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RESEARCH ARTICLE

Linking mesoscale landscape heterogeneity and biodiversity: gardens and tree cover significantly modify flower-visiting beetle communities

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Abstract

Context Maintaining biodiversity in multifunction landscapes is a significant challenge. Planning for the impacts of change requires knowledge of how species respond to landscape heterogeneity. Some insect groups are known to respond to heterogeneity at the mesoscale, defined here as hundreds of metres. However, for many taxa these effects are poorly known.

Objectives To identify key elements of mesoscale landscape heterogeneity influencing community composition in flower-visiting beetles, and whether landscape explains any variation in beetle communities beyond that driven by immediate habitat cover.

Methods Flower-visiting beetles were sampled from 36 transects, laid out using a 6 km^2 grid located in southern Britain. Landscape heterogeneity was measured for 30 and 200 m buffers around the transects and the relative response of beetle communities to each assessed using ordination analyses followed by variation partitioning.

Results The composition of immediately adjacent habitat (30 m) and mesoscale landscape heterogeneity (200 m) explained unique portions of the variation in flower-visiting beetle communities. A number of species, including those affiliated with deadwood habitats, were positively linked to tree cover in the surrounding mesoscale landscape. Gardens covered a smaller area than trees but modified beetle communities to the same extent.

Conclusions The local abundance of some flower-visiting beetles is modified by the composition of the surrounding landscape. Results highlight the importance of tree cover for maintaining insect biodiversity in agricultural landscapes, while suggesting that gardens associated with small urban areas may have a disproportionate influence on biodiversity.

Keywords Flower-visiting beetles · Landscape heterogeneity · Landscape mosaics · Mesoscale landscape · Urban biodiversity

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Introduction

The need for landscapes to maintain or even exceed current levels of biodiversity is well recognised, with both governmental and non-governmental conservation strategies increasingly adopting landscape-scale approaches (Lawton et al. 2010). This is a significant

challenge in lowland mosaic landscapes where urban development and agricultural intensification have fragmented habitats over long timescales, with variable but consistently negative impacts on biodiversity (Andrén 1994; Haila 2002; Fahrig 2003; Kappes et al. 2009; Fletcher et al. 2018). Successful management of landscapes for wildlife requires an understanding of how landscape heterogeneity determines patterns of species distribution and modifies community composition.

Landscape heterogeneity can be considered a function of both landscape composition—the amounts of different habitat cover types within the landscape—and landscape configuration, i.e., the heterogeneity of their spatial arrangement (Fahrig et al. 2011). Landscape heterogeneity is recognised as a key driver of species distributions in lowland agricultural landscapes for many taxonomic groups including birds (Fuller et al. 1997; Virkkala et al. 2013; Neumann et al. 2016a), bees and wasps (Fabian et al. 2013; Steckel et al. 2014), mammals (Mortelliti et al. 2011; Bender and Fahrig 2012) and plants (Jules and Shahani 2003).

However, whilst landscape conservation or landscape planning tends to consider landscape from an anthropogenic point of view, perhaps at a kilometres-wide scale, there is no single 'landscape scale' relevant to all species groups (Schweiger et al. 2005; Ekroos et al. 2013; Fuentes-Montemayor et al. 2017). Highly mobile species groups such as birds or Orthoptera respond to landscape composition even when examined at fairly broad scales, e.g., cricket species richness in 10-km^2 (Cherrill 2015) or bird community composition in 2-km tetrads (Neumann et al. 2016a). For invertebrates with more limited dispersal power, landscape heterogeneity within a radius of hundreds of metres is important, as seen for ground beetles (Carabidae) at a 400-m radius (Barbaro et al. 2007; Barbaro and Van Halder 2009) and Lepidoptera, hoverflies (Syrphidae) and bees at 600 m (Sjödin et al. 2008). In common with Barbaro et al. (2007), we describe this as a mesoscale landscape. This spatial scale is comparable to the size of common units of land management, with many new housing developments in the United Kingdom, for example, in the range of 5–20 ha.

Links between mesoscale landscape heterogeneity and biodiversity might therefore be successfully applied to the planning of new habitat networks as mitigation for single housing developments, or to the spatial optimisation of agri-environment schemes at a farm scale. These processes would ideally take account of biodiversity in all elements of the landscape, but whilst the synergistic effect of complete landscape mosaics has been shown to have an impact on community composition, species communities drawn from multiple mosaic components are less often considered (Bennett et al. 2006; Neumann et al. 2016b; Duflot et al. 2017). This is perhaps due to the challenge of gathering data from multiple habitats and taxonomic groups; methods that rapidly capture a 'snapshot' of landscape biodiversity by sampling a single species community would facilitate this.

Flower-visiting beetles cover a range of habitat affiliations within a single well-studied order, but few studies consider the effect of landscape heterogeneity on their distributions (Sjödin et al. 2008; Horak 2014). Among the flower-visitors are saproxylic beetles (one of the most threatened groups of species in Europe (Cálix et al. 2018) as well as many phytophagous and predatory species associated with tall sward and scrub habitats. By focussing on flower-visiting beetles, this study aims to provide a window into how mesoscale landscape heterogeneity influences the distribution of a diverse insect assemblage across a lowland agricultural mosaic.

Sampling was carried out on linear patches of flowering plants in the Apiaceaea (e.g., cow parsley, *Anthriscus sylvestris*, and hogweed, *Heraclium sphondylium*), which are very abundant in a range of lowland habitats across Northern Europe. Apiaceaea attract a diverse variety of insect visitors (Willis and Burkill 1892; Zych 2007a) and are key plant species in some ecological networks (Zych 2007b; Pocock et al. 2012). Their tendency to grow in dense stands alongside public roads and footpaths facilitates access to ready-made sampling transects. We also restricted sampling to Apiaceaea in order to reduce variation arising from e.g. flower preference among beetle species, which is not the focus of this study.

We asked the following key questions: (i) Is there a unique contribution of mesoscale landscape heterogeneity to flower-visiting beetle community composition apart from as a predictor of the immediate presence of suitable habitat? (ii) Which elements of landscape heterogeneity are the most important drivers of community composition? and (iii) In what way do they shape the community?

Appropriate scales of response to represent mesoscale (200 m buffer) and immediate habitat (30 m buffer) in the case of flower-visiting beetles were determined a priori from published estimates of beetle dispersal distances. The response of beetle communities to these two spatial scales was compared using variation partitioning.

Methods

Study site selection

The study area boundary was defined by a 6 km^2 grid, located in the northern part of the county of Hampshire, southern England (Fig. 1). From Land Cover Map 2015 (Rowland et al. 2017), the study area represents a heterogeneous mosaic of agricultural land (48% improved grassland, 26% arable), semi-natural habitats (woodland 23%) and small urban settlements (3%). The study area is low-lying (between 49 and 86 m above sea level) and has a temperate climate, with a mean annual maximum temperature of 14.5 °C and annual precipitation of 635 mm, both from Reading (10 km away) (Met Office 2017).

Within each of the resulting 36 1-km^2 grids, a 200-m sampling transect was established. Transects were situated along a road or public footpath, which in our study landscape are often bordered by dense linear stands of flowering Apiaceae. Transect locations were guided by the presence of flowering Apiaceae in the first visit in May (predominately cow parsley, *A. sylvestris*) as well as the vegetative presence of later-flowering species (e.g., hogweed, *H. sphondylium*) to ensure the continued usability of the transect through repeat visits. We selected transect locations with enough flower coverage to search for 30 min. Within those parameters, they were placed as close as possible to the centre of each 1-km square to maximise the distance between transects and reduce both spatial autocorrelation between samples and overlap in mesoscale landscape units. For the one case where no suitable transect was present within the square, a suitable location within the adjacent square was selected, maintaining the maximum possible separation with neighbouring transects.

Beetle sampling

Each transect was surveyed three times by a single observer. The first visit was made between 16th May and 10th June 2013, the second between 26th June and 8th July 2013 and the third between the 10th and 26th July 2013. Sampling was carried out between 10 a.m. and 6 p.m. in dry and non-windy conditions only. Transects were walked slowly in a single direction for 30 min. Flower heads were searched visually and all beetles detected captured in a plastic collecting tube (90 mm length × 25 mm diameter). Large aggregations of beetles were captured by shaking the flower head over a plastic funnel inserted into the mouth of the collecting tube, taking advantage of the fact that beetles tend to drop off vegetation when disturbed. Members of the family Nitidulidae were sampled as they are often present in very large numbers, associated with nearby flowering crops (e.g., *Meligethes aeneus*, a common pest of oilseed rape), but not included for analysis to prevent the response of other beetle species being swamped (Neumann et al. 2016a).

All beetles were identified to family using the keys of Duff (2012a) and nomenclature of the checklist of British beetles (Duff 2012b). All individuals besides members of the family Nitidulidae were subsequently identified to species (see Appendix 1 for a full table of references). Records from all three visits were pooled for each transect to give a final count of individuals and species. Voucher specimens for this study are held in the Centre for Wildlife Assessment & Conservation at the University of Reading.

The identity of all flowering Apiaceae species was recorded during each visit along with an estimate of the number of flowering stems within 5 m of the transect. To account for seasonal variability and variation in flower density and nectar richness, plant count data were transformed into an index where the maximum count for each survey period was 100. Weather data were recorded in the field (cloud cover in oktas) and from an automatic weather station 10 km away (rainfall on the previous day: yes/no) (University of Reading 2013). Start time was recorded to the nearest 5 min and later converted into three categories (Morning = 10:00–11:55, Noon = 12:00–13:55, Afternoon = later than 14:00). Those transects from which no beetles were recorded were excluded from the final analysis.

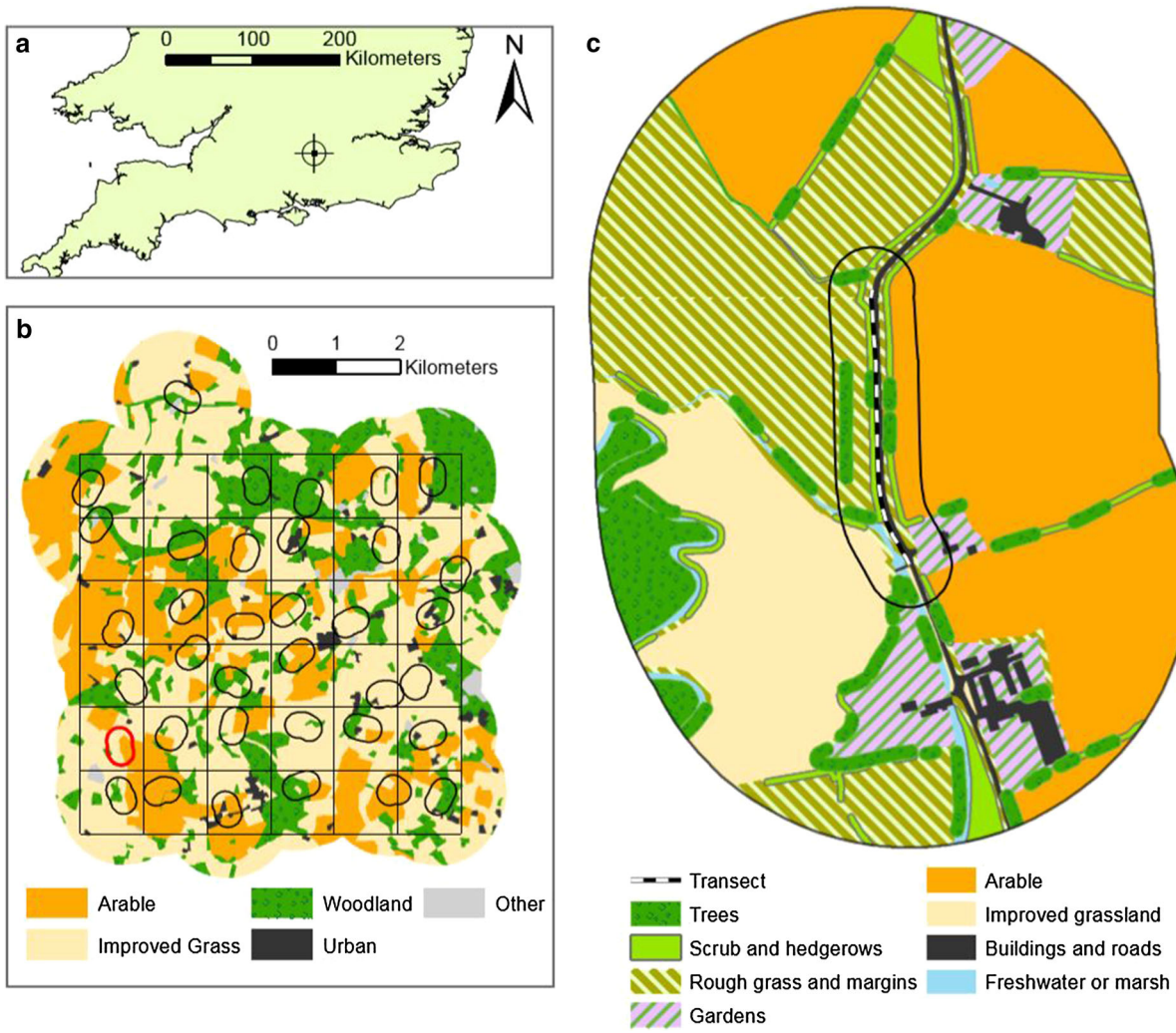

Fig. 1 **a** Location of the 6-km^2 grid used for selecting transect locations within southeast England. **b** Broad land cover from CEH Landcover Map 2015. **c** Example habitat classification of a 200-m buffer around a transect (outlined in red on **b**), based on OS Mastermap polygons (© Crown copyright 2018 Ordnance Survey)

Landscape data

Immediate habitat and mesoscale landscape buffers

Few studies address the local movement and dispersal of multiple beetle species. However, Irmler et al. (2010) provide a useful summary of the distances some saproxylic beetle species (many of them nectivorous) disperse away from patches of woodland habitat. The smallest dispersal category for species in Irmler et al. (2010) was 0–30 m. Using this figure as a guide, immediate habitat mix is defined here as habitat cover within 30 metres of the transect, with the assumption that flowers on the sampling transect are within a single flight range from this zone, even for species that only disperse short distances. The maximum flight distance found by Irmler et al. (2010) was > 80 m but for the majority of species dispersal was limited to < 80 m. Dispersal flight distances for beetles reported elsewhere generally fall within 200 ms (Schallhart et al. 2009; Torres-Vila et al. 2017; Rodwell et al. 2018). In this study mesoscale landscapes are therefore defined as the area within 200-m buffers from the sampling transect.

Mesoscale landscape composition (200-m buffer)

Landscape composition, which is the total area of different habitat cover types, was digitized for a 200-m buffer around each transect in ArcMap 10.4 (ESRI 2016), following the classification in Table 1. The delineation of patches and classification was based primarily on OS Mastermap (Ordnance Survey 2015). Where MasterMap categorised a patch as 'General Surface,' classifications were based on a combination of underlying land cover types from Land Cover Map 2007 (Morton et al. 2014) and visual inspection of aerial imagery (Getmapping Plc 2015).

Linear elements (composition)

Incorporating linear elements improves models of species and community distribution (Neumann et al. 2016b; Sullivan et al. 2017). Linear features not represented as patches in Mastermap were digitized as polylines following patch boundaries. These were classed as 'Line of Trees' (non-woodland trees where feature width was > 5 m), 'Hedges' (linear woody elements < 5 m wide) or 'Margin' (strips of non-woody vegetation along patch boundaries appearing more texturally complex in aerial imagery than adjacent habitats, for example road verges or field margins). Areas were assigned to linear elements based on the mean width of features measured with reference to aerial imagery in ArcMap. Forty measurements were taken for each linear feature type; the standard error was within 0.5 m of the mean value in each case.

'Line of Trees' was combined with patches of woodland cover to create the variable TREES. Many tree-dwelling beetles visit flowers as adults and utilise arboreal habitats outside of woodland, with open-grown oaks, for example, harbouring a higher species richness of saproxylic beetles than those in denser woodland (Koch Widerberg et al. 2012; Parmain and

Table 1 Summary of variables used to describe local habitat composition (30-m buffer) around transects

Variable	Description	Immediate habitat			Mesoscale landscape		
		Min	Mean	Max	Min	Mean	Max
Landscape composition							
ARABLE	Arable & Horticulture	0.00	0.37	1.26	0.0	6.1	16.7
IMPGRASS	Improved grassland	0.00	0.10	0.42	0.0	8.3	18.6
GARDEN	Suburban gardens	0.00	0.29	1.13	0.0	1.0	5.0
MANMADE	Buildings, roads, paths	0.00	0.17	0.40	0.0	1.1	6.7
ROUGH	Road and field margins, semi-natural grassland	0.00	0.22	0.73	0.0	1.7	9.0
TREES	Areas of tree cover with single canopy > 5 m wide (woodland, lines of trees)	0.07	0.45	1.06	0.2	1.6	10.9
SCRUB	Areas of woody vegetation without mature trees (scrub and hedgerows)	0.00	0.02	0.07	0.1	1.0	4.6
WET	Freshwater and marsh	0.00	0.01	0.15	0.0	0.7	4.5
	Buffer area	1.45	1.48	1.54	20.1	20.7	21.9
Landscape configuration							
WOODEDGE	Length of woodland edge and lines of trees (km)				0.60	2.82	6.10
SCRUBEDGE	Length of scrub edge and hedgerows (km)				0.00	0.48	1.75
MARGIN	Length of road verge and field margin (km)				0.09	1.20	3.01
GARHEDGE	Length of hedges per m^2 of garden (m/m^2)				0.0	7.5	58.2
ROUGHPATCH	Mean patch size in ROUGH composition variable (ha)				0.0	0.3	2.7
TRPATCH	Mean patch size in TREES composition variable (ha)				0.0	0.3	1.4
SCPATCH	Mean patch size in SCRUB composition variable (ha)				0.0	0.1	0.3
SHDI	Shannon's Diversity Index				0.3	1.2	1.8
CONTAGION	Contagion Index				51.2	65.5	87.8

Bouget 2018). 'Hedges' were further categorised as either Garden or Rural by selecting those that intersected with a patch of the Garden cover type for $> 50\%$ of their length. Rural Hedges were added to the Scrub cover type to form the variable SCRUB as they offer comparable insect habitat with a similar species mix of woody shrub species and small trees. Garden hedges were not incorporated into the composition data as they predominately overlapped with patches already categorised as gardens, representing a diverse mix of lawns, small trees, shrubs and hedges. Margins were incorporated into the composition variable ROUGH. An example of final landscape composition classification for a transect, including linear elements, is given in Fig. 1c.

Landscape configuration (200-m buffer)

Landscape configuration describes the spatial arrangement and geometry of the various landscape components and was represented here by the edge length and mean patch size of important cover types and two diversity metrics. Shannon's Diversity Index and Contagion Index were calculated for each buffer in Fragstats 4.1 (McGarigal and Ene 2012) and included as measures of landscape heterogeneity.

Edge habitats potentially provide a beneficial combination of larval habitats such as dead wood or herbaceous vegetation and abundant flowering plants frequented by adult beetles. Lengths of woodland edge (WOOD EDGE) and scrub edge (SCRUB EDGE) were therefore included as landscape configuration variables, calculated from the perimeters of the TREES and SCRUB composition variables, which for SCRUB EDGE included the lengths of rural hedges. Lengths of Margin identified in the linear feature analysis were combined with the edge length of land cover type MARGIN to create the variable MARGIN LENGTH, representing road verges and field margins that may serve as connecting features and host flowering Apiaceae. Potential patch area effects were assessed by including the mean patch size of three cover types, forming the variables TREE PATCH, SCRUB PATCH, and ROUGH PATCH.

Finally, the length of GARDEN HEDGE, weighted by total Garden Area, was included as a measure of potential habitat quality in urban areas. Areas of garden rich in hedges are likely to be different in character to those bordered by wooden fences or laid extensively to lawn with few boundary features.

Immediate habitat (30-m buffer)

Immediate habitat composition was obtained by clipping the landscape composition data to a 30-m buffer, representing the combination of habitats that were present immediately adjacent to the sampling transect. A summary of all variables used for analysis and their mean values is provided in Table 1.

Data analysis

All analyses were conducted in R 3.4.1 (R Core Team 2017) using package vegan 2.4-4 (Oksanen et al. 2017). Beetle data were examined as both the full community data incorporating abundance (full community) and species presence–absence (presence–absence). This follows the suggestion of Blanchet et al. (2014), who suggested that relevant information about less frequently encountered species can be obscured in ordination results driven by very common species. Species were included in the analysis if they occurred on three or more transects.

To address questions (ii) and (iii), the effects of immediate habitat composition (30 m composition), mesoscale landscape composition (200 m composition) and landscape configuration (200 m configuration) were determined using direct ordination methods. Presence–absence data were analysed using redundancy analysis (RDA). Preliminary analysis revealed a significant effect of survey time during the second visit (TIME2) on the full community data, with some species significantly more likely to occur on transects visited in the afternoon. This was entered as a conditional variable in a partial redundancy analysis (pRDA) (Borcard et al. 1992) to identify the true proportion of community variation attributable to either immediate habitat or landscape variables.

Both the full community and presence–absence data were transformed using the Hellinger distance (Rao 1995; Legendre and Gallagher 2001) in order to reduce the weight of rarely encountered species (which may not be truly biologically rare, merely less susceptible to the sampling method deployed here). All habitat and landscape variables representing an area were $\mathrm{Log}_{10}(x + 1)$ transformed so that the effect of potentially important semi-natural cover types was

not obscured by variation in dominant cover types such as arable or improved grassland (Neumann et al. 2016a).

Following a significant ($p < 0.05$) global permutation test on the combined effect of all variables, a reduced model providing the most parsimonious explanation for beetle community composition was identified using the Vegan function *OrdiR2step*. Variables were added to the final model if they were significant ($p < 0.05$) *and* increased the adj-R^2 of the model; provided this value did not exceed the adj-R^2 of the global model (Blanchet et al. 2008), this approach reduces the incidence of Type I errors and overestimation of explained variation.

Probability values for the global model, each variable retained in the reduced model and the constrained ordination axes were estimated using Monte Carlo tests with 9999 permutations. Multicollinearity between explanatory variables was accounted for using variance inflation factors (VIF, Neter et al. 1996); terms with the highest VIF were removed sequentially from the initial model until all VIF were < 3.0. Sites close to each other may have similar species communities, leading to spatial autocorrelation. This was assessed using Principle Coordinates of Neighbourhood Matrices (PCNM) based on the XY coordinate of the transect midpoints (Borcard and Legendre 2002). All PCNM were entered into a redundancy analysis as predictors of beetle community composition.

Variables from the reduced 200 m composition and 200 m configuration analyses were combined into final 200 m mesoscale landscape models. Any collinear (redundant) terms were discarded at this stage by inspecting VIF for the combined model. To address question (i), variation partitioning (function *varpart)* was used to unpick any unique explanatory contributions of 30 m habitat composition and the 200 m landscape variables (Borcard et al. 1992; Peres-Neto et al. 2006), expressed in terms of adjusted-R^2.

Results

Beetle community

Excluding Nitidulidae, 2662 beetles of 69 species from 18 families were collected during the three sampling visits. The lowest total species richness recorded at any one transect was five; the highest was 18, with a mean of 11.0 ± 0.7. The best represented families were Cantharidae (11 species), Cerambycidae (10 species), Scraptiidae (nine species) and Elateridae (seven species). All of these contain known flower-visiting species. The most widespread species were *Anaspis pulicaria* and *A. maculata* (Scraptiidae), *Anthrenus verbasci* (Dermestidae), *Agriotes pallidulus* (Elateridae) and *Rhagonycha fulva* (Cantharidae). *Anaspis* species are frequently found on *Apiaceae* and *Crateagus* spp. flowers in spring and early summer (Levey 2009), both *maculata* and *pulicaria* were ubiquitous in this study, appearing on 31 and 27, respectively, of the 36 transects. *Anthrenus verbasci* is a synanthropic species often found in homes, where the larvae feed on keratinaceous material, e.g., hair and skin (Peacock 1993). The adults are widespread on flowers in spring and summer but not usually found in numbers far from buildings (Woodroffe and Southgate 1954). Of the 20 most widespread species recorded, roughly equal numbers are broadly associated with trees and with open habitats (Table 2). Transects that were close to each other did not have more similar beetle communities, with no significant relationship between PCNM and full community composition ($F = 1.045$, $p = 0.305$) or species presence–absence ($F = 1.185$, $p = 0.113$).

Immediate habitat composition

28.8% of variation in the full community ($F = 1.412$, $p = 0.01$) and 29.0% of presence–absence ($F = 1.327$, $p = 0.002$) was explained by the combined effect of the 30 m habitat composition variables (Table 3). After forward selection, the reduced landscape composition model for full community explained 12.8% of variation. GARDEN ($p = 0.006$) and TREES ($p = 0.006$) were identified as significant predictors of community composition. The bi-plot (Fig. 2a) shows that the first constrained axis (RDA1, 8.0% variation explained, $p < 0.001$) represents a gradient from transects with high tree cover to ones with a relatively high proportion of garden cover. The second axis (RDA2, 4.8%, $p = 0.023$) represents a gradient from transects with large amounts of both gardens and trees to those with a more open rural character with low garden and tree cover. More species showed a moderate to strong positive association with trees than a negative one; those responding negatively include *A.*

Table 2 Summary of the 20 most widespread species (recorded in six or more transects) and their broad habitat associations

Family	Species	Bi-plot abbreviation	Locations (n = 35)	Total	Habitat association
Scraptiidae	*Anaspis maculata*	As.ma	31	410	Decaying wood
Scraptiidae	*Anaspis pulicaria*	As.pu	27	475	Tall sward, scrub
Dermestidae	*Anthrenus verbasci*	At.ve	22	439	Synanthropic
Elateridae	*Agriotes pallidulus*	Ag.pa	21	74	Tall sward, scrub
Cantharidae	*Rhagonycha fulva*	Rh.fu	18	126	Tall sward, scrub
Cerambydicae	*Grammoptera ruficornis*	Gr.ru	17	59	Decaying wood
Scraptiidae	*Anaspis humeralis*	As.hu	17	58	Decaying wood
Byturidae	*Byturus tomentosus*	By.to	15	60	Tall sward, scrub
Elateridae	*Athous haemorrhoidalis*	Ah.ha	14	22	Tall sward, scrub
Scraptiidae	*Anaspis frontalis*	As.fr	14	15	Decaying wood
Scraptiidae	*Anaspis costai*	As.co	13	79	Decaying wood
Oedemeridae	*Oedemera nobilis*	Oe.no	11	43	Tall sward, scrub
Cerambydicae	*Rutpela maculata*	Ru.ma	10	19	Decaying wood
Coccinellidae	*Propylea quatuordecimpunctata*	Pr.qu	10	12	Generalist
Dermestidae	*Anthrenus fuscus*	At.fu	9	14	Synanthropic, Trees
Scraptiidae	*Anaspis garneysi*	As.ga	8	13	Decaying wood
Byturidae	*Byturus ochraeus*	By.oc	7	18	Tall sward, scrub
Chrysomelidae	*Bruchus rufimanus*	Br.ru	7	7	Tall sward, scrub
Coccinellidae	*Coccinella septempunctata*	Co.se	6	50	Generalist

Table 3 Summary of redundancy analysis (RDA, presence–absence models) and partial redundancy analysis (pRDA, full community models) results

Global model shows the combined effect of all variables; reduced models were determined via forward selection to identify key explanatory variables

Significance of variation partitioning fractions: **p < 0.01

	Abundance					Presence–absence		
	F	p	Explained	Var-Part %		F	p	Explained (%)
				AB	PA			
Immediate habitat (30)								
All variables	1.412	0.010	28.8%			1.327	0.002	29.0
GARDEN	2.311	0.006	12.8%	2.4**	3.5**	1.776	0.003	14.8
TREES	2.248	0.006				2.071	< 0.001	
ROUGH	n/s					1.466	0.040	
Mesoscale landscape (200)								
All variables	1.412	0.009	29.2%			1.247	< 0.001	27.0
GARDEN	2.311	0.004	13.9%	3.7**	0.4	n/s		
TREES	2.248	0.003				n/s		
TRPATCH						2.198	< 0.001	6.2

pulicaria, which is thought to breed in more open habitats than other members of *Anaspis* spp (Levey 2009). More species responded negatively to gardens than positively. However, *A. verbasci* was very strongly associated with gardens and a few other species also showed weakly positive correlations with garden cover, including *Byturus tomentosus*, which is known as a pest of cultivated raspberries.

GARDEN ($p = 0.003$), TREES ($p = 0.001$) and ROUGH ($p = 0.040$) were significant predictors of species presence–absence, together explaining 14.8% of variation (Table 3). The first constrained axes

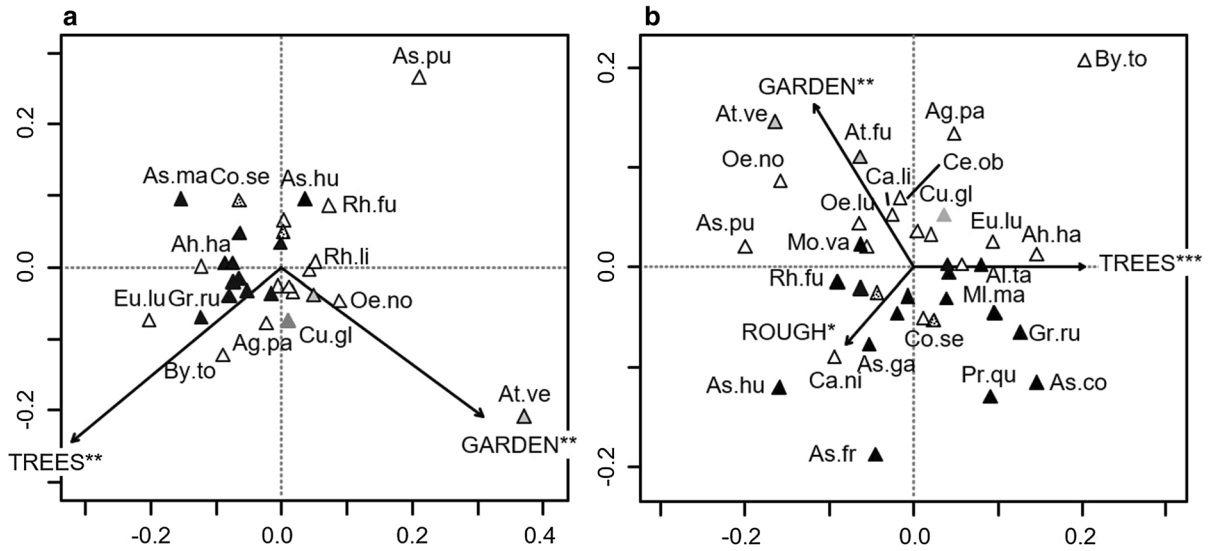

Fig. 2 Redundancy analysis bi-plots showing the key 30 m habitat composition variables that explain flower-visiting beetle community composition. **a** Shows analysis for full community data, **b** for presence–absence only. The length of arrows indicates the strength of correlation between the variables and the constrained axes. Symbols indicate habitat association; black triangle = deadwood associated, grey = other arboreal, grey fill = synanthropic, open triangle = tall sward or scrub, pattern fill = generalist. Significance of variables $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Species can be projected perpendicularly onto the arrows to infer the strength of the correlation between individual species and predictor variables. The highest scoring species on either axis or those otherwise mentioned in the text are labelled. Abbreviations for frequently encountered species are listed in Table 2; additional species labelled are *Alosterna tabacicolor* (Al.ta), *Cantharis livida* (Ca.li), *Cantharis nigricans* (Ca.ni), *Ceutorynchus obstrictus* (Ce.ob), *Curculio glandium* (Cu.gl), *Eusphalerum luteum* (Eu.lu), *Malthodes marginatus* (Ml.ma), *Mordellochroa variegata* (Mo.va), *Oedemera lurida* (Oe.lu) and *Rhagonycha limbata* (Rh.li)

(RDA1, 6.8%, $p < 0.001$) is a gradient from transects with low tree cover and higher proportion of rough vegetation and gardens to transects with high tree cover (Fig. 2b). The second constrained axis (RDA 2 5.1%, $p = 0.014$) is a gradient from transects with high garden cover and less rough vegetation to those with fewer gardens in the vicinity. Very abundant species that responded strongly in the full community analysis show a similar direction of response on the presence–absence bi-plot but are less dominant on each axis compared to other species. A stronger association with gardens is revealed for some species such as *Anthrenus fuscus* and *Oedemera nobilis* (Oedemeridae). *Anaspis humeralis, A. frontalis* and *Cantharis nigricans* were more likely to be found on transects with high rough vegetation cover.

Mesoscale landscape heterogeneity

Mesoscale landscape composition explained 29.2% of variation in the full community data ($F = 1.412$, $p = 0.009$) and 27.0% of presence–absence ($F = 1.327$, $p = 0.023$). Forward selection again identified GARDEN ($p = 0.004$) and TREES ($p = 0.003$) as significant predictors of full community composition, explaining 13.9% of total variation. Only TREES ($p < 0.001$) was retained in the reduced model for species presence–absence, explaining 5.9% of variation. Landscape configuration variables explained 26.0% of variation in the full community composition ($F = 1.453$, $p = 0.012$) and 27.0% of species presence–absence ($F = 1.247$, $p < 0.001$), with TRPATCH the only variable retained in the reduced model in both cases (both $p < 0.001$).

GARDEN and TREES were retained in a combined composition/configuration model for full community data. TRPATCH was removed as it was collinear with TREES and the model explained more variation with TREES included rather than TRPATCH. The bi-plot (Fig. 3a) is similar to that for local habitat composition but with some changes in the strength of association for individual species. *Rhagonycha fulva* was

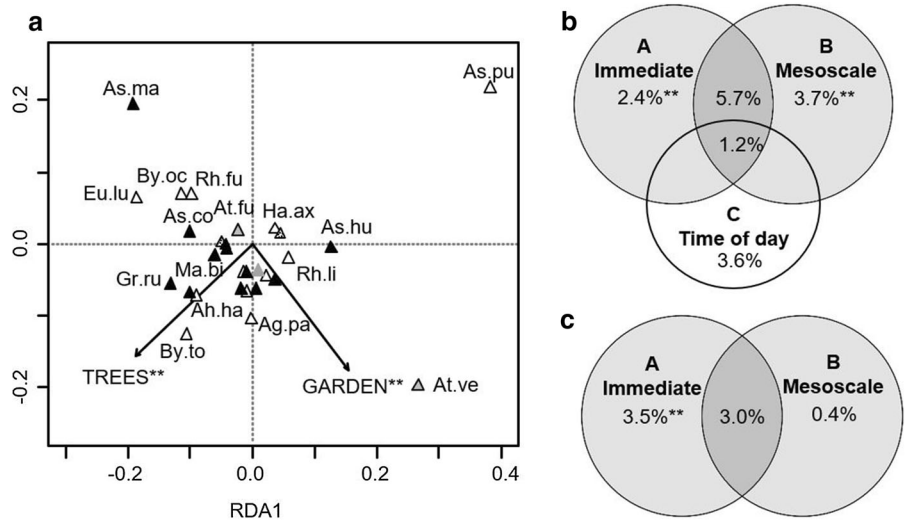

Fig. 3 **a** Redundancy analysis bi-plot showing the key 200 m landscape variables that explain flower-visiting beetle community composition. The length of arrows indicates the strength of correlation between the variables and the constrained axes. Significance of variables $*p < 0.05$, $**p < 0.01$, $***p < 0.001$. Species can be projected perpendicularly onto the arrows to infer the strength of the correlation between individual species and predictor variables. The highest-scoring species on either axis or those otherwise mentioned in the text are labelled. Abbreviations for frequently encountered species are listed in Table 2; additional species labelled are *Cantharis nigricans* (Ca.ni), *Eusphalerum luteum* (Eu.lu), *Harmonia axyridis* (Ha.ax), *Malachus bipustulatus* (Ma.bi), *Malthodes marginatus* (Ml.ma) and *Rhagonycha limbata* (Rh.li). Symbols as for Fig. 2. **b** Variation partitioning for full community and **c** presence–absence only data. Proportions of variation explained are expressed in terms of R^2-adj; A + B indicate the unique effect of the reduced model in each case; C is the joint effect. Significance of fractions: no symbol $p > 0.05$, $*p < 0.05$, $**p < 0.01$

negatively associated with tree cover on the local habitat bi-plot but showed a weak positive association at the mesoscale landscape level. *A. fuscus* was positively associated with gardens at local habitat scale but showed a weak preference for mesoscale landscapes with lower garden cover. The top-middle section of the bi-plot is empty, showing that no species had a strong negative association with both trees and gardens.

In the combined model for presence–absence, TREES and TRPATCH were collinear. TRPATCH was retained as it explained a larger proportion of variation (6.2%, $p < 0.001$). The one constrained axis explained 6.2% of the variation and described a gradient from landscapes with on average larger tree patch size to those with smaller patches of trees.

Variation partitioning

Variation partitioning for the full community showed that the reduced models for 30 m local habitat, 200 m landscape and the conditional variable TIME2 together explained 16.1% of variation in the full community data (Fig. 3b). The part of this attributable uniquely to local habitat was 2.4% ($p = 0.004$). 200 m landscape explained 3.7% ($p = 0.007$) and 5.7% was shared variation, not attributable to local habitat or landscape alone. The condition TIME2 explained 3.6% of variation ($p = 0.004$) and 1.2% was shared between all three elements. For the presence–absence data, the total variation explained was 6.9% (Fig. 3c). Of this, 3.5% was uniquely attributable to 30 m habitat composition ($p = 0.010$) and 0.4% to 200 m landscape; this portion was non-significant ($p = 0.272$). 3.0% was shared.

Discussion

Variation partitioning showed a unique contribution of mesoscale landscape heterogeneity at 200-m radius, similar in magnitude to the contribution of immediate habitat composition. This provides a clear yes to question (i). However, in the presence–absence analysis the landscape element was non-significant. This suggests that the *abundance* of some flower-visiting

beetles at a particular site is modified by features in the surrounding mesoscale landscape [contrary to Sjödin et al. (2008)], but that the *presence* of a species is determined only by the proximity or suitable habitat.

To answer question (ii), garden extent and tree cover were consistently identified as drivers of community composition. These relate to landscape composition; no measures of configuration were found to be significant. Mean tree patch size explained a significant portion of variation in the presence–absence data, confirming expectations for saproxylic beetles (Irmler et al. 2010) but not in a previous study of flower-visiting insects (Horak 2014). However, patch size did not uniquely explain any variation once partitioned with local habitat, suggesting that this variable is a proxy for patch size or habitat amount adjacent to the transect. Indeed, no landscape configuration variables (including diversity and contagion) were important, consistent with the suggestion of Barbaro et al. (2007) that, at the mesoscale, spatial heterogeneity is a proxy for composition.

Previous studies of other beetle communities at similar spatial scales have obtained variable results, with landscape composition within a 400-m radius the main driver of Carabid communities in Barbaro et al. (2007) but unimportant (at any scale between 200 and 2000 m radius) in Philpott et al. (2014). Landscape composition within a few hundreds of metres radius has also been linked to species richness in solitary bees and wasps (Steckel et al. 2014; Hardman et al. 2016).

In answer to question (iii), the overall community response (Figs. 2, 3a) is one of tree associated species positively correlated with the immediate presence of trees but negatively with gardens, while responses to tree and garden amount in the surrounding mesoscale landscape are less predictable. The following sections address in more detail how the flower-visiting beetle community is shaped by the main landscape elements identified.

Woodland and non-woodland trees

This study underlines the importance of trees—both inside and outside woodland—as habitat for a diverse community of beetles. Forest cover in the surrounding landscape has also been identified as the most significant driver of community composition in bees on wildflower strips (Fabian et al. 2013) and hoverflies in flower-rich grasslands (Sjödin et al. 2008).

Thirty-one of the species recorded are associated with trees, most of them saproxylic (dependent on dead or decaying wood). Higher tree cover both close to the transects and in the surrounding mesoscale landscape boosted the presence and abundance of a number of saproxylic species; tree cover has previously been identified as a proxy for deadwood availability (Götmark et al. 2011; Jacobsen et al. 2015).

Species positively correlated with trees, for which the main larval habitat is indeed arboreal, included *Grammoptera ruficornis* (Cerambycidae), *M. bipustulatus* (Malachiidae) and *Malthodes marginatus* (Cantharidae), while others such as *Eusphalerum luteum* (Staphylinidae) and *B. tomentosus* are not associated with trees in terms of larval habitat but could have a preference for shady conditions when feeding on flowers as adults.

Whilst some saproxylic beetles are known to be dispersal-limited (Irmler et al. 2010; Brin et al. 2016), this study found no evidence that mesoscale landscape configuration variables—i.e., measures of connectivity—influenced community composition. However, rarer species that are more often restricted by habitat connectivity were almost entirely absent from the community in our study, so we cannot conclude that landscape configuration at this scale is always unimportant for beetles.

Although one-third of the species recorded were associated with decaying wood, most that were detected on enough transects to be included in the analysis are associated with ephemeral habitats (e.g., *Anaspis* spp. in dead twigs and small branches) and so are likely to disperse relatively well (Southwood 1977; Nordén et al. 2014). During fieldwork, individuals of *Anaspis* were observed to fly readily and, being small-bodied (2.5–4.5 mm), could potentially travel some distance beyond the local dispersal flights away from habitat patches reported by Irmler et al. (2010), especially in convective conditions. No measure of habitat quality was included here and much of the unexplained variation in the community data, especially that pertaining to arboreal species, is likely to be related to the more precise distribution of habitat resources (e.g. tree species, stage of decay) within the generic cover type ‘Trees’.

Gardens

In the case of *A. verbasci*, a positive correlation with gardens is likely to be a proxy for buildings. For the rest of the beetle community, responses were varied. Roughly equal numbers of species responded positively and negatively to both the amount of garden cover immediately adjacent to the transect and garden cover in the surrounding mesoscale landscape. This suggests that the modifying impact of urban areas on biodiversity overall is more complex than a straightforward loss of habitat and thus biodiversity to impervious surfaces (McIntyre et al. 2001; Wolf and Gibbs 2004; Plascencia and Philpott 2017).

A large-scale study in France found that flower-visiting insect communities are functionally more homogenous in urban areas (Deguines et al. 2016). However, gardens with high canopy cover or diverse planting support more diverse arthropod communities (Lowenstein et al. 2014; Otoshi et al. 2015; Salisbury et al. 2015), and (Baldock et al. 2015) found that bee species richness and abundance were higher in urban gardens than in nearby farmland or nature reserves, showing that gardens are able to support relatively high levels of biodiversity. Gardens in our study landscape were mostly associated with small settlements. Rural villages and farmsteads have been identified as important reservoirs of bird diversity in agricultural landscapes (Rosin et al. 2016) and it is possible that small settlements similarly shape insect communities. The influence of gardens in our study landscape is perhaps surprising given that they covered an average of just 5% of the landscape buffers, with only one other landscape component identified as a significant driver of community composition.

Species ecology

A few species were most abundant on transects bordered by large amounts of their habitat. *G. ruficornis* and *Malachius bipustulatus* breed in decaying trunks or branches and under bark, respectively, and were both more abundant on tree-rich transects, though presence–absence for *M. bipustulatus* was not impacted by tree cover adjacent to the transect. *A. verbasci* was never found far from buildings by Woodroffe and Southgate (1954) and was strongly correlated with garden extent here. *Anaspis pulicaria* has been described as 'more of an open habitat species' (Levey 2009); the present study confirms this observation as the species was negatively correlated with tree cover.

In the presence–absence analysis, many species were correlated strongly with more than one explanatory variable. This may indicate a requirement for diverse resources associated with different life stages, such as dead branches for oviposition and larval development and more open sites with abundant nectar resources. Preferences for sunny sites (Kadej et al. 2018) and shady or sheltered ones (Dover et al. 1997) have both been observed in insects, though the response of beetles to small-scale habitat complexity varies (Ford et al. 2017).

Large amounts of rough vegetation, which in the present study refers mainly to vegetation dominated by a mix of Apiaceae, long grass, and common herbaceous plants such as nettle (*Urtica dioica*) or docks (*Rumex* ssp.) increased the probability that some species would be present on the transect. This may indicate preferences for large expanses of flowering Apiaceae to gather nectar, though the density of flowering stems was directly measured during sampling and not found to be a significant driver of community composition. Several species that were positively correlated with rough vegetation are predators of other insects (*C. nigricans, R. fulva, Harmonia axyridis, M. bipustulatus*), perhaps indicating that large extents of this cover type can support diverse insect communities, as seen in arable field margins (Thomas and Marshall 1999; Birkhofer et al. 2014).

Conclusions

Our results show that for flower-visiting beetles, mesoscale landscape composition explains a significant proportion of community composition. For those species sampled, landscape connectivity does not shape the community at this scale. The variable trees included non-woodland trees and increased variation explained when compared to models that only included woodland patches (Henry et al. 2017; Sullivan et al. 2017), underlining the importance of non-woodland trees for biodiversity in heterogeneous landscapes.

Gardens modified beetle communities despite representing a small part of our study landscape. Gardens can make a significant contribution to maintaining

biodiversity (Hunter and Hunter 2008; Goddard et al. 2010; Plascencia and Philpott 2017), further work on the role of small urban settlements within agricultural landscapes would help to assess whether their impact on insect biodiversity is indeed positive.

Author contributions CWF, JLN and GJH conceived and designed the study. CWF collected and analysed the data. CWF drafted the manuscript with significant input and critical revisions from JLN and GJH.

Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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