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The legacy of 20th Century landscape change on today’s woodland carabid communities

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ABSTRACT

Aim

For many species, the effects of landscape change can involve a time lag and result in an extinction debt. The landscape matrix plays a vital role in supporting species populations. However, the importance of the historical composition and configuration of landscape mosaics has received little attention, with studies focusing on the effects of loss and fragmentation of single (focal) habitat over time. We investigated the importance of historical and contemporary landscape heterogeneity (composition and configuration) to identify how landscape change has, and is continuing to have, an effect on current woodland carabid communities.

Location

Lowland Britain.

Methods

Carabids were sampled from woodlands in 36 tetrads of 4 km². Ordination methods analysed current community response to representations of contemporary and historical (1930’s) landscape heterogeneity. The effects of 80 years of landscape change on current carabid assemblages were compared among tetrads.

Results

Results are consistent with an extinction debt; carabid communities correlated significantly with the historical composition and configuration of the landscape, but not contemporary landscape configuration. Community assemblages have been shaped, and many species remain affiliated with landscape conditions that no longer exist, notably, large patches of
broadleaf woodland and semi-natural grassland. Recent introduction of conifer plantations has had a negative effect on the abundance of many woodland species. For many common, slow-dispersing species, contemporary and historical landscapes offered sub-optimum woodland coverage indicating a lag effect that exceeds 80 years. Increased arable landcover and loss of semi-natural grassland and heathland points towards an ongoing detrimental impact on carabid populations.

Main conclusions

Compared with focal-habitat studies, the landscape mosaic approach provides a more comprehensive understanding of the effects of widespread landscape change on species communities. Conservation guidance includes new planting, maintenance and restoration of semi-natural habitats, implemented across multiple spatial scales and where feasible, considering both historical and contemporary landscape heterogeneity.

Keywords Carabidae, community analysis, extinction debt, landscape change, landscape heterogeneity, landscape mosaic.
(A) INTRODUCTION

Landscape change poses a serious threat to global biodiversity and there is concern regarding the loss of species in wooded-agricultural environments (Hendrickx et al., 2007; Fahrig et al., 2011). Over the last 80 years, agricultural intensification has led to widespread landscape modification across much of Europe, Australia and North America (Lunt & Spooner, 2005; Schweiger et al., 2005). The loss and fragmentation of semi-natural habitats, plus transformation of land to intensive agriculture has fundamentally altered the compositional heterogeneity (the number and proportions of different landcover types) and configurational heterogeneity (the spatial arrangement of different landcover types) in the rural environment (Fahrig et al., 2011). Changes to landscape heterogeneity alter the ecological filters which affect species-landscape processes such as dispersal, resource availability and colonisation (Mayfield et al., 2010), ultimately influencing the abundance and diversity of species able to occupy habitats and exist in a landscape (Baessler & Klotz, 2006; Hendrickx et al., 2007).

While some species respond almost immediately to landscape change, often there is a time lag effect (relaxation time), whereby species persist in a habitat, but the conditions they require for long-term survival are no longer being met fully; this is commonly referred to as an ‘extinction debt’ (Diamond, 1972; Tilman et al., 1994). The present occupancy of species in a habitat patch may therefore, overestimate the carrying capacity of the current landscape and consequently, underestimate the threat to biodiversity even if no further landscape change occurs (Adriaens et al., 2006; Piqueray et al., 2011). Previous studies provide convincing evidence of extinction debts and lag effects across a range of habitats, taxa and spatial scales (see review by Kuussaari et al., 2009). As such, a key issue in conservation biogeography is to identify how species respond to current landscape heterogeneity, but also to consider the temporal aspect. Ascertaining how species communities have been affected
and might continue to change in response to ongoing landscape change provides an indication of how biodiversity might respond to future conservation and land management decisions.

In temporal landscape research, a frequently adopted approach is to quantify and assess the interactions which exist between contemporary and past landscapes and current species distributions (e.g. Lindborg & Eriksson, 2004; Piessens & Hermy, 2006; Kuussaari et al., 2009; Cristofoli et al., 2010; Piqueray et al., 2011; Husáková & Münzbergová, 2014). This approach reconstructs contemporary and past landscape configurations for a focal habitat of interest e.g., semi-natural grasslands (Sang et al., 2010) or old-growth forest (Berglund & Jonsson, 2005). The presence of an extinction debt is inferred if the variation in current species richness, or the response of a functional group of species, is better explained by historical rather than contemporary landscape conditions. However, the binary classification of landscapes as either ‘focal habitat’, where resources required for the study taxa are met, or ‘hostile matrix’ (Fahrig et al., 2011) means that conclusions regarding how species respond are solely based on contemporary and past configurations of one habitat type. It is however, known from studies that have analysed species response to current landscape conditions, that wider landscape heterogeneity is an important determinant of biodiversity (Haslem & Bennett, 2008; Duflot et al., 2014; Neumann et al., 2016). The ‘landscape mosaic’ approach, recognises that species are not only affected by the amount and spatial configuration of their focal habitat, but also by the composition of the heterogeneous matrix which can provide resources, alternative useable habitat and influence species dispersal (Fahrig et al., 2011). In landscapes where focal habitat has been recently destroyed or fragmented, species might have dispersed into new patches, found alternative habitats in the matrix or, remained as an isolated population in the now compromised habitat patch. The past composition and configuration of the matrix is therefore, likely to be of significant explanatory importance for current species assemblages. Despite this, the effect of historical landscape composition has
received minimal attention (but see Lunt & Spooner, 2005; Baessler & Klotz, 2006; Aguirre-Gutiérrez et al., 2015; Cousins et al., 2015).

Post WWII in Britain, large areas of broadleaf woodland were cleared for intensive agriculture, fragmented by urban infrastructure, or converted to commercial coniferous plantations (Fuller et al., 2007). This had a detrimental effect on woodland biodiversity (Hinsley et al., 1995; Bellamy et al., 1996; Mason, 2007). Landscape modification also occurred across other semi-natural habitats including species-rich grasslands and lowland heathland (Vickery et al., 2001; Warren et al., 2001). The alteration of landscape processes throughout the wider environment could potentially have affected species community assemblages in woodlands today.

This study investigated the response of woodland ground beetle communities (Coleoptera; Carabidae) to the contemporary and historical landscape heterogeneity (composition and configuration) of wooded-agricultural landscape mosaics in southern Britain (Fig. 1). Carabids were chosen as biological indicators as they are functionally diverse and sensitive to landscape change (Aviron et al., 2005; Barbaro & van Halder, 2009). We analysed carabid response at the community level to include both specialist and generalist species, without restricting natural community variability or biasing carabid response by relying on specialists (Adriaens et al., 2006). We asked, 1) do current woodland carabid communities exhibit a correlation with contemporary and historical landscapes when considering both the composition and configuration of landscape mosaics? 2) Is there evidence that current carabid distributions relate more strongly to representations of the historical landscape than the contemporary landscape, indicating a potential extinction debt? 3) Comparing results from contemporary and historical landscapes, is it possible to infer how landscape change might have had, or be having, an effect on current woodland carabid communities?
(A) METHODS

(B) Study region

The study was conducted in rural southern Britain (Fig. 1). The region is low-lying and temperate: average elevation 140 m a.s.l., mean annual temperature 10.2 °C, average annual precipitation 850 mm. In the 1930’s prior to the onset of intensive agriculture, semi-natural habitats including species-rich meadows, grazing pastures, lowland heath and large patches of broadleaf woodland dominated the landscape. Arable land existed as small-scale plots used for non-intensive cropping, market gardens and orchards (Southall et al., 2007). Today, the landscape is dominated by intensive arable farming (largely wheat, winter oil seed rape and barley) and improved grassland (for livestock, hay and silage production). Broadleaf woodland cover has been reduced into smaller, fragmented patches. Where larger woods have been retained, sizeable blocks have been converted to commercial coniferous plantations. Small areas of chalk downland, heathland and rough grassland exist as relict, isolated fragments (Fig. 1).

(B) Study design

The study set-up follows previous research conducted by the authors in 2011. We refer readers to Neumann et al., (2015) for a full detailed description of the methods. Thirty-six 2 x 2 km study tetrads were selected across the study region (Fig. 1); each was centred on a patch of broadleaf woodland, hereafter referred to as the sample woodland. Thirty of the sample woodlands were classified as Ancient Semi-Natural Woodland (Ancient Woodland Inventory – Natural England, 2013). The remaining six were continuously wooded for at least 165 years (County Series 1846-1969 maps – OS, 2013). Sample woodland size varied from 3 ha to 350 ha (median 51 ha). All were predominantly broadleaf although some larger woodlands contained stands of commercial coniferous plantation (Forestry Commission, 2013). The
composition of the landscape matrix within each tetrad was typical of the contemporary rural environment but tetrads differed in terms of their landscape configuration (i.e., amount, size, shape and arrangement of habitats). Tetrads contained uniform soil types, avoided areas of steep topography, large urban areas and coastal regions and did not overlap.

(B) Contemporary map data

Landcover Map 2007 (LCM2007) (Morton et al., 2011) and Ordnance Survey MasterMap Topography data (OSMM) (OS, 2010) were used to quantify contemporary land-use.

LCM2007 is an up-to-date UK land-use map representing the UK Biodiversity Action Plan Broad Habitats derived from 30 m resolution satellite imagery (NERC, 2011). The spatial and thematic accuracy of LCM2007 when validated against ground reference data was 83% and the minimum mappable area was 0.5 ha meaning small or complex-shaped features e.g., small water bodies, are not well represented (NERC, 2011). To overcome these inaccuracies the LCM2007 data were combined with the OSMM Topography data. OSMM details landscape features (e.g. buildings, roads, woodlands, water bodies) as individual polygons with 2.5 – 6.0 m spatial accuracy in rural areas but does not specify definitive landcover information (OS, 2010). For each tetrad, a comprehensive landcover dataset was created in ArcMap 10.1 (ESRI, 2011) using information from both datasets.

(B) Historical map data

The first systematic survey of land in Great Britain was carried out under the direction of Professor Dudley Stamp in the early 1930’s (Hooftman & Bullock, 2012). The Dudley Stamp Maps (DSM) categorised land-use at the one-inch-to-the-mile (1:63,360) scale and were printed between 1933 and 1949. Digitisation of the original paper maps was completed in 2011 (Clark, 2011). DSM maps seven Broad Habitats: (i) forest and woodland; (ii)
meadowland and permanent grasslands; (iii) arable land; (iv) water; (v) heath and moorland; (vi) urban core; (vii) suburban (gardens etc.) (Southall et al., 2007).

(B) Landscape heterogeneity spatial analysis

ArcMap 10.1 was used to quantify the contemporary and historical landscape heterogeneity (landscape composition and configuration) within each tetrad (Table 1). To facilitate comparisons between current and past landscapes, the contemporary LCM2007 data were classified to be comparable with the Broad Habitats represented in the DSM (see Table S1, Supporting Information).

(C) Landscape composition

Contemporary landscape composition in each tetrad was represented by the relative proportion of the eight Broad Habitat variables. Six were used to characterize the historical landscape composition; improved grassland and coniferous plantation were not present historically (Table 1).

(C) Landscape configuration

Landscape configuration metrics measured the number, amount, shape and spatial configuration of the Broad Habitat variables in each tetrad (Table 1). Discrete habitat patches had an edge-to-edge Euclidean distance of at least 20 m from another patch of the same type. Functionally, 20 m exceeds the ‘interaction distance’ for many common carabid species (Brouwers & Newton, 2009). The number of patches and mean patch area indicated the degree of structural fragmentation of a Broad Habitat type (Cristofoli et al., 2010).

(C) Additional constraining variables
The detection of true landscape effects on communities can be hampered by constraining variables (Table 1). For all analyses, the effects of carabid sampling date and spatial autocorrelation (where tetrads in close proximity to each other can possess more similar landscape or biotic conditions than those from a random set of observations) were accounted for (see below) (Heikkinen et al., 2004; Oliver et al., 2010).

(B) Sampling carabid communities

Carabid communities in each sample woodland were surveyed using 10 pitfall traps set between May and early August 2011. Two pitfall traps were placed at the centre of each sample woodland. Further pairs were set along the most northerly, southerly, easterly and westerly facing-woodland edge adjacent with the non-woodland habitat. Pitfall traps (diameter 60 mm, depth 80 mm) were one third filled with ethylene glycol (50%) and water (50%). In each tetrad, traps were set continuously for 14 days, randomly assigned between May and August to avoid clusters of tetrads in close proximity trapping species over the same time period. Individuals collected were pooled for each tetrad and identified to species using Luff (2007).

(B) Statistical analyses

The effects of contemporary and historical landscape heterogeneity on current woodland carabid communities were explored using partial canonical correspondence analyses (pCCA) in Canoco 5 (ter Braak & Šmilauer, 2012). Analyses followed a two-step process: 1) global permutation tests 2) interactive forward selection procedure. Partial methods were used in all tests to account for, and remove any variation explained by ‘sampling date’. The effect of spatial autocorrelation was addressed using principal coordinates of neighbour matrices (PCNM) (see Borcard & Legendre, 2002).
Four pCCA models were run; one each testing for an effect of landscape composition or landscape configuration in both contemporary and historical landscapes on woodland carabid communities. For each model, a constrained ordination containing all the explanatory variables (Table 1) was run to check for significance of the joint effects; a global permutation test was considered significant where p < 0.05 using 9999 Monte-Carlo permutations. The Monte-Carlo test repeatedly shuffled the species data while keeping the explanatory landscape variables (and ‘sampling date’ covariate) fixed to identify any biologically plausible structure in the data. Following a significant result, partial interactive forward selection (pIFS) was used to reduce the whole set of variables to a more parsimonious subset that explained a good proportion of the constrained variation in the carabid community composition. At each step, the landscape variable that added most to the explained community composition variation was selected (in addition to the effects of explanatory variables that had already been selected). The statistical significance of each variable was determined using Monte-Carlo permutations. The results of pIFS were displayed as bi-plots illustrating the 25 most important carabid species relationships with the selected landscape variables. On the bi-plots, arrows representing landscape variables point in the direction of the steepest increase in a variables value. Symbols representing beetle species can be perpendicularly projected onto the landscape variable line using a calibration arrow in the Canoco software to determine the optima of an individual species in respect to the value of that landscape variable. This interpretation is underpinned by some assumptions (see Legendre and Legendre, 1998), notably that species have a unimodal relationship of (log-transformed) abundance with the landscape variable and that the landscape gradient is long enough to allow a species to go from a sub-optimum low frequency and on to a level of past-optimum lower frequency. Nonetheless, use of the calibration arrow provides a useful indication of approximated species response, whereby ‘optimum’ represents the value of the
environmental variable in the study at which a species is predicted to have its highest (log) abundance.

Multicollinearity between explanatory variables is common in study tetrads where landcover composition sums to 1 (Heikkinen et al., 2004). The landscape composition variables (Table 1) were log (x+1) transformed to maximise the linearity of their relation to each other and to ensure that the ecological importance of all the landcover types for species was considered (Cleveland, 1993; ter Braak & Šmilauer, 2012). In all cases, the correlation matrix and variance inflation factors were consulted during the Global Permutation Test to check for collinearity (ter Braak & Šmilauer, 2012). Correlation coefficients among the final explanatory variables were all less than 0.6 (Table S2) (cf. Aviron et al., 2005, Radford & Bennett, 2007). The full matrix of carabid species were log (x+1) transformed to minimize the impact of abundant species on the analyses (Vanbergen et al., 2005).

(A) RESULTS

(B) Land-use change

Land-use changes are summarised in Table 2. Historically, study tetrads were dominated by semi-natural grasslands and broadleaf woodland. Approximately 25% of the landscape was used for arable production and 8% lowland heath and scrubland. Today, grasslands represented 3.6% of tetrad landcover; a relative decline of 91%. Grassland patches almost halved in number and decreased substantially in size. Lowland heath and scrub habitat underwent a relative loss of 95%. The majority of grassland and heathland habitat was converted to improved grassland and intensive arable land-use, together representing the largest proportion of landcover in the contemporary landscape (combined average 241.6 ha or 60.4%).
Broadleaf woodland habitat declined by 10 ha on average; a loss of 2.4%. Despite a relatively low level of loss, contemporary woodlands now exist as substantially smaller, more numerous patches with increased woodland edge habitat. Coniferous plantations were not present historically, but represented 14.2 ha (3.5%) of tetrad landcover today. Total woodland habitat inclusive of coniferous plantations increased by 1.1%. Urban land-use and transport infrastructure also increased over the 80 years.

Table S2 shows variable collinearity between different years. Variables of the same habitat type showed moderate to strong positive correlations over time; broadleaf woodland (r = 0.63), urban (r = 0.65), inland water (r = 0.67) and road length (r = 0.79). Pairwise comparisons indicated moderate positive correlation between historical semi-natural grassland and contemporary improved grassland cover (r = 0.56) and historical heathland and contemporary coniferous woodland cover (r = 0.45).

(B) Carabid community dynamics

4677 carabid beetles comprising 76 species were recorded from the 36 tetrads. 80% were from five widespread woodland and generalist habitat species: *Pterostichus madidus* (1809, 39% of the total), *Abax parallelepipedus* (1354, 29%), *Pterostichus melanarius* (303, 6%), *Nebria brevicollis* (162, 3%) and *Calathus rotundicollis* (155, 3%). Other species recorded frequently but in lower abundances included grassland, open habitat, agricultural and heathland species (Table S3).

(B) Effect of spatial autocorrelation

Principal coordinates of neighbouring matrices (PCNM) found no spatially conditioned variation in the contemporary landscape composition or configuration variables (p = 0.289)
and p = 0.740), nor the historical composition or configuration variables (p = 0.326 and p = 0.540) which could explain the carabid community composition.

**(B) Carabid community response to contemporary and historical landscape heterogeneity**

**(C) Contemporary landscape composition**

Woodland carabid community composition was significantly related to contemporary landscape composition (pCCA, F = 1.3, p = 0.009); the eight landscape composition variables explained 29.7% of the total community variation (Table 3; Fig. 2). pIFS selected four Broad Habitat variables that accounted for 18.0% of the total variation in carabid communities (Fig. 2). Species recorded less frequently during the study exhibited the strongest response; *C. rotundicollis* (C.rot) was the only one of the five commonly trapped species to appear on the bi-plot (Fig. 2). Most species associated negatively with contemporary expanses of arable land and coniferous plantation which respectively explained 4.9% (p = 0.015) and 3.9% (p = 0.098) of the total variation (Table 3; Fig. 2). Species associated with mature broadleaf woodlands including *Bembidion mannerheimii* (B.man), *Calodromius spilotus* (C.spi) and *Acupalpus dubius* (A.dub) were among those to respond most negatively to these two variables. Only heathland specialist *Nebria salina* (N.sal) and generalist woodland species *C. rotundicollis* (C.rot) had their highest relative (log) abundances in landscapes containing 35 – 40% arable landcover and 3 – 6% coniferous plantation; values typical of the contemporary landscape (Table 1; Fig. 2). *Notiophilus quadripunctatus* (N.qua), *Amara ovata* (A.ova) and *Paranchus albipes* (P.alp) were most abundant in tetrads containing 3 – 4% semi-natural grassland (mean cover 3.6%; Table 2, Fig. 2).

**(C) Historical landscape composition**
Woodland carabid community composition was significantly related to the historical landscape composition (pCCA, F = 1.3, p = 0.005); the six variables explained 23.0% of the total community variation (Table 3). Arable land (p = 0.008) and broadleaf woodland (p = 0.031) accounted for 10.2% of the total variation during pIFS (Table 3, Fig. 3). Thirteen of the 25 species represented on the bi-plot responded to both the contemporary and historical landscape composition (Figs. 2 and 3). However, with the exception of arable land, the two models identified different explanatory landscape variables as key determinants of community composition. Many species continued to display negative associations with historical levels of arable land (Fig. 3). With the exception of Calathus fuscipes (C.fus) (an inhabitant of arable fields) all other species represented on the bi-plot appeared at greater abundance in tetrads with a proportion of arable land below that of the historical average (23.5%). The approximate amount of broadleaf woodland cover that maximized the predicted abundance of all species represented (other than agricultural species Synuchus vivalis (S.viv) and Bembidion quadrivittatum (B.qua)) was slightly greater than the historical average of 26.6% (Table 2, Fig. 3). Pterostichus niger (P.nig) (a large-bodied (18.5 mm), flightless inhabitant of woodlands and damp grasslands) and Carabus problematicus (C.pro) (a very large (24 mm), flightless inhabitant of woodland and heathland) were recorded in over two-thirds of the study tetrads, but correlated only with historical landscape composition (Fig. 3).

(C) Contemporary landscape configuration

Woodland carabid communities exhibited a near-significant response to contemporary landscape configuration when testing the joint effects (pCCA; F = 1.3, p = 0.064). The 9 configuration variables explained 32.1% of the total variation. Length of woodland edge and mean woodland patch area explained the greatest proportion of the variation; 4.8% (p = 0.033) and 4.2% (p = 0.084) respectively (Table 3, Fig. 4). Grassland, heathland and open-habitat species were most prevalent on the bi-plot. Those located in the positive bi-plot
quadrant (top-right) had highest predicted abundance where woodland edge exceeded 22 km (contemporary mean 19.8 km). Woodland species including *Bembidion aeneum* (B.aen) and specialist *Leistus fulvibarbis* (L.ful) were most abundant where landscapes contained large woodland patches (~12 ha).

**C) Historical landscape configuration**

Variation in current woodland carabid communities was better explained by historical landscape configuration than contemporary landscape configuration when testing the joint effects (pCCA: F = 1.4, p = 0.006, 34.7%) (Table 3). Four historical configuration variables explained 17.7% of the total variation (Table 3, Fig. 5). Historically larger patches of broadleaf woodland (p = 0.062) and semi-natural grassland (p = 0.064) explained the greatest amount of carabid community variation (Table 3, Fig. 5). These two Broad Habitat types also contributed to the largest proportions of total historical landcover (Table 2). *C. rotundicollis* (C.rot), *A. parallelepipedus* (A.par) and *P. melanarius* (P.mel), three of the five most frequently trapped species, were optimally associated with landscapes containing 0.2 – 0.6 km of transport routes (historical average of 1.8 km) (Table 2). In addition to *C. problematicus* (C.pro) these common and widespread woodland species were found in greater abundance in tetrads with 10 – 11.5 km of woodland edge habitat (historical average 11.3 km) and woodland patches sized 16 – 26 ha (historical average 16.3 ha). Woodland species *B. mannerheimii* (B.man), *C. spilotus* (C.spi) and *A. dubius* (A.dub) positively associated with historically large patches (> 28 ha) of broadleaf woodland (Fig. 5). *N. quadripunctatus* (N.qua), *A. ovata* (A.ova) and *P. albipes* (P.alb) correlated strongly with landscapes that historically contained grassland patches larger than 60 ha (historical average 36.7 ha) (Table 2, Fig. 5).

**A) DISCUSSION**
Recently, it has become more widely accepted that species perceive landscapes in a complex manner and utilise resources from different landcover types beyond their focal habitat (Haslem & Bennett, 2008; Oliver et al., 2010; Fahrig et al., 2011). It has also been demonstrated that the response of many species to landscape change is typically not instant, but involves a time lag (Diamond, 1972). It was therefore, anticipated that populations would exhibit a response to a variety of habitats present in the contemporary landscape, but also those representative of the historical landscape (Kuussaari et al., 2009; Watts et al., 2010).

(B) Evidence of extinction debt for carabid communities in wooded-agricultural landscapes

Carabid communities correlated significantly with both contemporary and historical landscape composition, although more of the variation was explained by the contemporary landscape. However, the significant effect of historical landscape composition is indicative that some species may be experiencing a lag effect i.e., persisting as a result of landscape conditions which no longer exist placing them at heightened risk of future extinction (Lindborg & Eriksson, 2004). By contrast, the significant response of current carabid communities to historical but not contemporary landscape configuration is consistent with an extinction debt (Lindborg & Eriksson, 2004; Berglund & Jonsson, 2005; Sang et al., 2010).

In the landscape composition models, 13 of the same species represented on the bi-plots responded to both contemporary and historical conditions yet, apart from arable land, different explanatory variables were identified. This is strong evidence that past habitat availability is a key factor explaining current community assemblages (Sang et al., 2010), and also indicates that many of the same species are continuing to react to different, altered conditions in the contemporary landscape. The negative association of many species to historical amounts of arable land and positive relationship with historical availability of
broadleaf woodland is not unexpected as species will often respond most strongly to the extent of preferred or avoided elements in a landscape (Judas et al., 2002; Heikkinen et al., 2004; Airon et al., 2005). Indeed, the approach adopted in other temporal landscape studies assumes that species will correlate significantly with representations of their focal habitat. However, in this study, the same species did not yield a response to contemporary broadleaf woodland cover, despite only declining by 2.4% over the 80 years and with a moderately strong correlation between years (i.e., tetrads with greater woodland cover historically retained greater amounts of woodland today (Table S2)). What was observed was a continued negative association to the vast increase in arable land cover, and also to coniferous plantations which were not present historically. In lowland Britain, most conifer plantations are sited on heathland (Spencer & Haworth, 2005) (which showed moderate correlation between years), and within large patches of broadleaf, often ancient semi-natural woodland (Rackham, 2003; Natural England, 2013). The strong negative association with conifers was most evident for species typical or specialist of mature woodland including B. mannerheimii, C. spilotus and A. dubius; these species also optimally associated with large patches of broadleaf woodland in the historical model. The ongoing impacts of woodland conversion are likely to continue to be detrimental as abundance and richness measures within introduced coniferous plantations have consistently been found to be lower than those associated with mature broadleaf woodland (Wiezik et al., 2007; Oxborough et al., 2010). Contrarily, there is evidence that heathland soil structure and fertility is less altered by plantations, helping to support heathland specialists such as N. salina and offering potential areas for conservation restoration focus (Spencer & Haworth, 2005). In the landscape configuration models, carabid communities were most strongly associated with historically large patches of broadleaf woodland and semi-natural grasslands. These two habitats contributed to the largest proportion of historical landcover, again indicating a legacy
whereby current woodland carabid assemblages have been shaped, and remain affiliated to
traits which were dominant 80 years ago. The continued prevalence of *N. quadripunctatus*,
*A. ovata* and *P. albipes* (open/grassland habitat species) in landscapes that retain just 3 – 4%
grassland cover today, suggests that some species may only persist if landscape conditions
were exceptionally favourable previously, i.e., the highest abundance of these species was in
tetrads that historically included grassland patches larger than 60 ha (average historical patch
size 36.7 ha). Further studies adopting the temporal landscape mosaic approach but sampling
within grassland habitats would help confirm this assumption.

The degree of habitat fragmentation within a landscape has been found to be of significant
importance when it comes to identifying extinction debts (e.g. Cousins, 2009; Cristofoli *et al.*, 2010; Piqueray *et al.*, 2011; Rybicki & Hanski, 2013). Here, the break-up of woodland
into smaller, more numerous patches, leading to an increase in edge habitat but with little loss
in total woodland cover is indicative of fragmentation. Evidence from the contemporary
configuration model however, suggested that the effect on species was not uniform: larger
patches may be key for specialists like *L. fulvibarbis*, while greater amounts of woodland
edge appeared to benefit other grassland, heathland and open-habitat species; possibly by
acting as a buffer, providing alternative useable or refuge habitat following substantial semi-
natural habitat loss (Schweiger *et al.*, 2005; Hendrickx *et al.*, 2007; Neumann *et al.*, 2015).
This highlights the need for a landscape mosaic approach that ensures the values of other
landcover types are not ignored. Likewise, although a negative effect of fragmentation was
not conclusive, it must be noted that focal habitat studies focussing on the response of
specialists are more likely to observe a significant effect as species will express higher
sensitivity to changes in their specific habitat, particularly in the absence of other landcover
information (Sang *et al.*, 2010). Nonetheless, there is increasing recognition that landscape
change impacts on the process of community assembly (Mayfield *et al.*, 2010) and that the
response of generalists are equally important to fully understand the ongoing impacts on community structure (Cousins & Vanhosenacker, 2011; Piqueray et al., 2011).

(B) How might landscape change be having an effect on carabid communities?

This, and previous studies (e.g. Barbaro & Van Halder, 2009; Sang et al., 2010; Duflot et al., 2014; Neumann et al., 2015) indicate that specialists and carabids with lower dispersal ability may be at greater risk following landcover change. In this study, large-bodied and flightless carabids including P. niger, C. problematicus, A. parallelepipedus and P. melanarius responded only to historical landscape conditions. All however, are considered common and widespread (Luff, 2007) and were identified from more than two-thirds of the woodlands sampled. The dispersal of large-bodied, flightless, carabids takes several generations and successful colonisation of new patches may take hundreds of years (Jopp & Reuter, 2005).

Their frequency today should not be assumed to represent a stable and healthy population, but may be better viewed as persisting (Oliver et al., 2010) and in need of appropriate targeted land management actions. Indeed, the relative abundance of these species was greatest where the extent, shape and size of broadleaf woodland habitat was found to be greater than, or at the threshold of that provided in the landscape 80 years ago. Although a pertinent issue currently, the loss of woodland habitat in Britain can be dated back to the Neolithic (Rackham, 1986) suggesting that, for many species, the extinction debt currently being paid may relate to landscape conditions present well beyond the time period considered here.

(B) Value of the landscape mosaic approach

The landscape mosaic approach allows simultaneous consideration of landscape composition and configuration as complementary components. Until now, temporal landscape studies have only considered changes in the configuration of focal habitat (e.g. Lindborg & Eriksson,
overemphasise the effects of landscape change on biodiversity. In this study, the landscape mosaic approach stressed the importance of historical landscape conditions, but also highlighted which habitats in the modified environment served to bolster populations and those which were detrimental, providing a better understanding of how community assemblages have been, and may continue to be shaped.

(B) Conservation implications

The detection of an extinction debt provides an unknown deadline for future biodiversity loss, however, while species persist, there remains time for conservation measures to be applied. Lowland Britain will remain dominated by intensive agriculture for the foreseeable, thus a combination of management approaches are needed. For species with low dispersal power, maintaining or increasing the size of woodland patches is advocated, while facilitating species movement through the introduction and maintenance of linear features is a recognised option where intensive agriculture dominates the landscape (Lawton et al., 2010; Watts et al., 2010). There is good evidence that species-rich hedgerows also offer comparable conditions to woodland edges (Taboada et al., 2004), which if providing refuge habitat for species of open-habitats will ensure that linear features provide co-benefits throughout the matrix. Active conversion of plantation woodland back to native tree species or heathland is recognised (Spencer & Haworth, 2005) and guidance might consider restoration or new woodland planting to be conducted at a level equivalent to the amount of habitat lost to plantation. Restoration of heathland and species-rich grassland must be encouraged where feasible (Piessens & Hermy, 2006) especially smaller patches implemented under farm-level stewardship that connect larger restoration efforts. Finally, conservation actions should consider the composition and configuration of both the historical and contemporary landscape to ensure that efforts are applied where they are most suitable, encouraging
maximum biodiversity gain. For example, semi-natural grassland restoration might be best undertaken on nutrient-depleted ex-arable land that retains a history of being on (or near to) previous grassland sites to assist the development of species-rich swards (Walker et al., 2004). While such strategic conservation planning ideally requires access to historical spatial data, local knowledge will be invaluable where spatial datasets are unavailable.

(A) ACKNOWLEDGEMENTS

We are grateful to Chris Foster for his help with data collection and to landowners who granted us access to their land.

(A) REFERENCES


Forestry Commission. Data obtained under Ordnance Survey Open Data terms. Available at: http://www.forestry.gov.uk/forestry/infd-8g5bx3.


(A) DATA ACCESSIBILITY STATEMENT

Requests for access to data used and analysed in this study can be made by emailing the corresponding author.

(A) BIOSKETCH

The research team comprises individuals from UK academic and conservation research institutions with a broad range of expertise in landscape ecology and practical conservation across multiple taxonomic groups (http://www.reading.ac.uk/cwac/).

JLN and GHG conceptualised the study. JLN collected and analysed the data, GJH and AH assisted with carabid identification. JLN led the manuscript writing with input and editing provided by all authors.
Table 1: Summary of landscape composition and landscape configuration variables used to represent the contemporary and historical landscape heterogeneity in 36 study tetrads. Table also details additional constraining variables considered in the analyses.

<table>
<thead>
<tr>
<th>Main set</th>
<th>Sub set</th>
<th>Broad Habitat variables</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Landscape</strong></td>
<td><strong>Woodland land-use</strong></td>
<td>Amount (ha) of broadleaf woodland (“Woodland”)</td>
</tr>
<tr>
<td><strong>composition</strong></td>
<td><strong>Agricultural land-use</strong></td>
<td>Amount (ha) of coniferous plantation (“Coniferous”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Amount (ha) of arable land (“Arable”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Amount (ha) of improved grassland (“Improved grassland”)</td>
</tr>
<tr>
<td></td>
<td><strong>Semi-natural land-use</strong></td>
<td>Amount (ha) of semi-natural grasslands (“Grasslands”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Amount (ha) of inland water (“Water”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Amount (ha) of heathland and scrub (“Heath and scrub”)</td>
</tr>
<tr>
<td></td>
<td><strong>Urban land-use</strong></td>
<td>Amount (ha) of suburban and urban (“Urban”)</td>
</tr>
<tr>
<td><strong>Landscape</strong></td>
<td><strong>Woodland metrics</strong></td>
<td>Total number of woodland patches (“WP”)</td>
</tr>
<tr>
<td><strong>configuration</strong></td>
<td></td>
<td>Mean area (ha) of woodland patches (“MPA”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total length (km) of woodland edge (“WE”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Perimeter: Area ratio of the sample woodland (“PAR”)</td>
</tr>
<tr>
<td></td>
<td><strong>Semi-natural habitat metrics</strong></td>
<td>Total number of semi-natural grassland patches (“NPG”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean area (ha) of semi-natural grassland patches (“MPG”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total number of heathland and scrub patches (“NPH”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean area (ha) of heathland and scrub patches (“MPH”)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Total length (km) of main roads and railways (“RD”)</td>
</tr>
<tr>
<td><strong>Constraining</strong></td>
<td><strong>Sampling date</strong></td>
<td>Date of first carabid collection after 7 days (fortnight midpoint)</td>
</tr>
<tr>
<td><strong>variables</strong></td>
<td><strong>Spatial location</strong></td>
<td>British National Grid coordinate (XY) at tetrad midpoint</td>
</tr>
</tbody>
</table>

Abbreviations in brackets represent variable identification code on analysis bi-plots.
Table 2: Average change in the composition and configuration of Broad Habitats (BH) comparing between 2007 (contemporary landscape) and the 1930’s (historical landscape).

<table>
<thead>
<tr>
<th>Landscape composition (BH)</th>
<th>Contemporary</th>
<th>Historical</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean area (ha)</td>
<td>% cover of tetrad</td>
</tr>
<tr>
<td>Arable land</td>
<td>155.7 ha</td>
<td>38.9%</td>
</tr>
<tr>
<td>Improved grassland</td>
<td>85.9 ha</td>
<td>21.5%</td>
</tr>
<tr>
<td>Broadleaf woodland</td>
<td>96.6 ha</td>
<td>24.2%</td>
</tr>
<tr>
<td>Coniferous plantation</td>
<td>14.2 ha</td>
<td>3.5%</td>
</tr>
<tr>
<td>Heath and scrub</td>
<td>1.7 ha</td>
<td>0.4%</td>
</tr>
<tr>
<td>Grasslands</td>
<td>14.4 ha</td>
<td>3.6%</td>
</tr>
<tr>
<td>Inland water</td>
<td>1.0 ha</td>
<td>0.2%</td>
</tr>
<tr>
<td>Suburban and urban</td>
<td>25.4 ha</td>
<td>6.3%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Landscape configuration (BH)</th>
<th>Contemporary</th>
<th>Historical</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean values</td>
<td>Mean values</td>
</tr>
<tr>
<td>Number woodland patches</td>
<td>19 patches</td>
<td>11 patches</td>
</tr>
<tr>
<td>Area woodland patches</td>
<td>6.2 ha</td>
<td>16.3 ha</td>
</tr>
<tr>
<td>Length woodland edge</td>
<td>19.8 km</td>
<td>11.3 km</td>
</tr>
<tr>
<td>Number grassland patches</td>
<td>5 patches</td>
<td>9 patches</td>
</tr>
<tr>
<td>Area grassland patches</td>
<td>3.0 ha</td>
<td>36.7 ha</td>
</tr>
<tr>
<td>Number heath /scrub patches</td>
<td>9 patches</td>
<td>2 patches</td>
</tr>
<tr>
<td>Area heath/scrub patches</td>
<td>0.2 ha</td>
<td>15.3 ha</td>
</tr>
<tr>
<td>Length of roads and railways</td>
<td>2.2 km</td>
<td>1.8 km</td>
</tr>
</tbody>
</table>
Table 3: Response of woodland carabid communities to contemporary and historical landscape composition and landscape configuration across 36 tetrads. Results show the key explanatory variables identified by interactive forward selection for each model, following a significant (p < 0.05) global permutation test.

<table>
<thead>
<tr>
<th>Landscape composition</th>
<th>Global significance test</th>
<th>Interactive selection</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Contemporary</td>
<td>1.3</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Historical</td>
<td>1.3</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Landscape configuration</td>
<td>Global significance test</td>
<td>Interactive selection</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Contemporary</td>
<td>1.3</td>
<td>0.064</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Historical</td>
<td>1.4</td>
<td>0.006</td>
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</tbody>
</table>

Var = total variation in carabid community composition explained by all the landscape variables (global significance test) and the total amount of variation explained by each individual variable (identified during forward interactive selection). Refer to Table 1 for landscape variable abbreviations. Significance levels determined by Monte-Carlo global permutation tests.
Fig. 1: Location of the 36 2 x 2 km study tetrads in central southern England and a thematic representation of landscape change, comparing the historical and contemporary landscapes for one study tetrad.

Fig. 2: Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to contemporary landscape composition variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 11.6% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

Fig. 3: Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to historical landscape composition variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 10.2% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

Fig. 4: Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to contemporary landscape configuration variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 9.0% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.

Fig. 5: Partial Canonical Correspondence Analysis (pCCA) bi-plot illustrating the response of carabid communities to historical landscape configuration variables. Key explanatory variables identified by partial Interactive Forward Selection (pIFS). For legibility, bi-plot displays the 25 species that are well described by the first two ordination axes (which together explain 11.0% of the total variation) and are shown using bi-plot scaling. Refer to Table 1 for variable abbreviations and Table S3 for full species names.
Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1: Creation of Broad Habitat categories derived from LCM2007 and OSMM data.

Table S2: Pearson correlation matrices for landscape variables in each year and between time periods.

Table S3: Record of carabid species, bi-plot codes and species characteristics.