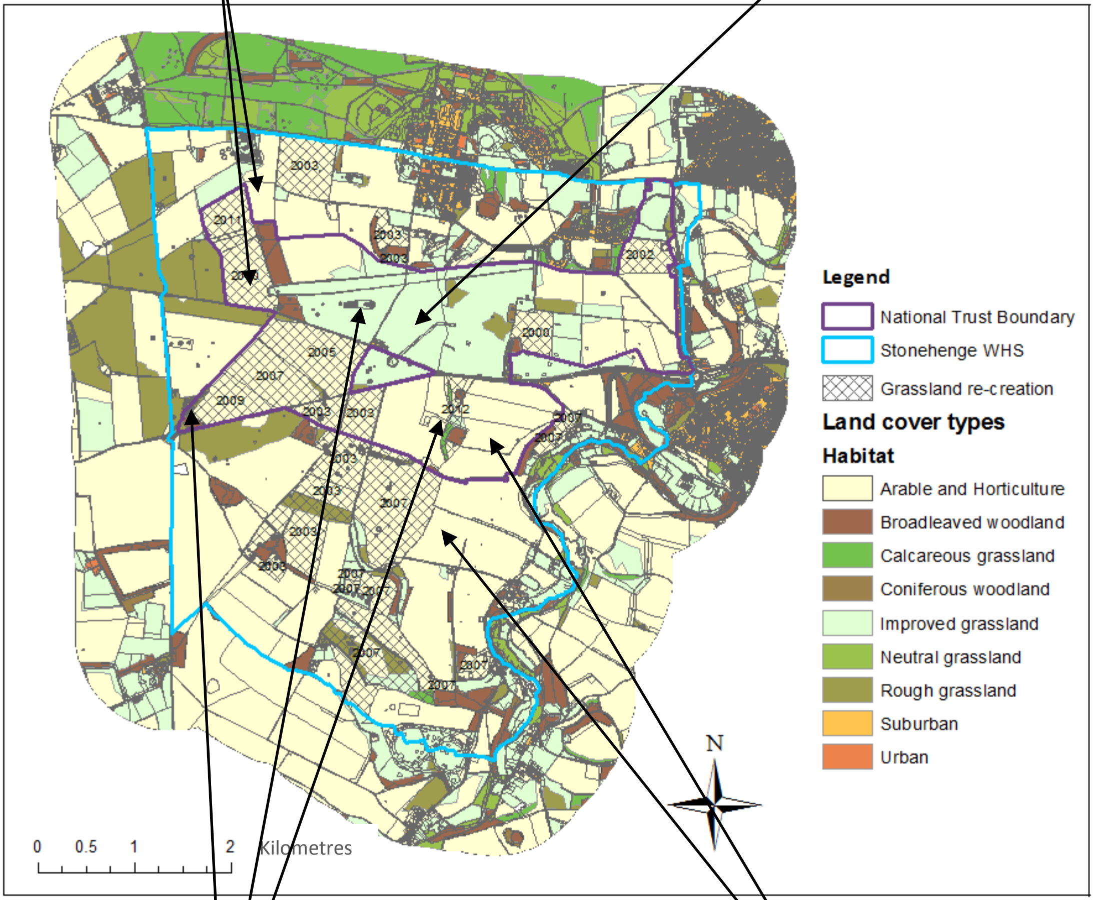
- **a)** Increase the area and quality of all grassland types
- **b)** Buffer existing chalk grassland fragments
- **c)** Enhance overall landscape connectivity with targeted management
- **d)** Be implemented alongside the enhancement and management of all types of land-cover

Newer grassland re-creation

- Prioritise patches adjacent to chalk grassland fragments and older re-creation
- Focus on the NW of the site where Salisbury Plain adjoins the World Heritage Site

Semi-improved pasture

- Varied grazing and mowing regime to increase permeability and disturbance
- Consider management to increase botanical diversity



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Chalk grassland fragments

- Varied grazing and mowing regime to enhance biodiversity
- Focus management on adjacent areas to encourage colonisation

Arable land

- Create grassy field margins using seed brush harvested on site
- Record and manage for rare arable plants

Figure 7-1. Landscape level recommendations for the Stonehenge World Heritage Site (WHS) landscape focussing of chalk grassland fragments, new grassland re-creation, semi-improved pasture and arable land.

7.5 Future research recommendations

The aims of this study covered some of the current knowledge gaps in landscape scale restoration and the results have highlighted the next set of research questions detailed below.

There are a variety of factors that have an impact of the effect of restoration actions on biodiversity enhancement and landscape connectivity. The scale and therefore, objectives of the policy that restoration actions are conducted at can be vital as there is often a mismatch between the scale of ecological processes and the scale of policy and management especially as governance and administrative boundaries are often smaller than large scale ecological processes such as metapopulation dynamics and ecosystem services (Guerrero *et al.* 2013; Henle *et al.* 2010; Young *et al.* 2005). International policies may cover these large scale ecological processes (e.g. Natura 2000 network) but the National (e.g. Sites of Special Scientific Interest) and Local (e.g. Local Nature Reserves) policies may not be effective in increasing biodiversity and landscape connectivity (Lawton *et al.* 2010). There are also the constraints and objectives of the coordination method e.g. Agri-environment schemes and New Environmental Land Management Scheme and these may not benefit all plants and animals (Andersson *et al.* 2013; Pocock *et al.* 2012). Additionally landscape scale restoration requires the collaboration and cooperation of many land owners and stake-holders (Menz *et al.* 2013; Young *et al.* 2005), these will not all have same objectives or training. Also what type of habitat is restored and for what target species can be an crucial factor in whether restoration has a positive effect on the biodiversity and connectivity of the target habitat and organism (Andersson *et al.* 2013; Fuentes-Montemayor *et al.* 2011; Pocock *et al.* 2012).

7.5.1 Are results transferable to all landscape scale grassland restoration in European temperate grasslands?

This study provides an example of a landscape scale grassland restoration project, other examples are available (Conrad & Tischew 2011; Fagan *et al.* 2008; Kiehl *et al.* 2006; Lengyel *et al.* 2012; Piqueray *et al.* 2011; Prach & Walker 2011), but few combine evaluative methods at a range of spatial scales and investigate the colonisation of these new habitats by mobile organisms. It is therefore apparent that future research that investigates the ecological implications of a collection of landscape scale restoration projects together, that evaluates the landscape scale implications of habitat restoration and that uses colonisation data to measure success would be beneficial.

Additional research that focuses on the combined evaluation of landscape scale restoration projects would provide an overview of the application and ecological benefits of restoration techniques at a landscape scale and the subsequent management recommendations. These types of project have to include early input from relevant stakeholders (Land managers, conservation NGOs and policy etc) and clear links to uptake of findings if they are to have real world impact. A meta-analysis of grassland restoration projects and the implications of the results for management is suggested or alternatively, a collaborative research project involving sites of grassland recreation across Europe. This would overcome the limitations of the transferability of conclusions based on the results from a single study area which is recommended for future restoration evaluation (Ruiz-Jaen & Aide 2005).

Future research that investigates the landscape connectivity of existing sites of grassland restoration is also advocated to quantify the impact of landscape scale grassland restoration on the functional connectivity of the wider landscape. This would involve the spatial analysis of maps covering a range of landscape scale restoration projects and evaluating them using some of the methods in this study including cost-distance analysis, habitat landscape metrics and target taxa with different mobility and ecological characteristics.

Current landscape scale restoration projects would benefit from additional research on evaluating the progression of sites by the colonisation of target mobile taxa and the subsequent ecological interactions.

7.5.2 How important is the behaviour of mobile taxa for landscape restoration and connectivity?

The behaviour of mobile organisms at habitat boundaries is a component in measuring and evaluating landscape connectivity (Tischendorf & Fahrig 2000) and metapopulation dynamics (Heinz *et al.* 2006). Therefore more research that includes behavioural research of mobile taxa, more experimental studies and the investigation of behaviour at a range of chalk grassland fragments at more than one study area, area recommended.

Experimental studies that use microcosms to investigate the behaviour of Lepidoptera at habitat, resource and structural boundaries are recommended, (see examples in Bergman *et al.* 2007; Merckx *et al.* 2003). These would benefit from being located using a large study area to increase the replication of experimental plots and to reduce the compounding effects of the surrounding landscape (thus not having the limitation of the study in Chapter 5). Studies that combine a variety of dispersal and behavioural methods are also advocated as behaviour may be best interpreted for conservation actions when used in combination with other methods of mark and recapture and genetic analysis for conservation strategies (Leidner & Haddad 2011). Investigating the behaviour of individuals in the matrix land cover is also advocated as this provides another measure of landscape connectivity (Tischendorf & Fahrig 2000).

Behavioural studies across different restoration projects would offer more replication and comparison and enable transferable and universal management recommendation for grassland restoration projects to be made. A selection of restoration sites across the UK or Europe where behaviour at habitat boundaries and in the matrix could be investigated and compared is recommended.

7.5.3 What sort of targeted restoration measures would be best for enhancing landscape connectivity?

Research into what restoration strategies are best for different landscapes is required. There are guidelines for different types of landscapes depending on the degree of fragmentation and degradation (McIntyre & Hobbs 1999) but these have not been evaluated using a selection of real landscapes.

This research would involve assessing the best set of restorative and management options for a particular landscape by comparing strategies with different aims. For example, at the Stonehenge World Heritage Site, landscape connectivity could measured and compared between best practice recommendations of restorative actions (Lawton *et al.* 2010; McIntyre & Hobbs 1999) with management that targets either sites of, (i) highest matrix permeability, (ii) least permeable or, (iii) intermediate permeability or, (iv) specific habitat patches as described in section (7.4.3). It would also be recommended to compare these to random selection of sites for restoration and to compare landscape connectivity under these scenarios with and without Agri-environment scheme options for grassy field margins in arable land. This has been done using scenarios for woodland (Watts *et al.* 2010) and similar methods could be used.

7.5.4 What should the aim of restoration be?

The effect of restoration measures of biodiversity enhancement and landscape connectivity is commonly measured in the short term as the similarity of diversity, vegetation structure and ecological processes to those of the reference site (Ruiz-Jaen & Aide 2005). However, the effect of restoration in the long term is more complex to measure as requires the presence of functional groups required for long-term stability, resilience to natural disturbances and self-sustainability (SER 2004). The restoration of ecological networks is vital for ecosystem services and the long term stability of these systems although is not always a result from restored communities and is not always measured (Forup *et al.* 2008; Henson *et al.* 2009).

To evaluate restoration projects in these ways requires a long-term commitment to monitoring and highlights that a set of restoration aims for the shot, medium and long term is recommended with measurable goals that combine similarity to reference habitat patches, ecological process and interactions and the long term sustainability. To achieve this collaboration between scientists, land managers and policy makers is required (Menz *et al.* 2013; Young 2000). Additionally, research into future threats to semi-natural grasslands and how this will change management recommendations such as climate change is required as these will need to be adaptively managed in the future (Lindenmayer *et al.* 2008; Poschlod & WallisDeVries 2002).

7.6 Conclusion

This study explored and highlighted landscape connectivity as a key to effective habitat restoration for butterflies in lowland agricultural landscapes. The behaviour of Lepidoptera at habitat and resource boundaries, their species richness and community compositions in restoration habitat and the structural and functional connectivity of the landscape is investigated. The results illustrated that there can be relatively rapid enhancement of biodiversity and landscape connectivity for Lepidoptera associated with grasslands, even new grassland re-creation can increase boundary crossing behaviour and the functional connectivity of the landscape has increased for this group as a result of the restoration project. However, species with low mobility and/or specialist larval host plants that do not establish in the grassland re-creation fields are restricted to the chalk grassland fragments and will require targeted management and conservation in the future to encourage colonisation of new habitats.

This study highlights that a range of management options at the habitat boundary, habitat patch and landscape scales are required to enhance landscape connectivity and thereby increase the rate at which the restoration of habitats at a landscape scale can achieve improvements for the biodiversity of target taxa. Restoration that improves biodiversity and landscape connectivity starts from the selection of appropriate seed source and location of receptor habitat patches, to ongoing targeted management right through to the consideration of the landscape context in which grassland restoration occurs.

Landscape connectivity is important as a connected and diverse landscape is more resilient and adaptable to land-use, ecological, community and climate change. In the UK one mechanism for implementing this is through site specific and targeted Agri-environment schemes. Measures of the effect of restoration on biodiversity and landscape connectivity will need to evolve; currently, for conditions need to represent that of the target habitat. However, for conservation, heterogeneity and adaptation to change are also important and this may call for a paradigm shift in the aims and objectives of habitat restoration.

Landscape scale restoration will require cooperation, collaboration and a shared vision from policy makers, land owners and managers. This collaborative approach is the only successful route given the complexity of landscape scale restoration and the many stakeholders responsible for its future success. Interdisciplinary and pan-European collaborative research into the restoration of habitats at a landscape scale is therefore advocated.

Chapter 8

8.1 Appendix A

8.1.1 Twiston-Davies. G., J. Mitchley, and S. R. Mortimer. 2011. The Stonehenge Landscape Restoration Project- Conservation opportunities for rare butterflies? Aspects of Applied Biology. 108. 259-265.

8.1.2 Twiston-Davies. G., S. R. Mortimer, and J. Mitchley. (*In press*). Restoration of species rich grassland in the Stonehenge World Heritage Site, UK. In: Kiehl. K., (Ed). Guidelines for native seed production and grassland restoration. Cambridge Scholars.

8.2 Appendix B, C, D and E on Disc

Chapter 9 References

Allen, R., and P. Brash. 2008. Nature Conservation Evaluation 2007 Survey. The National Trust. Conservation Directorate, Stonehenge Wiltshire.

Andersson, G. K. S., K. Birkhofer, M. Rundlöf, and H. G. Smith. 2013. Landscape heterogeneity and farming practice alter the species composition and taxonomic breadth of pollinator communities. Basic and Applied Ecology **14**:540-546.

Anon. 1998. Lowland Calcareous grassland. UK Biodiversity group: Tranche 2 Action Plans.

Antwi, E. K., R. Krawczynski, and G. Wiegleb. 2008. Detecting the effect of disturbance on habitat diversity and land cover change in a post-mining area using GIS. Landscape and Urban Planning **87**:22-32.

Asher, J., M. S. Warren, R. Fox, P. T. Harding, G. Jeffcoate, and S. Jeffcoate 2001. The Millennium Atlas of Butterflies of Britain and Ireland. Oxford University Press, Oxford.

Auffret, A. G., R. Schmucki, J. Reimark, and S. A. O. Cousins. 2012. Grazing networks provide useful functional connectivity for plants in fragmented systems. Journal of Vegetation Science **23**:970-977.

Aviron, S., F. Burel, J. Baudry, and N. Schermann. 2005. Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. Agriculture, Ecosystems & Environment **108**:205-217.

Aviron, S., P. Kindlmann, and F. Burel. 2007. Conservation of butterfly populations in dynamic landscapes: The role of farming practices and landscape mosaic. Ecological Modelling **205**:135-145.

Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. Ecography **26**:153-160.

Baguette, M., S. Blanchet, D. Legrand, V. M. Stevens, and C. Turlure. 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews **88**:310-326.

Baguette, M., J. Clobert, and N. Schtickzelle. 2011. Metapopulation dynamics of the bog fritillary butterfly: experimental changes in habitat quality induced negative density-dependent dispersal. Ecography **34**:170-176.

Barbosa, O., and P. A. Marquet. 2002. Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. Oecologia **132**:296-306.

Bartomeus, I., S. G. Potts, I. Steffan-Dewenter, B. E. Vaissiere, M. Woyciechowski, K. M. Krewenka, T. Tscheulin, S. P. M. Roberts, H. Szentgyorgyi, C. Westphal, and R. Bommarco. 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ **2**:e328.

Bartuszevige, A. M., D. L. Gorchov, and L. Raab. 2006. The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. Ecography **29**:213-222.

Batary, P., B. Andras, D. Kleijn, and T. Tscharntke. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proceedings of the Royal Society B-Biological Sciences **278**:1894-1902.

Batary, P., A. Holzschuh, K. M. Orci, F. Samu, and T. Tscharntke. 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. Agriculture Ecosystems & Environment **146**:130-136.

Benini, L., V. Bandini, D. Marazza, and A. Contin. 2010. Assessment of land use changes through an indicator-based approach: A case study from the Lamone river basin in Northern Italy. Ecological Indicators **10**:4-14.

Bennie, J., M. O. Hill, R. Baxter, and B. Huntley. 2006. Influence of slope and aspect on long-term vegetation change in British chalk grasslands. Journal of Ecology **94**:355-368.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution **18**:182-188.

Berg, A., K. Ahrne, E. Ockinger, R. Svensson, and B. Soderstrom. 2011. Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. Biological Conservation **144**:2819-2831.

Berg, A., K. Ahrne, E. Ockinger, R. Svensson, and J. Wissman. 2013. Butterflies in semi-natural pastures and power-line corridors - effects of flower richness, management, and structural vegetation characteristics. Insect Conservation and Diversity **6**:639-657.

Berggren, A., B. Birath, and O. Kindvall. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). Conservation Biology **16**:1562-1569.

Berggren, A., A. Carlson, and O. Kindvall. 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets *Metrioptera roeseli*. Journal of Animal Ecology **70**:663-670.

Bergman, M., K. Gotthard, D. Berger, M. Olofsson, D. J. Kemp, and C. Wiklund. 2007. Mating success of resident versus non-resident males in a territorial butterfly. Proceedings of the Royal Society B-Biological Sciences **274**:1659-1665.

Beyer, L. J., and C. B. Schultz. 2010. Oviposition selection by a rare grass skipper Polites mardon in montane habitats: Advancing ecological understanding to develop conservation strategies. Biological Conservation **143**:862-872.

Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemueller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313**:351-354.

Bink, F. A. 1992. Ecologische atlas van de dagvlinders van Nordwest-Europa. Haarlem Schuyt.

Binzenhofer, B., B. Schroder, B. Strauss, R. Biedermann, and J. Settele. 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths - The example of *Zygaena carniolica* and *Coenonympha arcania*. Biological Conservation **126**:247-259.

Bloom, S. A. 1981. Similarity indeces in community studies - potential pitfalls. Marine Ecology Progress Series **5**:125-128.

Brudvig, L. A. 2011. The restoration of Biodiversity: Where has reserach been and where does it need to go? American Journal of Botany **98**:549-558.

Brudvig, L. A., S. A. Wagner, and E. I. Damschen. 2012. Corridors promote fire via connectivity and edge effects. Ecological Applications **22**:937-946.

Brueckmann, S. V., J. Krauss, and I. Steffan-Dewenter. 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology **47**:799-809.

Bulman, C. R., R. J. Wilson, A. R. Holt, L. G. Bravo, R. I. Early, M. S. Warren, and C. D. Thomas. 2007. Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. Ecological Applications **17**:1460-1473.

Buri, P., R. Arlettaz, and J. Y. Humbert. 2013. Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation. Agriculture Ecosystems & Environment **181**:22-30.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment **2**:529-536.

Calaclura, B., and O. Spinell. 2008. Management of Natura 2000 habitats. 6210 Semi-natural dry grasslands and scrubland facies on calcareous substrates (*Festuco-Brometalia*). European Commission.

Campbell, H. 2009. Monitoring the Success of Calcicolous Grassland Reversion at Stonehenge. School of Biological Sciences. University of Reading, Reading, UK.

Carvalheiro, L. G., W. E. Kunin, and J. C. Biesmeijer. 2013. Species Richness declines and biotic homogenization have slowed down for NW-European pollinators and plants. Ecology Letters **16**:1416-1417.

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. Biological Conservation **103**:33-49.

Catchpole, R. 2006. Planning for Biodiversity- opportunity mapping and habitat networks in practice: a technical guide. English Nature Research Reports No. 687.

Chen, I. C., H. J. Shiu, S. Benedick, J. D. Holloway, V. K. Cheye, H. S. Barlow, J. K. Hill, and C. D. Thomas. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. Proceedings of the National Academy of Sciences of the United States of America **106**:1479-1483.

Chippindale, C. 1983. Stonehenge Complete. Thames and Hudson, Leipzig.

Clausen, H. D., H. B. Holbeck, and J. Reddersen. 2001. Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. Biological Conservation **98**:167-178.

Clobert, J., R. A. Ims, and F. Rousset 2004. Causes, Mechanisms and Consequences of Dispersal In: Hanski. I and Gaggiotti. O. E. 2004. Ecology, Genetics and Evolution of Metapopulations. Elsevier Inc, San Diego.

Collinge, S. K. 2000. Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology **81**:2211-2226.

Conrad, M. K., and S. Tischew. 2011. Grassland restoration in practice: Do we achieve the targets? A case study from Saxony-Anhalt/Germany. Ecological Engineering **37**:1149-1157.

Conradt, L., E. J. Bodsworth, T. J. Roper, and C. D. Thomas. 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implication for metapopulation models. Proceedings of the Royal Society B-Biological Sciences **267**:1505-1570.

Conradt, L., and T. J. Roper. 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: Implications for dispersal. Ecology **87**:125-132.

Cowley, M. J. R., C. D. Thomas, D. B. Roy, R. J. Wilson, J. L. Leon-Cortes, D. Gutierrez, C. R. Bulman, R. M. Quinn, D. Moss, and K. J. Gaston. 2001. Density-distribution relationships in British butterflies. I. The effect of mobility and spatial scale. Journal of Animal Ecology **70**:410-425.

Crawley, M. J. 2007. The R Book. John Wiley and Sons Ltd, Chichester.

Craythorne, R. 2007. Grassland Reversion at Stonehenge- Monitoring and Assessment. School of Biological Sciences. University of Reading, Reading, UK.

Cristescu, R. H., J. Rhodes, C. Frere, and P. B. Banks. 2013. Is restoring flora the same as restoring fauna? Lessons learned from koalas and mining rehabilitation. Journal of Applied Ecology **50**:423-431.

Crofts, A., and R. G. Jefferson. 1999. The Lowland Grassland Management Handbook (2nd edition). English Nature/The Wildlife Trusts.

Curran, P., D. Smedley, P. Thompson, and A. T. Knight. 2012. Mapping restoration opportunity for collaborating with land managers in a carbon credit-funded restoration program in the Makana municipality, Eastern Cape, South Africa. Restoration Ecology **20**:56-64.

Darvill, T. 2007. Stonehenge the Biography of a Landscape. Tempus, Stroud.

Davies, H., T. M. Brereton, D. B. Roy, and R. Fox. 2007. Government targets for protected area management: will threatened butterflies benefit? Biodiversity and Conservation **16**:3719-3736.

Davies, K. F., C. R. Margules, and K. F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? Ecology **81**:1450-1461.

Davis, J. D., D. M. Debinski, and B. J. Danielson. 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecology **22**:1341-1354.

de Bello, F., J. N. Price, T. Münkemüller, J. Liira, M. Zobel, W. Thuiller, P. Gerhold, L. Götzenberger, S. Lavergne, J. Lepš, K. Zobel, and M. Pärtel. 2012. Functional species pool framework to test for biotic effects on community assembly. Ecology **93**:2263-2273.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342-355.

DEFRA. 2009. England biodiversity strategy indicators- A1 (b) populations of butterflies on farmland in England.

Delattre, T., F. Burel, A. Humeau, V. M. Stevens, P. Vernon, and M. Baguette. 2010a. Dispersal mood revealed by shifts from routine to direct flights in the meadow brown butterfly Maniola jurtina. Oikos **119**:1900-1908.

Delattre, T., J.-B. Pichancourt, F. Burel, and P. Kindlmann. 2010b. Grassy field margins as potential corridors for butterflies in agricultural landscapes: A simulation study. Ecological Modelling **221**:370-377.

Delattre, T., P. Vernon, and F. Burel. 2013. An agri-environmental scheme enhances butterfly dispersal in European agricultural landscapes. Agriculture Ecosystems & Environment **166**:102-109.

Dennis, R. L. H., J. G. Hodgson, R. Grenyer, T. G. Shreeve, and D. B. Roy. 2004. Host plants and butterfly biology. Do host-plant strategies drive butterfly status? Ecological Entomology **29**:12-26.

Dennis, R. L. H., T. G. Shreeve, and H. Van Dyck. 2003. Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos **102**:417-426.

Deri, E., T. Magura, R. Horvath, M. Kisfali, G. Ruff, S. Lengyel, and B. Tothmeresz. 2011. Measuring the short-term success of grassland restoration: the use of habitat affinity indices in ecological restoration. Restoration Ecology **19**:520-528.

Diacon-Bolli, J., T. Dalang, R. Holderegger, and M. Bürgi. 2012. Heterogeneity fosters biodiversity: Linking history and ecology of dry calcareous grasslands. Basic and Applied Ecology **13**:641-653.

Diamond, S. E., A. M. Frame, R. A. Martin, and L. B. Buckley. 2011. Species' traits predict phenological responses to climate change in butterflies. Ecology **92**:1005-1012.

Diekotter, T., R. Billeter, and T. O. Crist. 2008. Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. Basic and Applied Ecology **9**:298-307.

Diepenbrock, L. M., and D. L. Finke. 2013. Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. Insect Conservation and Diversity **6**:671-679.

Doerr, V. A. J., T. Barrett, and E. D. Doerr. 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson *et al.* Journal of Applied Ecology **48**:143-147.

Donald, P. F., and A. D. Evans. 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. Journal of Applied Ecology **43**:209-218.

Dover, J., and J. Settele. 2009. The influences of landscape structure on butterfly distribution and movement: a review. Journal of Insect Conservation **13**:3-27.

Dover, J. W., and G. L. A. Fry. 2001. Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape. Entomologia Experimentalis Et Applicata **100**:221-233.

Dover, J. W., A. Rescia, S. Fungarino, J. Fairburn, P. Carey, P. Lunt, R. L. H. Dennis, and C. J. Dover. 2010. Can hay harvesting detrimentally affect adult butterfly abundance? Journal of Insect Conservation **14**:413-418.

Driscoll, D. A., and T. Weir. 2005. Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. Conservation Biology **19**:182-194.

Duelli, P., and M. K. Obrist. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology **4**:129-138.

Ebeling, A., A. M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos **117**:1808-1815.

ECNC. 2010. European Centre for Nature Conservation. http://www.ecnc.org. Date accessed 09/09/2010.

Edwards, A. R., S. R. Mortimer, C. S. Lawson, D. B. Westbury, S. J. Harris, B. A. Woodcock, and V. K. Brown. 2007. Hay strewing, brush harvesting of seed and soil disturbance as tools for the enhancement of botanical diversity in grasslands. Biological Conservation **134**:372-382.

European Commission. 2014. From Land Cover to Landscape Diversity in the European Union. http://ec.europa.eu/agriculture/publi/landscape. Date accessed 20/08/2014.

European Commission. 2014. About Corine Land Cover. http://ec.europa.eu/agriculture/publi/landscape/about.htm. Date acccessed 20/08/2014.

Ewers, R. M., S. Thorpe, and R. K. Didham. 2007. Synergistic interactions between edge and area effects in a heavily fragmented landscape. Ecology **88**:96-106.

Eycott, A. E., M. Marzano, and K. Watts. 2011. Filling evidence gaps with expert opinion: The use of Delphi analysis in least-cost modelling of functional connectivity. Landscape and Urban Planning **103**:400-409.

Eycott, A. E., G. B. Stewart, L. M. Buyung-Ali, D. E. Bowler, K. Watts, and A. S. Pullin. 2012. A meta-analysis on the impact of different matrix structures on species movement rates. Landscape Ecology **27**:1263-1278.

Fagan, K. C., R. F. Pywell, J. M. Bullock, and R. H. Marrs. 2008. Do restored calcareous grasslands on former arable fields resemble ancient targets? The effect of time, methods and environment on outcomes. Journal of Applied Ecology **45**:1293-1303.

Fagan, K. C., R. F. Pywell, J. M. Bullock, and R. H. Marrs. 2010. The seed banks of English lowland calcareous grasslands along a restoration chronosequence. Plant Ecology **208**:199-211.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation **100**:65-74.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography **40**:1649-1663.

Fibrophos. 2014. http://www.fibrophos.co.uk. Date accessed 01/03/2014.

Filz, K. J., J. O. Engler, J. Stoffels, M. Weitzel, and T. Schmitt. 2013. Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands in south-western Germany. Biodiversity and Conservation **22**:2223-2241.

Fleishman, E., C. Ray, P. Sjogren-Gulve, C. L. Boggs, and D. D. Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology **16**:706-716.

Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. Journal of Applied Ecology **45**:742-752.

Fox, R., M. S. Warren, J. Asher, T. Brereton, and D. Roy. 2007. The state of Britain's butterflies 2007, Wareham, Dorset, UK.

Frampton, G. K., T. Cilgi, G. L. A. Fry, and S. D. Wratten. 1995. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera, Carabidae) on farmland. Biological Conservation **71**:347-355.

Fuentes-Montemayor, E., D. Goulson, and K. J. Park. 2011. The effectiveness of agri-environment schemes for the conservation of farmland moths: assessing the importance of a landscape-scale management approach. Journal of Applied Ecology **48**:532-542.

Fuller, R. M. 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: A review of grassland surveys 1930–1984. Biological Conservation **40**:281-300.

Gibbs, M., C. J. Breuker, and H. Van Dyck. 2010. Flight during oviposition reduces maternal egg provisioning and influences offspring development in *Pararge aegeria* (L.). Physiological Entomology **35**:29-39.

Gibbs, M., and H. Van Dyck. 2009. Reproductive plasticity, oviposition site selection, and maternal effects in fragmented landscapes. Behavioral Ecology and Sociobiology **64**:1-11.

Gibbs, M., and H. Van Dyck. 2010. Butterfly flight activity affects reproductive performance and longevity relative to landscape structure. Oecologia (Berlin) **163**:341-350.

Gonzalez-Varo, J. P., J. C. Biesmeijer, R. Bommarco, S. G. Potts, O. Schweiger, H. G. Smith, I. Steffan-Dewenter, H. Szentgyoergyi, M. Woyciechowski, and M. Vila. 2013. Combined effects of global change pressures on animal-mediated pollination. Trends in Ecology & Evolution **28**:524-530.

Goodwin, B. J., and L. Fahrig. 2002. How does landscape structure influence landscape connectivity? Oikos **99**:552-570.

Gossner, M. M., S. Getzin, M. Lange, E. Pašalić, M. Türke, K. Wiegand, and W. W. Weisser. 2013. The importance of heterogeneity revisited from a multiscale and multitaxa approach. Biological Conservation **166**:212-220.

Guerrero, A. M., R. R. J. McAllister, J. Corcoran, and K. A. Wilson. 2013. Scale mismatches, conservation planning, and the value of social-network analyses. Conservation Biology **27**:35-44.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. 2013. Predicting species distributions for conservation decisions. Ecology Letters **16**:1424-1435.

Gurnell, J., S. P. Rushton, P. W. W. Lurz, A. W. Sainsbury, P. Nettleton, M. D. F. Shirley, C. Bruemmer, and N. Geddes. 2006. Squirrel poxvirus: Landscape scale strategies for managing disease threat. Biological Conservation **131**:287-295.

Gustafson, E. J., and G. R. Parker. 1994. Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning **29**:117-130.

Gutierrez, D. 2005. Effectiveness of existing reserves in the long-term protection of a regionally rare butterfly. Conservation Biology **19**:1586-1597.

Haaland, C., and L. F. Bersier. 2011. What can sown wildflower strips contribute to butterfly conservation?: an example from a Swiss lowland agricultural landscape. Journal of Insect Conservation **15**:301-309.

Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. Ecological Applications **9**:612-622.

Haddad, N. M., and J. J. Tewksbury. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecological Applications **15**:250-257.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea-cinxia*. Ecology **75**:747-762.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature **404**:755-758.

Hardy, P. B., T. H. Sparks, N. J. B. Isaac, and R. L. H. Dennis. 2007. Specialism for larval and adult consumer resources among British butterflies: implications for conservation. Biological Conservation **138**:440-452.

Haynes, K. J., and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. Ecology **84**:2856-2866.

Haynes, K. J., and J. T. Cronin. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos **113**:43-54.

Haynes, K. J., T. Diekotter, and T. O. Crist. 2007a. Resource complementation and the response of an insect herbivore to habitat area and fragmentation. Oecologia **153**:511-520.

Haynes, K. J., F. P. Dillemuth, B. J. Anderson, A. S. Hakes, H. B. Jackson, S. E. Jackson, and J. T. Cronin. 2007b. Landscape context outweighs local habitat quality in its effects on herbivore dispersal and distribution. Oecologia **151**:431-441.

Heath, J. H., and A. M. Emmet 1985. The Moths and Butterlies of Great Britain and Ireland: Cossidae to Heliodinidae. Harley Books.

Heer, P., J. Pellet, A. Sierro, and R. Arlettaz. 2013. Evidence-based assessment of butterfly habitat restoration to enhance management practices. Biodiversity and Conservation **22**:239-252.

Heinz, S. K., C. Wissel, and K. Frank. 2006. The viability of metapopulations: individual dispersal behaviour matters. Landscape Ecology **21**:77-89.

Helsen, K., M. Hermy, and O. Honnay. 2013. Spatial isolation slows down directional plant functional group assembly in restored semi-natural grasslands. Journal of Applied Ecology **50**:404-413.

Hendrickx, F., J. P. Maelfait, W. Van Wingerden, O. Schweiger, M. Speelmans, S. Aviron, I. Augenstein, R. Billeter, D. Bailey, R. Bukacek, F. Burel, T. Diekotter, J. Dirksen, F. Herzog, J. Liira, M. Roubalova, V. Vandomme, and R. Bugter. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44**:340-351.

Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. Biodiversity and Conservation **13**:207-251.

Henle, K., W. Kunin, O. Schweiger, D. S. Schmeller, V. Grobelnik, Y. Matsinos, J. Pantis, L. Penev, S. G. Potts, I. Ring, J. Simila, J. Tzanopoulos, S. van den Hove, M. Baguette, J. Clobert, L. Excoffier, E. Framstad, M. Grodzinska-Jurczak, S. Lengyel, P. Marty, A. Moilanen, E. Porcher, D. Storch, I. Steffan-Dewenter, M. T. Sykes, M. Zobel, and J. Settele. 2010. Securing the conservation of biodiversity across administrative levels and spatial, temporal, and ecological scales-research needs and approaches of the SCALES project. Gaia-Ecological Perspectives for Science and Society **19**:187-193.

Henson, K. S. E., P. G. Craze, and J. Memmott. 2009. The restoration of parasites, parasitoids, and pathogens to heathland communities. Ecology **90**:1840-1851.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology **12**:450-455.

Hill, J. K., C. D. Thomas, R. Fox, M. G. Telfer, S. G. Willis, J. Asher, and B. Huntley. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. Proceedings of the Royal Society of London Series B-Biological Sciences **269**:2163-2171.

Hobbs, R. J. 2007. Setting effective and realistic restoration goals: Key directions for research. Restoration Ecology **15**:354-357.

Hodgson, J. A., A. Moilanen, B. A. Wintle, and C. D. Thomas. 2011. Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology **48**:148-152.

Hodgson, J. A., C. D. Thomas, B. A. Wintle, and A. Moilanen. 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology **46**:964-969.

Hodgson, J. G., J. P. Grime, P. J. Wilson, K. Thompson, and S. R. Band. 2005. The impacts of agricultural change (1963-2003) on the grassland flora of Central England: processes and prospects. Basic and Applied Ecology **6**:107-118.

Hughes, C. L., J. K. Hill, and C. Dytham. 2003. Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:S147-S150.

Humbert, J.-Y., J. Ghazoul, N. Richner, and T. Walter. 2012. Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. Biological Conservation **152**:96-101.

Jacquemyn, H., C. Van Mechelen, R. Brys, and O. Honnay. 2011. Management effects on the vegetation and soil seed bank of calcareous grasslands: An 11-year experiment. Biological Conservation **144**:416-422.

Jauker, F., T. Diekotter, F. Schwarzbach, and V. Wolters. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology **24**:547-555.

JNCC 1990. Handbook for phase 1 habitat survey.

JNCC. 2010. Joint Nature Conservation Committee. http://www.jncc.gov.uk. Date accessed 11/06/2010.

Kahmen, S., P. Poschlod, and K. F. Schreiber. 2002. Conservation management of calcareous grasslands. Changes in plant species composition and response of functional traits during 25 years. Biological Conservation **104**:319-328.

Kalarus, K., P. Skorka, and P. Nowicki. 2013. Resource use in two contrasting habitat types raises different challenges for the conservation of the dryad butterfly *Minois dryas*. Journal of Insect Conservation **17**:777-786.

Keller, D., M. J. van Strien, M. Herrmann, J. Bolliger, P. J. Edwards, J. Ghazoul, and R. Holderegger. 2013. Is functional connectivity in common grasshopper species affected by fragmentation in an agricultural landscape? Agriculture Ecosystems & Environment **175**:39-46.

Kiehl, K., A. Kirmer, T. W. Donath, L. Rasran, and N. Hölzel. 2010. Species introduction in restoration projects –evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. Basic and Applied Ecology **11**:285-299.

Kiehl, K., and J. Pfadenhauer. 2007. Establishment and persistence of target species in newly created Calcareous grasslands on former arable fields. Plant Ecology **189**:31-48.

Kiehl, K., A. Thormann, and J. Pfadenhauer. 2006. Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. Restoration Ecology **14**:148-156.

King, C., G. Ballantyne, and P. G. Willmer. 2013. Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. Methods in Ecology and Evolution **4**:811-818.

Kleijn, D., and F. van Langevelde. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology **7**:201-214.

Knight, A. T., R. M. Cowling, M. Difford, and B. M. Campbell. 2010. Mapping human and social dimensions of conservation opportunity for the scheduling of conservation action on private land. Conservation Biology. **24**:1348-1358.

Kohler, F., J. Verhulst, R. van Klink, and D. Kleijn. 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology **45**:753-762.

Komonen, A., A. Grapputo, V. Kaitala, J. S. Kotiaho, and J. Paivinen. 2004. The role of niche breadth, resource availability and range position on the life history of butterflies. Oikos **105**:41-54.

Korpela, E. L., T. Hyvonen, S. Lindgren, and M. Kuussaari. 2013. Can pollination services, species diversity and conservation be simultaneously promoted by sown wildflower strips on farmland? Agriculture Ecosystems & Environment **179**:18-24.

Kuefler, D., B. Hudgens, N. M. Haddad, W. F. Morris, and N. Thurgate. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology **91**:944-950.

Kumar, S., S. E. Simonson, and T. J. Stohlgren. 2009. Effects of spatial heterogeneity on butterfly species richness in Rocky Mountain National Park, CO, USA. Biodiversity and Conservation **18**:739-763.

Langmaid, J. R., A. M. Emmet, and J. H. Heath 1989. The Butterflies of Great Britain and Ireland: Hesperiidae-Nymphalidae. Harley Books.

Larsen, T. H., N. M. Williams, and C. Kremen. 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters **8**:538-547.

Lawson, C. R., J. Bennie, J. A. Hodgson, C. D. Thomas, and R. J. Wilson. 2014. Topographic microclimates drive microhabitat associations at the range margin of a butterfly. Ecography **37**:732-740.

Lawson, C. R., J. J. Bennie, C. D. Thomas, J. A. Hodgson, and R. J. Wilson. 2012. Local and landscape management of an expanding range margin under climate change. Journal of Applied Ecology **49**:552-561.

Lawton, J. H., P. N. M. Brotherton, V. K. Brown, C. Elphick, A. Fitter, J. Forshaw, R. W. Haddow, S. Hilborne, R. N. Leafe, G. M. Mace, M. P. Southgate, W. J. Sutherland, T. E. Tew, J. Varley, and

G. R. Wynne. 2010. Making Space for Nature: a review of England's wildlife sites and ecological network. Report to Defra. UK.

Leidner, A. K., and N. Haddad. 2011. Combiningmeasures of dispersal to identify conservation strategies in fragmented landscapes. Conservation Biology **25**:1022-1031.

Lengyel, S., K. Varga, B. Kosztyi, L. Lontay, E. Deri, P. Torok, and B. Tothmeresz. 2012. Grassland restoration to conserve landscape-level biodiversity: a synthesis of early results from a large-scale project. Applied Vegetation Science **15**:264-276.

Lenoir, L., and T. Lennartsson. 2010. Effects of timing of grazing on arthropod communities in semi-natural grasslands. Journal of Insect Science **10**.

Li, H., D. Li, T. Li, Q. Qiao, J. Yang, and H. Zhang. 2010. Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake-case study of Wolong Nature Reserve in China. Ecological Modelling **221**:944-952.

Lindborg, R., J. Bengtsson, Å. Berg, S. A. O. Cousins, O. Eriksson, T. Gustafsson, K. P. Hasund, L. Lenoir, A. Pihlgren, E. Sjödin, and M. Stenseke. 2008. A landscape perspective on conservation of semi-natural grasslands. Agriculture, Ecosystems & Environment **125**:213-222.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. M. Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters **11**:78-91.

MacArthur, R. H., and E. O. Wilson 1967. The theory of island biogeography. Princeton University Press.

Maccherini, S., and E. Santi. 2012. Long-term experimental restoration in a calcareous grassland: identifying the most effective restoration strategies. Biological Conservation **146**:123-135.

MAGIC. 2014. http://magic.gov.uk. Date accessed 14/01/2014.

Major, R. E., F. J. Christie, G. Gowing, G. Cassis, and C. A. M. Reid. 2003. The effect of habitat configuration on arboreal insects in fragmented woodlands of south-eastern Australia. Biological Conservation **113**:35-48.

Marini, L., E. Öckinger, K.-O. Bergman, B. Jauker, J. Krauss, M. Kuussaari, J. Pöyry, H. G. Smith, I. Steffan-Dewenter, and R. Bommarco. 2013. Contrasting effects of habitat area and connectivity on evenness of pollinator communities. Ecography **37**:544-551.

Matter, S. F., and J. Roland. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. Ecological Entomology **27**:308-316.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4:Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachsetts, Amherst. Available at the following web site: http//www.umass.edu/landeco/research/fragstats/fragstats.html. Date accessed 09/01/2014.

McIntyre, S., and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conservation Biology **13**:1282-1292.

Menendez, R., D. Gutierrez, and C. D. Thomas. 2002. Migration and Allee effects in the six-spot burnet moth *Zygaena filipendulae*. Ecological Entomology **27**:317-325.

Menz, M. H. M., K. W. Dixon, and R. J. Hobbs. 2013. Hurdles and Opportunities for Landscape-Scale Restoration. Science **339**:526-527.

Menz, M. H. M., R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends in Plant Science **16**:4-12.

Merckx, T., R. E. Feber, R. L. Dulieu, M. C. Townsend, M. S. Parsons, N. A. D. Bourn, P. Riordan, and D. W. MacDonald. 2009. Effect of field margins on moths depends on species mobility: field-based evidence for landscape-scale conservation. Agriculture Ecosystems & Environment **129**:302-309.

Merckx, T., and H. Van Dyck. 2007. Habitat fragmentation affects habitat-finding ability of the speckled wood butterfly, *Pararge aegeria* L. Animal Behaviour **74**:1029-1037.

Merckx, T., H. Van Dyck, B. Karlsson, and O. Leimar. 2003. The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies. Proceedings of the Royal Society of London Series B-Biological Sciences **270**:1815-1821.

Mitchell, M. G. E., E. M. Bennett, and A. Gonzalez. 2013. Linking landscape connectivity and ecosystem service provision: current knowledge and research gaps. Ecosystems **16**:894-908.

Mitchley, J., I. Jongepierova, and K. Fajmon. 2012. Regional seed mixtures for the re-creation of species-rich meadows in the White Carpathian Mountains: results of a 10-yr experiment. Applied Vegetation Science **15**:253-263.

Mitchley, J., and P. Xofis. 2005. Landscape structure and management regime as indicators of calcareous grassland habitat condition and species diversity. Journal for Nature Conservation **13**:171-183.

Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: Effects of habitat quality and landscape structure. Ecology **79**:2503-2515.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology **83**:1131-1145.

Mortimer, S. R., R. G. Booth, S. J. Harris, and V. K. Brown. 2002. Effects of initial site management on the Coleoptera assemblages colonising newly established chalk grassland on ex-arable land. Biological Conservation **104**:301-313.

Morton, D., C. Rowland, C. Wood, L. Meek, C. Marston, G. Smith, and I. C. Simpson. 2011. CS Technical Report No 11/07 NERC/Centre for Ecology and Hydrology (CEH project number: C03259).

Mouissie, A. M., P. Vos, H. M. C. Verhagen, and J. P. Bakker. 2005. Endozoochory by free-ranging, large herbivores: Ecological correlates and perspectives for restoration. Basic and Applied Ecology **6**:547-558.

Natura England. 2008. Lowland calcareous grassland BAP priority habitat inventory for England. version 2.0.1.

Natural England. 2012. Assessing whether created or restored grassland is BAP Priority Habitat in Natural England Technical Information Note 110.

Natural England. 2014. Nature Improvement Areas (NIAs). Page Overview on Nature Improvement Areas. http://www.naturalengland.org.uk/ourwork/conservation/biodiversity/funding/nia/default.aspx. Date accessed 06/01/2014.

Naumann, C. M., G. M. Tarmann, and W. G. Tremewan 1999. The Western Palaearctic Zygaenidae. Apollo Books.

NCC (Nature Conservation Committee). 1986. The Management of Chalk Grasslands for Butterflies. (JNCC) Focus on nature conservation.

Nieminen, M., H. Rita, and P. Uuvana. 1999. Body size and migration rate in moths. Ecography **22**:697-707.

Ockinger, E., K.-O. Bergman, M. Franzen, T. Kadlec, J. Krauss, M. Kuussaari, J. Poyry, H. G. Smith, I. Steffan-Dewenter, and R. Bommarco. 2012. The landscape matrix modifies the effect of habitat fragmentation in grassland butterflies. Landscape Ecology **27**:121-131.

Ockinger, E., M. Franzen, M. Rundlof, and H. G. Smith. 2009. Mobility-dependent effects on species richness in fragmented landscapes. Basic and Applied Ecology **10**:573-578.

Ockinger, E., and H. G. Smith. 2007a. Asymmetric dispersal and survival indicate population sources for grassland butterflies in agricultural landscapes. Ecography **30**:288-298.

Ockinger, E., and H. G. Smith. 2007b. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology **44**:50-59.

Ockinger, E., and H. Van Dyck. 2012. Landscape Structure Shapes Habitat Finding Ability in a Butterfly. PLoS One **7**.

Oliver, T., D. B. Roy, J. K. Hill, T. Brereton, and C. D. Thomas. 2010. Heterogeneous landscapes promote population stability. Ecology Letters **13**:473-484.

Ouin, A., S. Aviron, J. Dover, and F. Burel. 2004. Complementation/supplementation of resources for butterflies in agricultural landscapes. Agriculture Ecosystems & Environment **103**:473-479.

Ouin, A., M. Martin, and F. Burel. 2008. Agricultural landscape connectivity for the meadow brown butterfly (*Maniola jurtina*). Agriculture Ecosystems & Environment **124**:193-199.

Ovaskainen, O., A. D. Smith, J. L. Osborne, D. R. Reynolds, N. L. Carreck, A. P. Martin, K. Niitepold, and I. Hanski. 2008. Tracking butterfly movements with harmonic radar reveals an effect of population age on movement distance. Proceedings of the National Academy of Sciences of the United States of America **105**:19090-19095.

Pacha, M. J., and S. Petit. 2008. The effect of landscape structure and habitat quality on the occurrence of *Geranium sylvaticum* in fragmented hay meadows. Agriculture, Ecosystems & Environment **123**:81-87.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology **13**:1860-1872.

Pe'er, G., M. A. Tsianou, K. W. Franz, Y. G. Matsinos, A. D. Mazaris, D. Storch, L. Kopsova, J. Verboom, M. Baguette, V. M. Stevens, and K. Henle. 2014. Toward better application of minimum area requirements in conservation planning. Biological Conservation **170**:92-102.

Pemberton, C. 2011. Monitoring the success of Chalk Grassland Restoration in the Stonehenge Landscape. School of Biological Sciences. University of Reading, Reading, UK.

Pfadenhauer, J. 2001. Some remarks on the socio-cultural background of restoration ecology. Restoration Ecology **9**:220-229.

Pickens, B. A., and K. V. Root. 2009. Behavior as a tool for assessing a managed landscape: a case study of the Karner blue butterfly. Landscape Ecology **24**:243-251.

Piqueray, J., G. Bottin, L.-M. Delescaille, E. Bisteau, G. Colinet, and G. Mahy. 2011. Rapid restoration of a species-rich ecosystem assessed from soil and vegetation indicators: The case of calcareous grasslands restored from forest stands. Ecological Indicators **11**:724-733.

Pither, J., and P. D. Taylor. 1998. An experimental assessment of landscape connectivity. Oikos **83**:166-174.

Plue, J., and S. A. O. Cousins. 2013. Temporal dispersal in fragmented landscapes. Biological Conservation **160**:250-262.

Pocock, M. J. O., D. M. Evans, and J. Memmott. 2012. The robustness and restoration of a network of ecological networks. Science **335**:973-977.

Pollard, E., and T. J. Yates 1993. Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme. Springer.

Poschlod, P., S. Kiefer, U. Trankle, S. Fischer, and S. Bonn. 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. Applied Vegetation Science **1**:75-90.

Poschlod, P., and M. F. WallisDeVries. 2002. The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. Biological Conservation **104**:361-376.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25**:345-353.

Powney, G. D., L. K. Broaders, and T. H. Oliver. 2012. Towards a measure of functional connectivity: local synchrony matches small scale movements in a woodland edge butterfly. Landscape Ecology **27**:1109-1120.

Prach, K., I. Jongepierova, and K. Rehounkova. 2013. Large-scale restoration of dry grasslands on ex-arable land using a regional seed mixture: establishment of target species. Restoration Ecology **21**:33-39.

Prach, K., and L. R. Walker. 2011. Four opportunities for studies of ecological succession. Trends in Ecology & Evolution **26**:119-123.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation **19**:1205-1223.

Proença, V., and H. M. Pereira. 2013. Species–area models to assess biodiversity change in multi-habitat landscapes: the importance of species habitat affinity. Basic and Applied Ecology **14**:102-114.

Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences of the United States of America **105**:20770-20775.

Pywell, R. F., J. Bullock, D. Roy, P. Rothery, L. Warman, P. Bellamy, and K. Walker. 1999. A review of the ecological characteristics of wildflower species in relation to the sucess of restoration. Institute of Terrestrial Ecology, Centre for Ecology and Hydrology.

Pywell, R. F., J. M. Bullock, A. Hopkins, K. J. Walker, T. H. Sparks, M. J. W. Burke, and S. Peel. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied Ecology **39**:294-309.

Pywell, R. F., J. M. Bullock, D. B. Roy, L. I. Z. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. Journal of Applied Ecology **40**:65-77.

Pywell, R. F., M. S. Heard, R. B. Bradbury, S. Hinsley, M. Nowakowski, K. J. Walker, and J. M. Bullock. 2012. Wildlife-friendly farming benefits rare birds, bees and plants. Biology Letters **8**:772-775.

Racz, I. A., E. Deri, M. Kisfali, Z. Batiz, K. Varga, G. Szabo, and S. Lengyel. 2013. Early changes of orthopteran assemblages after grassland restoration: a comparison of space-for-time substitution versus repeated measures monitoring. Biodiversity and Conservation **22**:2321-2335.

Rakosy, L., and T. Schmitt. 2011. Are butterflies and moths suitable ecological indicator systems for restoration measures of semi-natural calcareous grassland habitats? Ecological Indicators **11**:1040-1045.

R Core Team. 2010. R: A language for statistical computing. R Foundation for statistical computing. Version 2.12.0. URL http://www.R-project.org., Vienna, Austria.

R Core Team. 2013. R: A language for statistical computing. R Foundation for statistical computing. Version 3.0.0. URL http://www.R-project.org, Vienna, Austria.

Reeve, J. D., J. T. Cronin, and K. J. Haynes. 2008. Diffusion models for animals in complex landscapes: incorporating heterogeneity among substrates, individuals and edge behaviours. Journal of Animal Ecology **77**:898-904.

Renton, M., N. Shackelford, and R. J. Standish. 2012. Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. Global Change Biology **18**:2057-2070.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist **158**:87-99.

Riedinger, V., M. Renner, M. Rundlof, I. Steffan-Dewenter, and A. Holzschuh. 2014. Early mass-flowering crops mitigate pollinator dilution in late-flowering crops. Landscape Ecology **29**:425-435.

Ries, L., and D. M. Debinski. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. Journal of Animal Ecology **70**:840-852.

Ries, L., and T. D. Sisk. 2008. Butterfly edge effects are predicted by a simple model in a complex landscape. Oecologia **156**:75-86.

Rodwell, J. 1992. British Plant Communities, Volume 3- Grasslands and Montane communities. Cambridge University Press, Cambridge.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine Parnassius butterfly dispersal: effects of landscape and population size. Ecology **81**:1642-1653.

Rook, A. J., B. Dumont, J. Isselstein, K. Osoro, M. F. WallisDeVries, G. Parente, and J. Mills. 2004. Matching type of livestock to desired biodiversity outcomes in pastures - a review. Biological Conservation **119**:137-150.

Rosin, Z. M., L. Myczko, P. Skorka, M. Lenda, D. Moron, T. H. Sparks, and P. Tryjanowski. 2012. Butterfly responses to environmental factors in fragmented calcareous grasslands. Journal of Insect Conservation **16**:321-329.

Ruiz-Jaen, M. C., and T. M. Aide. 2005. Restoration success: how is it being measured? Restoration Ecology **13**:569-577.

Rusterholz, H. P., and A. Erhardt. 2000. Can nectar properties explain sex-specific flower preferences in the Adonis Blue butterfly *Lysandra bellargus*? Ecological Entomology **25**:81-90.

Samnegard, U., A. S. Persson, and H. G. Smith. 2011. Gardens benefit bees and enhance pollination in intensively managed farmland. Biological Conservation **144**:2602-2606.

SCALES. 2014. Securing the Conservation of biodiversity across Administrative Levels and spatial, temporal and Ecological Scales. http://www.scales-project.net/. Date accessed 21/02/2014.

Schneider, C., J. Dover, and G. L. A. Fry. 2003. Movement of two grassland butterflies in the same habitat network: the role of adult resources and size of the study area. Ecological Entomology **28**:219-227.

Schtickzelle, N., and M. Baguette. 2003. Behavioural responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in framented landscapes. Journal of Animal Ecology **72**:533-545.

Schultz, C. B., A. M. A. Franco, and E. E. Crone. 2012. Response of butterflies to structural and resource boundaries. Journal of Animal Ecology **81**:724-734.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. Ecology **77**:1210-1225.

Schweiger, O., J. Settele, O. Kudrna, S. Klotz, and I. Kuhn. 2008. Climate change can cause spatial mismatch of trophically interacting species. Ecology **89**:3472-3479.

SER. 2004. Society for Ecological Restoration international science and policy working group. The SER international primer on ecological restoration. Society for Ecological Restoration.

Severns, P. M., E. J. B. McIntire, and C. B. Schultz. 2013. Evaluating functional connectivity with matrix behavior uncertainty for an endangered butterfly. Landscape Ecology **28**:559-569.

Shreeve, T. G., and R. L. H. Dennis. 2011. Landscape scale conservation: resources, behaviour, the matrix and opportunities. Journal of Insect Conservation **15**:179-188.

Shreeve, T. G., R. L. H. Dennis, D. B. Roy, and D. Moss. 2001. An ecological classification of British butterflies: Ecological attributes and biotope occupancy. Journal of Insect Conservation **5**:145-161.

Skorka, P., P. Nowicki, M. Lenda, M. Witek, E. B. Sliwinska, J. Settele, and M. Woyciechowski. 2013. Different flight behaviour of the endangered scarce large blue butterfly *Phengaris teleius* (Lepidoptera: Lycaenidae) within and outside its habitat patches. Landscape Ecology **28**:533-546.

Slamova, I., J. Klecka, and M. Konvicka. 2013. Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae). Insect Conservation and Diversity **6**:243-254.

Smart, S. 2001. MAVIS Plot Analyser. DART Computing.

Smith, M., J. Chetcuti, D. Moseley, and C. Quine. 2012. Addressing issues of conservation concern based on principles of landscape ecology- application to quick wins and the long march. Forest Research.

Stace, C. 2010. New Flora of the British Isles. Cambridge University Press, Cambridge.

Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The Effects of Edge Permeability and Habitat Geometry on Emigration from Patches of Habitat. American Naturalist **129**:533-552.

Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies, and T. Tscharntke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421-1432.

Steffan-Dewenter, I., and T. Tscharntke. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands - a mini review. Biological Conservation **104**:275-284.

Stewart, K. E. J., N. A. D. Bourn, and J. A. Thomas. 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. Journal of Applied Ecology **38**:1148-1154.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution **19**:305-308.

Tambosi, L. R., A. C. Martensen, M. C. Ribeiro, and J. P. Metzger. 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. Restoration Ecology **22**:169-177.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos **68**:571-572.

ter Braak, C. J. F., and P. Smilauer 2012. Canoco reference manual and user's guide: software for ordination (version 5.0). Microcomputer Power, Ithaca, NY, USA.

Thomas, C. D. 2000. Dispersal and extinction in fragmented landscapes. Proceedings of the Royal Society B-Biological Sciences **267**:139-145.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001a. Ecological and evolutionary processes at expanding range margins. Nature **411**:577-581.

Thomas, C. D., P. K. Gillingham, R. B. Bradbury, D. B. Roy, B. J. Anderson, J. M. Baxter, N. A. D. Bourn, H. Q. P. Crick, R. A. Findon, R. Fox, J. A. Hodgson, A. R. Holt, M. D. Morecroft, N. J. O'Hanlon, T. H. Oliver, J. W. Pearce-Higgins, D. A. Procter, J. A. Thomas, K. J. Walker, C. A. Walmsley, R. J. Wilson, and J. K. Hill. 2012. Protected areas facilitate species' range expansions. Proceedings of the National Academy of Sciences of the United States of America **109**:14063-14068.

Thomas, J. A. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae) in Britain. Journal of Applied Ecology **20**:59-83.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Philosophical Transactions of the Royal Society B-Biological Sciences **360**:339-357.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001b. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. Proceedings of the Royal Society of London Series B-Biological Sciences **268**:1791-1796.

Thomas, J. A., and R. T. Clarke. 2004. Extinction rates and butterflies - Response. Science **305**:1563-+.

Thomas, J. A., D. J. Simcox, and R. T. Clarke. 2009. Successful conservation of a threatened Maculinea butterfly. Science **325**:80-83.

Thomas, J. A., M. G. Telfer, D. B. Roy, C. D. Preston, J. J. D. Greenwood, J. Asher, R. Fox, R. T. Clarke, and J. H. Lawton. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science **303**:1879-1881.

Thomson, J. R., A. J. Moilanen, P. A. Vesk, A. F. Bennett, and R. M. Nally. 2009. Where and when to revegetate: a quantitative method for scheduling landscape reconstruction. Ecological Applications **19**:817-828.

Tischendorf, L., and L. Fahrig. 2000. On the usage and measurement of landcape connectivity. Oikos **90**:7-19.

Toeroek, P., E. Vida, B. Deak, S. Lengyel, and B. Tothmeresz. 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodiversity and Conservation **20**:2311-2332.

Travis, J. M. J., M. Delgado, G. Bocedi, M. Baguette, K. Barton, D. Bonte, I. Boulangeat, J. A. Hodgson, A. Kubisch, V. Penteriani, M. Saastamoinen, V. M. Stevens, and J. M. Bullock. 2013. Dispersal and species' responses to climate change. Oikos **122**:1532-1540.

Tropek, R., M. Hejda, T. Kadlec, and L. Spitzer. 2013. Local and landscape factors affecting communities of plants and diurnal Lepidoptera in black coal spoil heaps: implications for restoration management. Ecological Engineering **57**:252-260.

Tscharntke, T., and R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. Annual Review of Entomology **49**:405-430.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecological Research **17**:229-239.

Twiston-Davies, G., S. R. Mortimer, and J. Mitchley *in press*. Restoration of species rich grassland in the Stonehenge World Heritage Site, UK. In Kiehl. K., (Ed). Guidelines for native seed production and grassland restoration Cambridge Scholars, Cambridge.

Uuemaa, E., U. Mander, and R. Marja. 2013. Trends in the use of landscape spatial metrics as landscape indicators: a review. Ecological Indicators **28**:100-106.

Valladares, G., A. Salvo, and L. Cagnolo. 2006. Habitat fragmentation effects on trophic processes of insect-plant food webs. Conservation Biology **20**:212-217.

van Noordwijk, C. G. E., P. Boer, A. A. Mabelis, W. Verberk, and H. Siepel. 2012a. Life-history strategies as a tool to identify conservation constraints: a case-study on ants in chalk grasslands. Ecological Indicators **13**:303-313.

van Noordwijk, C. G. E., D. E. Flierman, E. Remke, M. F. WallisDeVries, and M. P. Berg. 2012b. Impact of grazing management on hibernating caterpillars of the butterfly *Melitaea cinxia* in calcareous grasslands. Journal of Insect Conservation **16**:909-920.

van Swaay, C. A. M. 2002. The importance of calcareous grasslands for butterflies in Europe. Biological Conservation **104**:315-318.

Van Swaay, C. A. M., A. Cuttelod, S. Collins, D. Maes, M. Lopez Munguira, M. Sasic, J. Settele, R. Verovnik, T. Verstrael, M. S. Warren, M. Wiemers, and I. Wynhof. 2010. European Red List of Butterflies, Luxembourg.

Van Teeffelen, A. J. A., C. C. Vos, and P. Opdam. 2012. Species in a dynamic world: consequences of habitat network dynamics on conservation planning. Biological Conservation **153**:239-253.

Vergnes, A., I. Le Viol, and P. Clergeau. 2012. Green corridors in urban landscapes affect the arthropod communities of domestic gardens. Biological Conservation **145**:171-178.

Wagner, H. H., Y. Rico, H. Lehnert, and H. J. Boehmer. 2013. Process-based long-term evaluation of an ecological network of calcareous grasslands connected by sheep herding. Ecography **36**:374-382.

Walker, K. J., P. A. Stevens, D. P. Stevens, J. O. Mountford, S. J. Manchester, and R. F. Pywell. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation **119**:1-18.

WallisDeVries, M. F., and S. H. Ens. 2010. Effects of habitat quality and isolation on the colonization of restored heathlands by butterflies. Restoration Ecology **18**:390-398.

WallisDeVries, M. F., P. Poschlod, and J. H. Willems. 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. Biological Conservation **104**:265-273.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley, D. B. Roy, M. G. Telfer, S. Jeffcoate, P. Harding, G. Jeffcoate, S. G. Willis, J. N. Greatorex-Davies, D. Moss, and C. D. Thomas. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature **414**:65-69.

Watts, K., A. E. Eycott, P. Handley, D. Ray, J. W. Humphrey, and C. P. Quine. 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecology **25**:1305-1318.

Watts, K., and P. Handley. 2010. Developing a functional connectivity indicator to detect change in fragmented landscapes. Ecological Indicators **10**:552-557.

Wiens, J. A. 1997. Metapopulation Dynamics and Landscape Ecology. Pages 43-62 in H. Ilkka, and E. G. Michael, editors. Metapopulation Biology. Academic Press, San Diego.

Wilkerson, M. L. 2013. Invasive plants in conservation linkages: a conceptual model that addresses an underappreciated conservation issue. Ecography **36**:1319-1330.

Wilson, R. J., Z. G. Davies, and C. D. Thomas. 2010. Linking habitat use to range expansion rates in fragmented landscapes: a metapopulation approach. Ecography **33**:73-82.

Wilson, R. J., D. Gutierrez, J. Gutierrez, and V. J. Monserrat. 2007. An elevational shift in butterfly species richness and composition accompanying recent climate change. Global Change Biology **13**:1873-1887.

Woodcock, B. A., J. M. Bullock, S. R. Mortimer, T. Brereton, J. W. Redhead, J. A. Thomas, and R. F. Pywell. 2012a. Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment. Biological Conservation **155**:50-58.

Woodcock, B. A., J. M. Bullock, S. R. Mortimer, and R. F. Pywell. 2012b. Limiting factors in the restoration of UK grassland beetle assemblages. Biological Conservation **146**:136-143.

Woodcock, B. A., A. R. Edwards, C. S. Lawson, D. B. Westbury, A. J. Brook, S. J. Harris, V. K. Brown, and S. R. Mortimer. 2008. Contrasting success in the restoration of plant and phytophagous beetle assemblages of species-rich mesotrophic grasslands. Oecologia **154**:773-783.

Woodcock, B. A., A. R. Edwards, C. S. Lawson, D. B. Westbury, A. J. Brook, S. J. Harris, G. Masters, R. Booth, V. K. Brown, and S. R. Mortimer. 2010. The restoration of phytophagous beetles in species-rich chalk grasslands. Restoration Ecology **18**:638-644.

Woodcock, B. A., M. Edwards, J. Redhead, W. R. Meek, P. Nuttall, S. Falk, M. Nowakowski, and R. F. Pywell. 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: behavioural differences and diversity responses to landscape. Agriculture Ecosystems & Environment **171**:1-8.

Young, C., A. Chadburn, and I. Bedu. 2009. Stonehenge World Heritage Site Management Plan 2009. English Heritage, London, UK.

Young, T. P. 2000. Restoration ecology and conservation biology. Biological Conservation **92**:73-83.

Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters **8**:662-673.