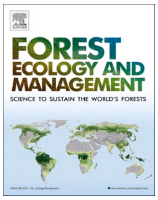
Forest Ecology and Management 593 (2025) 122885

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Agricultural landscapes impede woodland ground-dwelling beetle colonisation and establishment in planted woodlands

Samuel P. Rogerson [a,*], Ben A. Woodcock [b], Elisa Fuentes-Montemayor [a], Kevin Watts [a,c], Emily H. Waddell [a], Matt Guy [c], Ian Hayward [a], Kirsty J. Park [a]

[a] University of Stirling, Stirling, Scotland FK9 4LA, UK
[b] UK Centre for Ecology & Hydrology, Maclean Building, Crowmarsh Gifford, Wallingford OX10 8BB, UK
[c] Forest Research, Alice Holt Lodge, Farnham, Surrey GU10 4LH, UK

ARTICLE INFO

Keywords:
Woodland ecology
Insect ecology
Restoration
Coleoptera
Colonisation credit
Woodland creation

ABSTRACT

Global insect declines have been partly attributed to habitat loss and agricultural intensification. Large-scale habitat restoration is crucial to address this biodiversity crisis, with woodlands representing a key habitat that supports diverse insect communities, particularly beetle assemblages. However, little is known about beetle colonisation and establishment processes as woodland is created. Using data from a long-term natural experiment (the WrEN project), we investigate the relative importance of local and landscape characteristics on ground-dwelling beetle colonisation and establishment across 60 UK secondary broadleaved woodlands. Our sites, planted 12 – 160 years ago, range in size between 0.5 – 32 ha and are embedded in landscapes ranging from 20 – 90 % agriculture. Using structural equation models, we show that woodland generalist and specialist beetles were more abundant in larger woodlands and more species-rich in woodlands with a lower proportion of surrounding agriculture. Woodland specialists were more abundant in woodlands with lower tree densities, a positive indirect effect of woodland age. Beetle community composition varied according to woodland age and structure, with younger and more homogenous woodlands having more non-woodland species. These findings suggest that the agricultural matrix may hinder woodland beetle colonisation into newly established woodlands in farmed landscapes. To enhance beetle biodiversity, woodland restoration initiatives should prioritise planting larger sites, and active management such as selective thinning that reduces tree density and increases structural heterogeneity. We highlight a potential paradox between the benefits of restoration that avoids landscapes with high agriculture to promote beetle colonisation vs. targeting these landscapes in efforts to enhance biodiversity.

1. Introduction

Large-scale restoration efforts are underway globally to mitigate climate change (Canadell and Raupach, 2008) and tackle the ongoing biodiversity crisis (Leclère et al., 2020). Ambitious initiatives such as the UN’s REDD+ , the Bonn Challenge, and the UN Decade on Ecosystem Restoration aim to reverse centuries of habitat loss by restoring degraded landscapes and expanding forests to enhance carbon stocks and increase biodiversity (FAO, 2020). While the benefits of increased tree cover for carbon storage and climate change mitigation are relatively predictable (Banin et al., 2022), forecasting biodiversity outcomes is more challenging (Bastin et al., 2019). This complexity arises partly from significant temporal lags, known as ‘colonisation credits’, between restoration efforts and subsequent species colonisation and establishment (Jackson and Sax, 2010). Colonisation credits reflect the time a habitat needs to develop sufficient biotic and abiotic complexity to support a diverse range of species. Such lags have been widely observed for various species and diverse ecosystems, operating over broad spatial and temporal scales (Watts et al., 2020). They may be particularly pronounced in habitats like temperate woodlands, characterised by slow development rates (Fuentes-Montemayor, Watts, et al., 2022).

Within woodlands, beetles fulfil vital ecological functions (e.g., nutrient cycling; Nichols et al., 2008), serve as a crucial food source for many taxa (e.g., birds and small mammals; Holland, 2002), and act as valuable indicators of forest health (Pearce and Venier, 2006). Many ground beetle species have experienced substantial declines across Europe (Kotze and O’Hara, 2003), including woodlands and pasture (e.

---

* Corresponding author.
E-mail address: spr1@stir.ac.uk (S.P. Rogerson).

https://doi.org/10.1016/j.foreco.2025.122885
Received 17 February 2025; Received in revised form 30 May 2025; Accepted 1 June 2025

g. a 30 % decline in overall abundance in most habitats from 1994 to 2008 in the UK; Brooks et al., 2012). Historical woodland loss and subsequent qualitative degradation are recognised as major contributors to beetle population declines in Europe (Seibold et al., 2019). Despite recent increases in woodland cover in parts of Europe since the mid-20th century (Fuchs et al., 2015), these gains often represent non-native coniferous forests for timber, rather than mixed or broadleaf woodlands for biodiversity. Transitions from traditional management practices (such as coppicing and pasture woodlands) to high forest systems, where trees are grown to maturity with closed canopies and relatively uniform age structures, may have fundamentally altered habitat quality for many specialist species. These changes in woodland structure, management practices, and the resulting impact on connectivity between suitable habitat patches likely play significant contributory roles in species losses (Lange et al., 2014; Neumann et al., 2017).

Given these historical changes in ongoing woodland restoration efforts, understanding the factors that facilitate beetle colonisation in newly created woodlands is crucial. Woodlands created on former agricultural land face two potential barriers for beetle colonisation and subsequent establishment. The first is the degree to which the surrounding landscape aids or hampers movement across the habitat. Agricultural land, often characterised by continuous disturbance through intensive agricultural practices (e.g. monocultures, pesticide use, continuous stocking), may present a challenging environment for woodland beetles to traverse (Eycott et al., 2012). This is particularly true for flightless beetles or those with limited dispersal mechanisms (Hanson et al., 2016; Woodcock et al., 2012). For example, many large flightless carabids (e.g. *Carabus* spp.) can be restricted to ungrazed habitats (Petit and Usher, 1998) and woody features are required to facilitate the dispersal of woodland carabids across agricultural landscapes (Petit, 1994). Increasing habitat connectivity by creating networks of corridors, such as roadside verges, hedgerows, and connected woodland patches, can allow beetles to disperse more effectively (Della Rocca et al., 2023; Noordijk et al., 2011).

The second barrier is whether species, having reached a new woodland, can establish a self-sustaining population. Beetle species vary in their response to local habitat characteristics, partly due to differences in their habitat specificity, with woodland specialists typically displaying a stronger association with local woodland characteristics than generalists. In young, naturally regenerated woodlands, beetle communities generally harbour fewer species and lower abundances than mature woodlands (Johansson et al., 2016). This is primarily due to the limited availability of resources and habitat complexity in younger stands, which affects species groups such as Carabidae (ground beetles) and Curculionidae (weevils, bark beetles, and allies). Mature woodlands, on the other hand, can support a higher diversity and abundance of beetles, including rare and specialised species, due to the presence of old trees, dead wood, and a more stable microclimate (Hülsmann et al., 2019; Johansson et al., 2016). Complex structures such as leaf litter, deadwood, and diverse vegetation layers in mature woodlands provide niches for various beetle species, enhancing their diversity and abundance (Lassau et al., 2005). Furthermore, woodland size can also influence beetle community composition, as larger woodlands tend to support a higher abundance of woodland specialist species, whilst generalist species tend to be more abundant in smaller patches (Gaublomme et al., 2008; Neumann et al., 2017). It is evident that to better inform restoration projects, we need to consider the relative and combined effects of local and landscape characteristics on beetle communities.

Despite considerable research on beetle populations in primary and secondary woodlands (e.g., Gaublomme et al., 2008; Johansson et al., 2016) studies over expansive spatial and temporal scales are limited (Hülsmann et al., 2019; Lassau et al., 2005). In this study we assess the relative influence of local and landscape characteristics on ground-dwelling beetle communities in 60 planted secondary woodlands over 160 years and across 15,000 km^2 in agricultural landscapes in Scotland and England. We employed Structural Equation Modelling to examine whether woodland age directly influenced beetle abundance, richness, and community composition, or whether these effects were mediated by age indirectly through changes in woodland characteristics.

We predicted beetle species abundance and richness responses to woodland creation and local and landscape variables (such as the amount of deadwood and the proportion of surrounding agriculture) to vary according to the degree of habitat preference (woodland specialists and generalists vs. non-woodland species). We also expected differences in beetle community composition across gradients of woodland age, size, and proportion of surrounding agriculture, with a gradual community shift towards specialists as woodlands mature.

2. Methods

2.1. Site selection and study design

This study is part of the WrEN (Woodland Creation and Ecological Networks) project, a natural experiment investigating the responses of a range of biota to woodland creation (Watts et al., 2016; wren-project.com). We employed a systematic approach to select 60 deciduous woodlands from the National Forest Inventory (NFI; Forestry Commission, 2012), which allowed us to identify broadleaf woodland patches planted over the last 160 years on previously agricultural land in Scotland and England. Sites were selected to represent a gradient in size (0.5 – 32 ha) and surrounding agricultural characteristics of fragmented woodland patches in UK lowland agricultural landscapes (see 2.3 for methods). The Scottish sites covered a ~7000 km ^{2} area in central Scotland, and England sites an ~8000 km ^{2} area in central England. We selected predominantly broadleaved/mixed woodland patches, and these were dominated by oak (*Quercus* spp.) and birch (*Betula* spp.) in lowland agricultural landscapes (Scotland = 57 %, England = 80 % agricultural cover; Fig. 1) to minimise variation in topography (39 Scottish sites: mean elevation = 116.8 ± 68 m; 21 English sites: mean elevation = 92.6 ± 27.4 m). Woodland sites were chosen to be a minimum of 1 km from each other to facilitate spatial independence at the landscape-scale (Scotland: mean = 34.9 ± 8.2 km; England: mean = 50.1 ± 9.3 km). The age of the restoration site was estimated using digital scans of Ordnance Survey maps from the 1840s-1990s (An Ordnance Survey/EDINA supplied service http://digimap.edina.ac.uk/) identifying the first appearance of each woodland patch (for details see: Watts et al., 2016).

2.2. Ground-dwelling beetle surveys

We sampled ground-dwelling beetles using pitfall traps for ten weeks from June to August 2013 and 2014. Scottish sites were sampled in 2013 (n = 20) and 2014 (n = 19), and English sites were sampled in 2014 (n = 21). Each site was sampled in one year only. Pitfall traps had an aperture of 70 mm and were filled with a 30 % propylene glycol-water solution with a small quantity of unscented detergent. Traps were covered with a rain cover and arranged in a transect running from the edge to the centre of the woodland patch at 0, 1, 2, 5, 10, 25, 50 m and thereafter at 25 m intervals to 250 m to capture species with varying degrees of woodland affinity (e.g. specialists, generalists). The number of points on this transect depended on woodland patch size so that the smallest sites only had six trapping locations along the transect (0–25 m transect) and the largest 15 (0–250 m transect). Sample collections occurred at 2-week intervals. Beetles were only included in the study if identified to species level (94.39 % of total catch). All specimens identified to genus (0.01 %) or sub-family level (5.6 %), such as the taxonomically complex Aleocharinae (Staphylinidae), were excluded from analyses. For the purposes of this study, data from all traps across all sampling periods were combined at the site level.

We further categorised all species into three distinct categories (woodland specialists, woodland generalists, and non-woodland) using

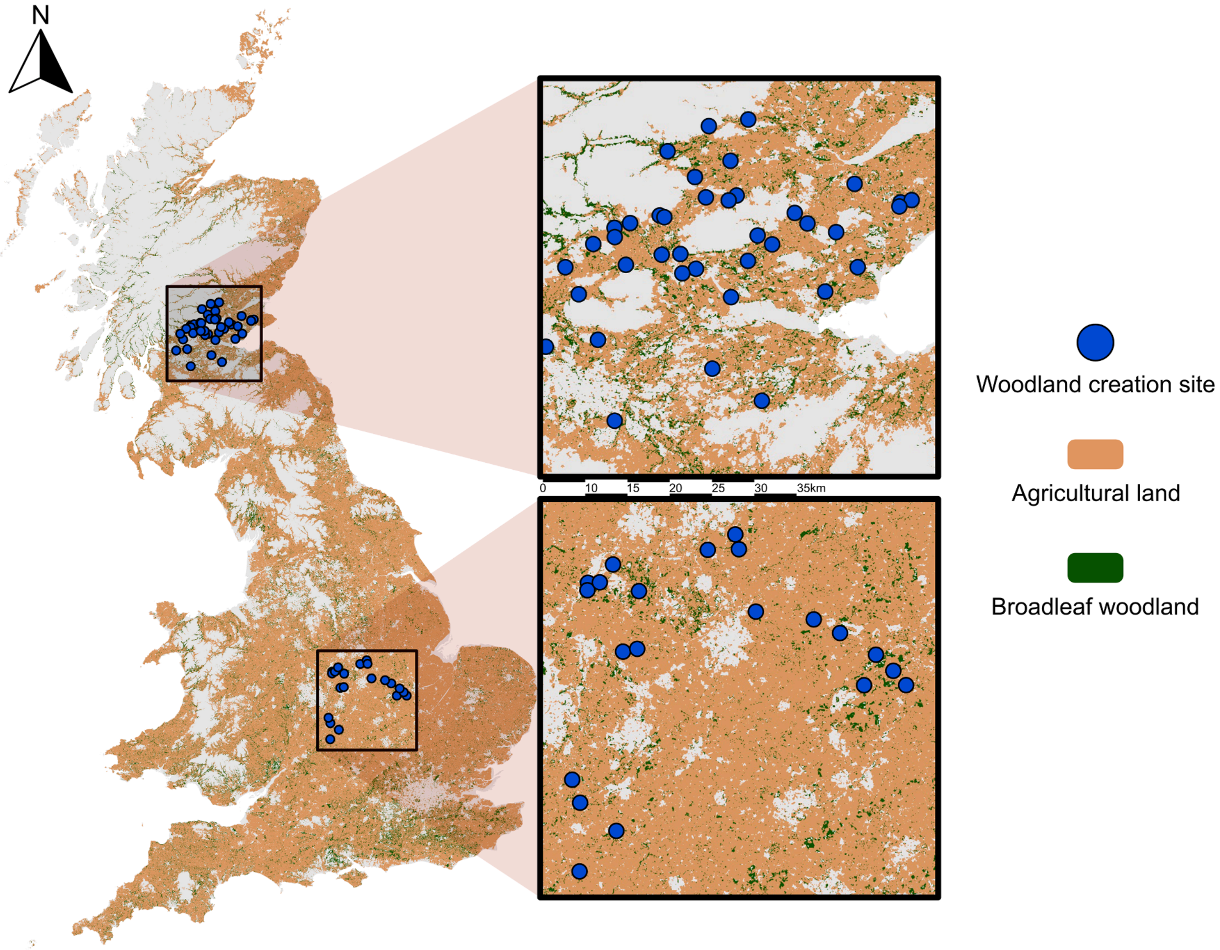


Fig. 1. Map of Great Britain with Scottish (n = 39) and English (n = 21) woodland creation sites highlighted. Land cover at 25 m resolution shows agriculture (including arable, horticulture, and improved grassland) and woodland (including broadleaf, mixed, and yew woodland). Raster from Land Cover Map 2015 (Rowland et al., 2017).

a range of sources (Hubble, 2012; Luff, 1998, 2007; Webb et al., 2017). Here, we consider woodland specialists to be species with an obligate association with woodland habitats, depending on them for most of their life cycle. We define 'woodland generalists' as beetle species that utilise a broad range of resources and habitats and, while frequently found in woodlands, are not restricted to them (Gaublomme et al., 2008). We chose these groups as there is widespread evidence to suggest that woodland specialist invertebrates have undergone declines over the past few decades (Bowler et al., 2023). In contrast, woodland generalist and non-woodland species (those that are typically associated with other habitat types such as grasslands or agricultural systems) have experienced mixed trends (Bowler et al., 2023; Brooks et al., 2012).

2.3. Local woodland characteristics

We conducted field surveys during the summers (June – August) of 2013 and 2014 to characterise the vegetation structure of all woodland sites using the point-centred quarter method along an edge-to-interior transect (Ferris-Kaan et al., 1992). At each designated point along the transect, a cross-shaped marker was established using two perpendicular lines (one aligned with the transect direction) to divide the surrounding area into four quadrants. Within each quadrant, the distance from the centre point to the nearest tree was measured (used subsequently to calculate tree density), the species identified, and its diameter at breast height (DBH) was recorded (only trees $\geq$7 cm were included). The standard deviation of DBH measurements (tree DBH S.D.) was calculated as our proxy for structural heterogeneity. A 2 × 2 m quadrat was positioned at the centre point to visually assess the woody debris on the ground using an index ranging from 1 to 3: 1 represented leaf litter and small twigs ($\leq$1 cm in diameter), 2 denoted larger branches ($\leq$10 cm), and 3 indicated coarse woody debris (>10 cm), including fallen trees. We then calculated an overall site deadwood score by taking the mean of these categorical scores across all quadrats for each woodland. Canopy cover (%) was evaluated using a sighting tube with an internal crosshair (Ferris-Kaan et al., 1992). Ten measurements were taken at 1 m intervals perpendicular to the transect at each transect point. For each measurement, the presence of canopy vegetation was recorded if the crosshair intersected canopy vegetation.

2.4. Surrounding landscape characteristics

We quantified landscape metrics within a range of buffer sizes around each woodland creation site: 100, 250, 500, 1000, 1500, 2000, 2500, and 3000 m from the woodland edge. We used LCM (2015 Landcover Map data; (Rowland et al., 2017) data to quantify the proportion of agricultural land (arable and agriculturally improved grassland) and NFI data (25 m resolution; Forestry Commission, 2012) to calculate inter-patch connectivity of broadleaf woodland. The broadleaf woodland connectivity index was calculated using an adapted Incidence Function Model (IFM) from Watts and Handley (2010) to assess potential connectivity at the landscape-scale. This metric combines the areas of woodland patches and a dispersal function to calculate connectivity among patches, providing a measure of ecological connectivity influenced by patch size, total woodland area, isolation, and configuration (see Supplementary Information Appendix 1 for more detail). At the maximum buffer of 3 km from the perimeter of each focal patch, the connectivity index ranged from 9 – 21231, with low values indicating a landscape with poor broadleaf woodland connectivity and high values denoting well-connected broadleaf woodland. All spatial analyses were calculated using the 'Simple Features' (Pebesma, 2018) and 'Raster' (Hijmans et al., 2023) packages in R Statistical Software (R Core Team., 2021).

2.5. Data analyses

All statistical analyses were conducted using R Statistical Software version (v4.3.2; R Core Team., 2023) within RStudio 2023.12.1 + 402 "Ocean Storm" release (RStudio Team., 2023).

2.5.1. Beetle abundance and richness in woodland creation sites

We used structural equation models (SEMs) to quantify the relative importance of local and landscape-scale characteristics on beetle abundance and richness. SEMs are a multivariate technique that can test whether *a priori* hypothesised direct and indirect causal relationships between variables are supported by observed data and compare the relative effect sizes of predictor variables (Lefcheck, 2016). We developed a metamodel examining how landscape and local characteristics influence beetle communities.

For our analyses, we used the proportion of agricultural land and broadleaf woodland connectivity measured at the 3000 m radius buffer, as this scale showed the strongest relationships with beetle richness during preliminary multi-scale analyses (see Supplementary Appendix 2 for buffer selection approach). These landscape metrics were hypothesised to influence beetle colonisation. At the local scale, we included patch size, age, and vegetation characteristics, which were hypothesised to directly and indirectly influence beetle establishment (Fig. 2). For instance, woodland age could directly affect beetle colonisation simply because older woodlands have had more time for beetles to discover them, while also indirectly affecting colonisation through its influence on vegetation structural characteristics. See Supporting Information Appendix 3 for full details on SEM variable selection, hypotheses, and model specification for each direct and indirect pathway.

Our approach to accounting for sampling effort follows the principles established by Gotelli and Colwell (2001), who distinguish between species richness (the number of species for a standardised number of individuals) and species density (the number of species per unit area). In ecological studies, species richness is the more appropriate measure for testing theoretical relationships, as abundance-based standardisation accounts for the inherently non-linear relationship between sampling effort and species accumulation (Gotelli and Colwell, 2001). To implement this approach, we log-transformed the total number of traps per site and incorporated it into our models as an offset for beetle abundance, thereby standardising abundance by sampling effort. We then modelled species richness as a function of this standardised abundance, which appropriately accounts for differences in sampling intensity across sites while maintaining the ecological relationship between abundance and species richness. This standardised abundance will be referred to simply as 'abundance' throughout the remainder of this paper.

Following our metamodel (Fig. 2), we ran three separate models, one each for woodland specialists, generalists, and non-woodland species. For all three models, abundance was modelled with a negative binomial error distribution due to overdispersion in our count data, which is typical in ecological datasets. For species richness, we used different distributions based on data characteristics: Poisson distributions for woodland specialist and non-woodland richness, which showed lower counts with limited variance typical of rare species groups, and a Gaussian distribution for woodland generalist richness, which displayed higher values with greater variance and a more symmetrical distribution. We specified richness as a response to abundance, assuming that sampling more beetles would result in more species being found.

In SEMs, the model output can also highlight significant pathways not initially specified in the metamodel. We have incorporated these into the final SEM, where a plausible ecological relationship exists. Where significant correlations exist between variables but the direction of causality is ambiguous or potentially bidirectional, these relationships are included as correlated errors in the statistical model. Correlated errors acknowledge important ecological relationships without imposing potentially incorrect causal directionality. These correlations are incorporated in the model fitting but are not shown as directional paths in the output diagrams. All correlated errors included in our models are documented in Table S2.

We log-transformed area in our models to align with the natural logarithmic scaling observed in species-area relationships (Lomolino, 2000). Tree DBH S.D. (standard deviation of tree DBH, a measure of the variation in tree size) was log-transformed to reduce skew and meet model assumptions. We further opted to use tree density rather than canopy cover as these variables were positively correlated ($r^2 = 0.45$) in our sites. Additionally, tree density was selected as it represents a more practical metric for woodland managers, who can directly manipulate stand density through thinning operations

SEMs were performed using the "psem" function in the "piecewiseSEM" R package (Lefcheck et al., 2024). Shipley's test of directed separation (Fisher's C) assessed global SEM fit, where values of $p > 0.05$

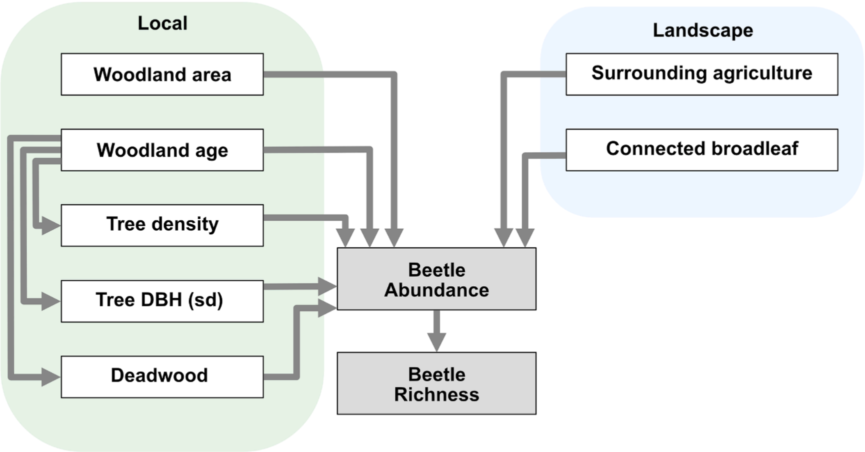


Fig. 2. Hypothetical structural equation metamodel showing potential local and landscape drivers of woodland beetle species colonisation and establishment within planted woodlands. Full details on these variables are within the main text and Supporting Information Appendix 3.

indicate that observed data supports the model. Predicted outcomes for beetle abundance and richness at varying degrees of surrounding agricultural proportion were calculated using the ‘predict’ function as part of the ‘effects’ package (Fox et al., 2022). We assessed spatial autocorrelation within the data by conducting a Moran’s I test, part of the DHARMa package (Hartig and Lohse, 2022), to account for the potential influence of region (Scotland and England) on beetle abundance and richness. There were no statistically significant patterns in spatial autocorrelation ($p > 0.05$).

2.5.2. Beetle community composition across woodland age categories

To compare the composition of the full beetle community (woodland specialists, generalists, and non-woodland species) across woodland development stages, we categorised woodland creation sites into three

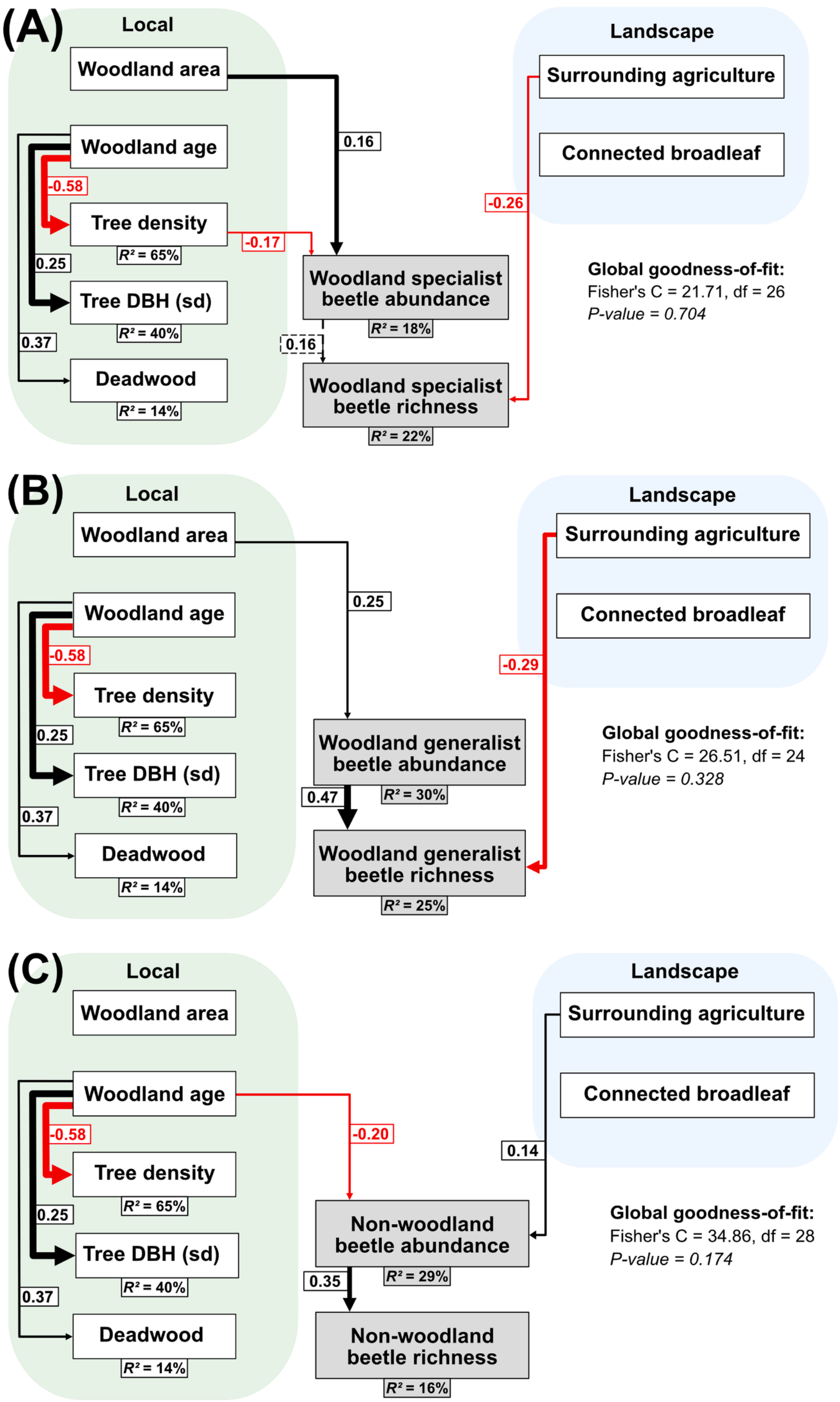


Fig. 3. Structural equation models showing local and landscape-level drivers of beetle species abundance and richness for (A) woodland specialists, (B) woodland generalists, and (B) non-woodland species within 60 planted woodlands in Scotland and England. Significant positive relationships are shown with black lines, and significant negative relationships are shown with red lines. The thickness of each line denotes the strength of the relationship, with thicker lines showing a stronger relationship and dashed lines representing marginal significance (<0.10). Numbers are standardised path coefficients from the SEM. Significant correlated errors (i.e. correlated variables with no causal explanation) included in the model are not shown (see Supporting Information Appendix 3 for more details).

distinct temporal categories based on forest stand dynamics described by Oliver and Larson (1996). These classifications are relevant for deciduous woodland systems in the UK. The categories—'stand initiation' (10–30 years), 'stem exclusion' (31–80 years), and 'understorey reinitiation' (81–160 years; hereby referred to as 'initiation', 'young', and 'mature' respectively)—were applied to all 60 sites, resulting in 18 initiation, 13 young, and 29 mature woodlands.

All of the following analyses and functions were performed with the 'vegan' package (Oksanen et al., 2024). We conducted an ordination using non-metric multi-dimensional scaling (NMDS) on a Bray-Curtis dissimilarity matrix. Ordinations were conducted on site-level data based on the proportion of total captures that each species comprised at each site. For each site, species data were pooled across all collection sessions and trap locations. We used a pairwise ANOSIM approach to determine differences between the centroid (the geometric centre of each group) of each woodland development stage group.

As with the SEMs, we assessed the effect of the development stage, surrounding landscape (proportion of agricultural land and broadleaf woodland connectivity), and woodland structure (deadwood, tree DBH S.D., tree density, woodland area) on community composition using a permutational multivariate analysis of variance (PERMANOVA; 'adonis' function), with 9999 permutations to calculate significance. Finally, a similarity percentage procedure (SIMPER) was performed to determine which beetle species contributed the most to the differences between the development stages.

3. Results

3.1. Abundance and richness of woodland specialists, generalists, and non-woodland beetles in planted woodlands

We recorded 23,244 beetles of 163 species over 37,310 trap days in 60 woodlands; of these, 109 species were categorised as woodland generalists, 16 as woodland specialists, and 38 as non-woodland species (Table S3). Woodland generalists comprised the majority of beetles ($n = 23,244$; 90.2 % of the total catch), with specialist ($n = 176$) and non-woodland ($n = 2355$) species representing a smaller fraction (9.8 % of the total catch). Carabidae ($n = 13,764$, $SR = 54$), Staphylinidae ($n = 11,045$, $SR = 66$), and Hydrophilidae ($n = 574$, $SR = 1$) were the most abundant families (Table S4).

As expected, abundance (corrected for sampling effort by including log-transformed number of traps per site as an offset) and richness were positively associated for all beetle groups (Figs. 3a, 3b & 3c; Table S5). Woodland specialists were more abundant in larger, low-density, and older (an indirect effect mediated by tree density) woodlands and were less species-rich in woodlands with a greater extent of surrounding agriculture (Fig. 3a & Table S5). Similarly, woodland generalist beetles were more abundant in larger woodlands and less species-rich in woodlands with more surrounding agriculture (Fig. 3b & Table S5). For specialists and generalists, increasing arable proportion from 20 – 90 % decreased richness from 1.97 to 0.59 and 20.2–14.1 per site, respectively (a reduction of approximately 70–30 %). In contrast, non-woodland beetles were more abundant in younger woodlands with a higher proportion of agriculture in the surrounding landscape (Fig. 3c & Table S5),

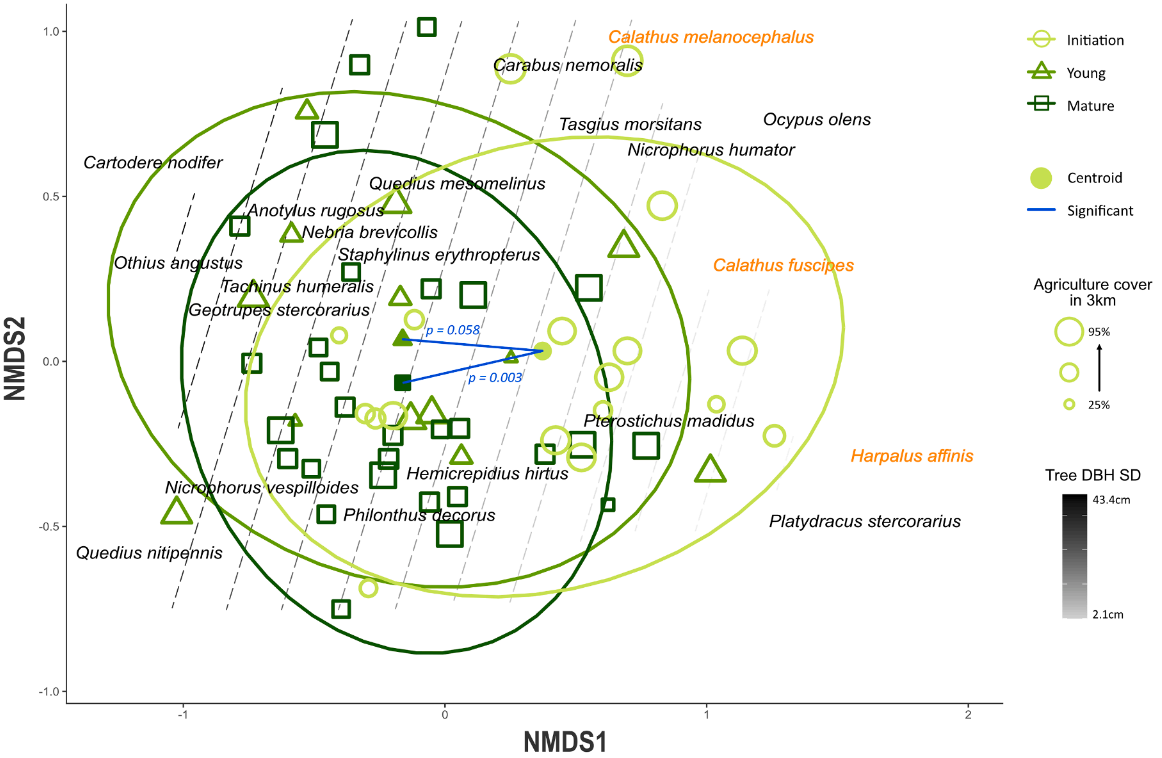


Fig. 4. Non-metric multidimensional scaling (NMDS) of beetle community composition based on relative abundance data (the proportion of total captures per site for each species; Bray-Curtis index) for initiation (10–30 years, $n = 18$), young (31–80 years, $n = 13$), and mature (81–160 years, $n = 29$). Each symbol is shaped according to the development category it represents, depicting one woodland community based on the relative abundance of all beetle species found within woodland sites, including woodland specialists, woodland generalists, and non-woodland species. The size of the shapes indicates the proportion of agriculture in the surrounding landscape, with larger symbols representing higher agricultural coverage. The full shapes indicate the geometric centre of each group (the centroids). The blue significance lines illustrate the results of the pairwise ANOSIM analysis of the centroids (see Table S6 for results). Contour lines illustrate the variation in woodland heterogeneity (as measured by the standard deviation of tree DBH). Species names include the 21 species identified as the ten most influential for each pairwise comparison of development stages (see Table S7 for full results), which were significant at $p < 0.05$ based on permutation-based p-values. They are coloured by their habitat affiliation: generalists = black, non-woodland = orange.

with abundance increasing 208 % from 16.5 to 50.8 in woodlands with 20–90 % agriculture in the surrounding 3 km buffer. The amount of deadwood did not affect beetle abundance or richness in any of our models.

3.2. Beetle community response

Beetle communities showed marked differences between mature woodlands (81–160 years) and those at the initiation stage (10–30 years; Fig. 4 & Table S6), with a marginally significant difference also observed between young and initiation stage woodlands (Fig. 4 & Table S6). While woodland development stage influenced beetle community composition, PERMANOVA analysis revealed a stronger effect of structural heterogeneity (tree DBH S.D.; Table S6) and the proportion of surrounding agriculture (Table S6). We found a greater prevalence of non-woodland beetle species in younger sites with lower structural heterogeneity and higher proportions of surrounding agricultural land (Fig. 4). Beetle communities were more variable in woodlands with a higher proportion of agriculture in the surrounding landscape (Fig. 4 & Table S6).

The SIMPER analysis identified 45 species (Fig. 4 & Table S7) that significantly contributed to driving part of the observed differences in the species compositions between different development stages. Three non-woodland species (*Calathus fuscipes, Harpalus affinis,* and *Harpalus rufipes*) and woodland generalists including *Tasgius morsitans, Pterostichus madidus,* and *Ocypus olens*, were more common in initiation woodlands (10 – 30 years; Fig. 4 & Table S7). Shifts in the occurrence and abundance of woodland generalist species primarily drove changes in community composition between young (31 – 80 years) and mature (81 – 160) woodlands. Woodland generalists *Nebria brevicollis*, *Nicrophorus vespilloides, and Anotylus rugosus* were more associated with young woodlands (Fig. 4 & Table S7), whilst *Serica brunnea* was the only species significantly associated with mature woodlands (Table S7).

4. Discussion

In this study, woodlands with a greater extent of surrounding agricultural land tend to harbour fewer woodland specialist and generalist beetle species while supporting higher abundances of non-woodland species. In contrast, woodland specialist and generalist species are more abundant in larger woodlands. As expected, older woodlands had lower tree density, increased structural heterogeneity (tree DBH S.D.), and more deadwood. Woodland specialists were more abundant in older woodlands with reduced tree density, and non-woodland beetles were more abundant in younger woodlands. Woodland age had a direct negative effect on the abundance of non-woodland beetle species, but an indirect positive effect on woodland specialists, as mediated by reduced tree density within older woodlands. Additionally, we found that differences in overall beetle community composition were driven by several key woodland characteristics - age, tree DBH, and the amount of surrounding agriculture. Specifically, non-woodland beetle species were more prevalent in younger woodlands with more agricultural land in the surrounding landscape.

4.1. Responses of beetles with differing habitat preferences

As hypothesised, we found that the beetle abundance and richness responses varied according to their degree of habitat specificity. Woodland specialist richness was 70 % lower in sites with 90 % surrounding agriculture compared to sites with 20 % surrounding agriculture, while generalist richness was 30 % lower across the same gradient, highlighting the disproportionate impact of agricultural intensification on woodland specialists (Table S8). Several interacting mechanisms may explain this heightened vulnerability. Resource limitations, particularly the reduced availability of deadwood and leaf litter in agricultural matrices (Taboada et al., 2006) combine with dispersal constraints across inhospitable agricultural environments to impact specialist species (Davies and Margules, 1998; Driscoll and Weir, 2005). These effects are exacerbated by agricultural management practices, with grazing pressure significantly constraining woodland carabid distributions (Petit and Usher, 1998). For example, flightless carabids in agricultural landscapes (e.g., *Carabus* spp.) exhibit particular sensitivity to grazing, being largely restricted to ungrazed areas where complex habitat structures and taller vegetation provide both means of dispersal and refuge. This suggests that woodland specialist flightless carabids would face similar or even greater challenges when attempting to disperse through grazed agricultural matrices.

It is important to note that our study sites were embedded in landscapes dominated by intensive agricultural practices, characteristic of much of the UK's agricultural matrix. While agricultural landscapes have been a feature of European ecosystems since the Neolithic times, the intensity of modern farming practices is a significant departure from historical land management, especially in the post-war period (Robinson and Sutherland, 2002). The effects we observe in this study may potentially be less pronounced in landscapes with less intensive agricultural systems that retain natural features that aid beetle movement and dispersal.

The impacts of agricultural intensification extend beyond habitat modification to create physiologically challenging conditions for both generalist and specialist beetles. Landscape modification can create temperature and humidity gradients that penetrate hundreds of metres into woodland patches (Zellweger et al., 2019). While all beetles face physiological challenges in intensively managed landscapes - for instance, Tiede et al., (2022) found that increasing cropland coverage correlated with declining ladybird (Coccinellidae) body condition - woodland specialists are particularly vulnerable. Typically adapted to stable woodland conditions, these specialists often lack the physiological plasticity to cope with environmental fluctuations (Lövei and Sunderland, 1996; Ng et al., 2018). Such physiological impacts may reduce reproductive success, survival rates, and biological control efficacy across Coleoptera families, with specialists experiencing more severe effects due to their limited adaptive capacity.

Specialist vulnerability raises important questions about ecosystem functionality. While generalist species may persist and continue to perform some ecological functions, specialists often fulfil unique roles that cannot be fully replicated by generalists (Olden, 2006). For example, many woodland specialist beetles have co-evolved with specific microhabitats. Predatory carabids and Staphylinids may specialise in hunting under loose bark, soil, or accumulated leaf litter, playing crucial roles in regulating prey population and maintaining natural trophic structures (Antvogel and Bonn, 2001; Gossner et al., 2013). The loss of specialist predators can have cascading effects on agricultural systems - Petit and Usher (1998) demonstrated how the decline of specialist carabid beetles from woodland refuges can lead to outbreaks of pest species such as slugs, which generalist predators may be less efficient at controlling. Furthermore, it has been suggested that the physiological adaptations that make specialists vulnerable to agricultural intensification could be the same traits that make them particularly effective at their ecological roles (Winqvist et al., 2014). For example, morphological adaptations such as specialised body sizes and shapes that allow predatory carabids to hunt efficiently in woodland leaf litter could also reduce their mobility in open agricultural landscapes (Ng et al., 2018). When specialists are replaced by generalists, key ecosystem functions may be performed less efficiently or lost entirely, potentially reducing both the stability and resilience of woodland ecosystems (Clavel et al., 2011). This suggests that maintaining woodland specialist communities is crucial for preserving ecosystem functionality, particularly in increasingly fragmented landscapes.

Non-woodland beetle abundance increased by 208 % in sites as the surrounding agriculture rose from 20 % to 90 % agricultural cover (Table S8). This dramatic increase suggests that agricultural intensification actively facilitates the spillover of open-habitat species into woodland patches (Tscharntke et al., 2012). These species are typically better adapted to disturbed conditions, possessing broader physiological tolerances that allow them to thrive in human-modified landscapes (Didham et al., 2007). This pattern could represent a form of biotic homogenisation (McKinney and Lockwood, 1999; Olden, 2006), where agricultural species increasingly dominate woodland communities, creating novel competitive pressures that may compound habitat modification effects and accelerate woodland specialist decline. Such fundamental reshaping of beetle communities could have significant implications for woodland ecosystem functioning, as species adapted to agricultural conditions replace those co-evolved with woodland habitats.

Contrary to our expectations, we did not detect significant effects of increased woodland connectivity on beetle communities (Sverdrup-Thygeson et al., 2017). This may be due to the generally low numbers of specialists in our study system, limiting our ability to discern connectivity effects. Additionally, the relatively isolated nature of most study sites likely constrained colonisation opportunities, potentially masking any connectivity effects that might be apparent in more connected woodland networks.

An important limitation is that our connectivity metric focused solely on broadleaf woodland patch connectivity and did not incorporate potential dispersal corridors such as hedgerows or other linear landscape features that may serve as critical movement pathways for woodland beetles (Neumann et al., 2017). This omission could explain the lack of detected connectivity effects, as beetles may utilise these landscape elements for dispersal between otherwise isolated woodland patches. Furthermore, specialists within our study may exhibit various dispersal behaviours and responses to different landscape elements, such that simplified connectivity metrics do not uniformly predict their distribution patterns (Driscoll et al., 2013; Hendrickx et al., 2009). Further investigation incorporating these linear connecting habitats into connectivity measures and examining the dispersal traits of different beetle functional groups could help elucidate these patterns.

4.2. Influence of woodland size

Woodland patch size significantly influenced beetle abundance, which in turn tends to drive beetle species richness in all cases (although this was marginal with specialists). Consistent with island biogeography principles, both woodland specialist and generalist beetles showed higher abundance in larger woodland patches (Debinski and Holt, 2000). This pattern likely emerges from the more stable microclimates and reduced edge effects that larger woodland interiors provide (Davies and Margules, 1998). Notably, specialist beetle species responded more strongly to woodland area, suggesting a greater dependence on the specific environmental conditions maintained within larger woodland interiors (Ewers and Didham, 2006; Neumann et al., 2017).

The ecological conditions within woodlands vary according to their size, with larger woodlands typically providing more diverse microhabitats and resources. Larger woodlands tend to maintain more stable environmental conditions including temperature, humidity, and light regimes that benefit woodland-associated species. In contrast, smaller woodlands are characterised by proportionally greater edge effects - with steep gradients in light exposure, temperature, and moisture levels (Zellweger et al., 2019). These environmental variations, coupled with the higher edge-to-interior ratio in smaller patches, could influence the composition of beetle communities.

4.3. Influence of woodland age and structure

Our results demonstrate that woodland maturation drives shifts in beetle community composition. Clear compositional differences were evident between initiation-stage woodlands (10 – 30 years) and both young (31 – 80 years) and mature woodlands (81 – 160 years), though young and mature woodlands supported more similar assemblages. Non-woodland species dominated younger woodlands, while specialist abundance decreased in dense stands. These patterns reflect the gradual development of woodland structure and associated microhabitats over time, particularly through changes in structural complexity (Fuentes-Montemayor, Park, et al., 2022; Gaublomme et al., 2008).

Structural heterogeneity, specifically variability in tree DBH S.D., emerged as a significant driver of beetle community composition. This metric represents the diversity of tree sizes and ages within a stand, which creates varied light regimes, temperature profiles, and microhabitats that can support different beetle assemblages (Parisi et al., 2021). Similar patterns have been observed in other taxonomic groups, such as plants and hoverflies (Fuller et al., 2018; Waddell et al., 2024). Lower specialist abundance within dense, homogeneous stands appears linked to their specific environmental requirements for activities such as hunting and foraging (Gaublomme et al., 2008; Vodka et al., 2009).

Contrary to expectations, we found no significant relationship between deadwood and beetle communities, despite its documented importance for woodland biodiversity (Gossner et al., 2013, 2016). This could be because Carabids – the most abundant family in our study – show less dependency on deadwood compared to other beetle groups (Kacprzyk et al., 2021). Carabids primarily use deadwood for shelter and overwintering rather than feeding, and few studies have demonstrated strong positive relationships between Carabid abundance and deadwood volume (Fuller et al., 2008; Kacprzyk et al., 2021). While pitfall traps effectively sample ground-dwelling beetles, they are less suitable for capturing saproxylic species, which are typically surveyed using emergence traps or direct sampling of deadwood habitats. Therefore, deadwood availability may influence our sampled communities less than studies focusing on saproxylic beetles. The lack of relationship may also partly reflect our methodological approach, which only provided a coarse index (1–3) of deadwood availability and potentially missed important metrics relating to volume and decay stages.

5. Conclusions and implications

This study reveals that ground-dwelling beetle communities respond to woodland characteristics across multiple spatial scales. Our findings present an important restoration paradox: while woodland creation and restoration may be most successful at promoting specialist beetle colonisation in landscapes with lower agricultural cover, there may be greater biodiversity gains from targeting interventions within intensive agricultural landscapes where woodland habitat is scarce. The influences of tree density and structural heterogeneity on woodland specialist abundance and beetle community composition, respectively, suggest that management interventions such as variable-density thinning and diversification of age classes could enhance habitat conditions for these species, regardless of landscape context. While our results focus on ground-dwelling beetles, the observed relationships between habitat specificity, landscape context, and structural complexity extend to other taxonomic groups (Fuller et al., 2018; Waddell et al., 2024). Understanding how these patterns influence ecosystem processes - particularly given specialists' unique and irreplaceable functional roles compared to their more persistent generalist counterparts (Clavel et al., 2011) - would provide valuable insights for conservation planning.

Author Contributions

All authors contributed to the conceptualisation of the research. KJP, KW and EFM designed the methodology. EFM co-led the data collection alongside field assistants. MG calculated the landscape metrics. SPR analysed the data and wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CRediT authorship contribution statement

Emily H. Waddell: Writing – review & editing, Supervision, Conceptualization. **Kevin Watts:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Elisa Fuentes-Montemayor:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Ben A. Woodcock:** Writing – review & editing, Supervision, Conceptualization. **Samuel P. Rogerson:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Conceptualization. **Kirsty J. Park:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Ian Hayward:** Data curation. **Matt Guy:** Writing – review & editing, Data curation, Conceptualization.

Funding

Thank you to our funders: Forestry Commission, University of Stirling, Natural England, Department for Environment, Food and Rural Affairs, The National Forest Company, and Scottish Natural Heritage. Sam Rogerson was supported by the Natural Environment Research Council (NERC) via an IAPETUS2 Doctoral Training Partnership (Grant: NE/S007431/1).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We extend a huge gratitude to those involved with data collection: Morgan Felix for collection and habitat surveys; Mark Ferryman, Thomas Armitage, and Jamie Irvine for processing, and Lloyd Garvey for all the identification. Finally, we are especially thankful to all the landowners who allowed access to their woodlands.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122885.

Data availability

Data collected for this study will be deposited in the Stirling data repository (STORRE).

References

Antvogel, H., Bonn, A., 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24 (4), 470–482. https://doi.org/10.1111/j.1600-0587.2001.tb00482.x.

Banin, L.F., Raine, E.H., Rowland, L.M., Chazdon, R.L., Smith, S.W., Rahman, N.E.B., Butler, A., Philipson, C., Applegate, G.G., Axelsson, E.P., Budiharta, S., Chua, S.C., Cutler, M.E.J., Elliott, S., Gemita, E., Godoong, E., Graham, L.L.B., Hayward, R.M., Hector, A., Burslem, D.F.R.P., 2022. The road to recovery: a synthesis of outcomes from ecosystem restoration in tropical and sub-tropical Asian forests. Philos. Trans. R. Soc. B: Biol. Sci. 378 (1867), 20210090. https://doi.org/10.1098/rstb.2021.0090.

Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., Crowther, T.W., 2019. The global tree restoration potential. Science 365 (6448), 76–79. https://doi.org/10.1126/science.aax0848.

Bowler, D.E., Cunningham, C.A., Beale, C.M., Emberson, L., Hill, J.K., Hunt, M., Maskell, L., Outhwaite, C.L., White, P.C.L., Pocock, M.J.O., 2023. Idiosyncratic trends of woodland invertebrate biodiversity in Britain over 45 years. Insect Conserv. Divers., icad.12685 https://doi.org/10.1111/icad.12685.

Brooks, D.R., Bater, J.E., Clark, S.J., Monteith, D.T., Andrews, C., Corbett, S.J., Beaumont, D.A., Chapman, J.W., 2012. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. J. Appl. Ecol. 49 (5), 1009–1019. https://doi.org/10.1111/j.1365-2664.2012.02194.x.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320 (5882), 1456–1457. https://doi.org/10.1126/science.1155458.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9 (4), 222–228. https://doi.org/10.1890/080216.

Davies, K.F., Margules, C.R., 1998. Effects of habitat fragmentation on carabid beetles: experimental evidence. J. Anim. Ecol. 67 (3), 460–471. https://doi.org/10.1046/j.1365-2656.1998.00210.x.

Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14 (2), 342–355. https://doi.org/10.1046/j.1523-1739.2000.98081.x.

Della Rocca, F., Jansson, N., Chiari, S., Zauli, A., Carpaneto, G.M., 2023. Micro-habitat drivers of saproxylic beetle assemblages in old woodlands of Mediterranean cork oak (Quercus suber). Agric. For. Entomol. 25 (1), 77–90. https://doi.org/10.1111/afe.12532.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M., 2007. Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol. Evol. 22 (9), 489–496. https://doi.org/10.1016/j.tree.2007.07.001.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., Smith, A.L., 2013. Conceptual domain of the matrix in fragmented landscapes. Trends Ecol. Evol. 28 (10), 605–613. https://doi.org/10.1016/j.tree.2013.06.010.

Driscoll, D.A., Weir, T., 2005. Beetle Responses to Habitat Fragmentation Depend on Ecological Traits, Habitat Condition, and Remnant Size. Conserv. Biol. 19 (1), 182–194. https://doi.org/10.1111/j.1523-1739.2005.00586.x.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. Camb. Philos. Soc. 81 (1), 117–142. https://doi.org/10.1017/S1464793105006949.

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., Pullin, A.S., 2012. A meta-analysis on the impact of different matrix structures on species movement rates. Landsc. Ecol. 27 (9), 1263–1278. https://doi.org/10.1007/s10980-012-9781-9.

FAO. (2020). Restoring the Earth - The next decade: Unasylva No. 252 - Vol. 71 2020/1. FAO. https://doi.org/10.4060/cb1600en.

Ferris-Kaan, R., Patterson, G.S., & Patterson, G.S. (1992). *Monitoring vegetation changes in conservation management of forests* (1. publ). HMSO.

Forestry Commission, 2012. National Forest Inventory GB 2012. ⟨https://data-forestry.opendata.arcgis.com/datasets/951a84d62b86428192202590c016beee⟩.

Fox, J., Weisberg, S., Price, B., Friendly, M., Hong, J., Andersen, R., Firth, D., Taylor, S., & R. Core Team. (2022). *effects: Effect Displays for Linear, Generalized Linear, and Other Models* (Version 4.2-2) [Computer software]. ⟨https://cran.r-project.org/web/packages/effects/index.html⟩.

Fuchs, R., Herold, M., Verburg, P.H., Clevers, J.G.P.W., Eberle, J., 2015. Gross changes in reconstructions of historic land cover/use for Europe between 1900 and 2010. Glob. Change Biol. 21 (1), 299–313. https://doi.org/10.1111/gcb.12714.

Fuentes-Montemayor, E., Park, K.J., Cordts, K., Watts, K., 2022. The long-term development of temperate woodland creation sites: From tree saplings to mature woodlands. For.: Int. J. For. Res. 95 (1), 28–37. https://doi.org/10.1093/forestry/cpab027.

Fuentes-Montemayor, E., Watts, K., Sansum, P., Scott, W., Park, K.J., 2022. Moth community responses to woodland creation: The influence of woodland age, patch characteristics and landscape attributes. Divers. Distrib. 28 (9), 1993–2007. https://doi.org/10.1111/ddi.13599.

Fuller, L., Fuentes-Montemayor, E., Watts, K., Macgregor, N.A., Bitenc, K., Park, K.J., 2018. Local-scale attributes determine the suitability of woodland creation sites for Diptera. J. Appl. Ecol. 55 (3), 1173–1184. https://doi.org/10.1111/1365-2664.13035.

Fuller, R.J., Oliver, T.H., Leather, S.R., 2008. Forest management effects on carabid beetle communities in coniferous and broadleaved forests: Implications for conservation. Insect Conserv. Divers. 1 (4), 242–252. https://doi.org/10.1111/j.1752-4598.2008.00032.x.

Gaublomme, E., Hendrickx, F., Dhuyvetter, H., Desender, K., 2008. The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biol. Conserv. 141 (10), 2585–2596. https://doi.org/10.1016/j.biocon.2008.07.022.

Gossner, M.M., Floren, A., Weisser, W.W., Linsenmair, K.E., 2013. Effect of dead wood enrichment in the canopy and on the forest floor on beetle guild composition. For. Ecol. Manag. 302, 404–413. https://doi.org/10.1016/j.foreco.2013.03.039.

Gossner, M.M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K.E., Steffan-Dewenter, I., Schulze, E.-D., Weisser, W.W., 2016. Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? Biol. Conserv. 201, 92–102. https://doi.org/10.1016/j.biocon.2016.06.032.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4 (4), 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Hanson, H.I., Palmu, E., Birkhofer, K., Smith, H.G., Hedlund, K., 2016. Agricultural land use determines the trait composition of ground beetle communities. PLoS ONE 11. https://doi.org/10.1371/journal.pone.0146329.

Hartig, F., Lohse, L., 2022. DHARMa: Residual Diagn. Hierarchical (Multi-Lev. / Mixed) Regres. Models (Version 0. 4. 6) [Comput. Softw. ⟨https://cran.r-project.org/web/packages/DHARMa/index.html⟩.

Hendrickx, F., Maelfait, J.-P., Desender, K., Aviron, S., Bailey, D., Diekotter, T., Lens, L., Liira, J., Schweiger, O., Speelmans, M., Vandomme, V., Bugter, R., 2009. Pervasive effects of dispersal limitation on within- and among-community species richness in agricultural landscapes. Glob. Ecol. Biogeogr. 18 (5), 607–616. https://doi.org/10.1111/j.1466-8238.2009.00473.x.

Hijmans, R.J., Etten, J. van, Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J.A., Hiemstra, P., Hingee, K., Ilich, A., Geosciences, I. for M.A., … Wueest, R. (2023). raster: Geographic Data Analysis and Modeling (Version 3.6-26) [Computer software]. ⟨https://cran.r-project.org/web/packages/raster/index.html⟩.

Holland, J.M. (Ed.). (2002). *The agroecology of carabid beetles*. Intercept.

Hubble, D., 2012. Keys to the adults of seed and leaf beetles of Britain and Ireland: Coleoptera: Orsodacnidae, Megalopodidae and Chrysomelidae. FSC Publications.

Hülsmann, M., Boutaud, E., Buse, J., Schuldt, A., Assmann, T., 2019. Land-use legacy and tree age in continuous woodlands: Weak effects on overall ground beetle assemblages, but strong effects on two threatened species. J. Insect Conserv. 23 (3), 623–633. https://doi.org/10.1007/s10841-019-00156-8.

Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends Ecol. Evol. 25 (3), 153–160. https://doi.org/10.1016/j.tree.2009.10.001.

Johansson, T., Hjältén, J., Olsson, J., Dynesius, M., Roberge, J.-M., 2016. Long-term effects of clear-cutting on epigaeic beetle assemblages in boreal forests. For. Ecol. Manag. 359, 65–73. https://doi.org/10.1016/j.foreco.2015.09.041.

Kacprzyk, M., Błońska, E., Wojas, T., 2021. Deadwood, soil and carabid beetle-based interaction networks—an initial case study from montane coniferous forests in Poland. Article 4. Forests 12 (4). https://doi.org/10.3390/f12040382.

Kotze, D.J., O'Hara, R.B., 2003. Species decline—but why? explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia 135 (1), 138–148. https://doi.org/10.1007/s00442-002-1174-3.

Lange, M., Türke, M., Pašalić, E., Boch, S., Hessenmöller, D., Müller, J., Prati, D., Socher, S.A., Fischer, M., Weisser, W.W., Gossner, M.M., 2014. Effects of forest management on ground-dwelling beetles (Coleoptera; Carabidae, Staphylinidae) in Central Europe are mainly mediated by changes in forest structure. For. Ecol. Manag. 329, 166–176. https://doi.org/10.1016/j.foreco.2014.06.012.

Lassau, S.A., Hochuli, D.F., Cassis, G., Reid, C.A.M., 2005. Effects of habitat complexity on forest beetle diversity: Do functional groups respond consistently? Divers. Distrib. 11 (1), 73–82. https://doi.org/10.1111/j.1366-9516.2005.00124.x.

Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., De Palma, A., DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Young, L., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. Nature 585 (7826), 551–556. https://doi.org/10.1038/s41586-020-2705-y.

Lefcheck, J.S., 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7 (5), 573–579. https://doi.org/10.1111/2041-210X.12512.

Lefcheck, J., Byrnes, J., & Grace, J. (2024). *piecewiseSEM: Piecewise Structural Equation Modeling* (Version 2.3.0.1) [Computer software]. 〈https://cran.r-project.org/web/packages/piecewiseSEM/index.html〉.

Lomolino, M.V., 2000. Ecology's most general, yet protean 1 pattern: the species-area relationship. J. Biogeogr. 27 (1), 17–26. https://doi.org/10.1046/j.1365-2699.2000.00377.x.

Lövei, G.L., Sunderland, K.D., 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. 41 (41, 1996), 231–256. https://doi.org/10.1146/annurev.en.41.010196.001311.

Luff, M. L. (with Natural Environment Research Council). (1998). Provisional atlas of the ground beetles <Coleoptera: Carabidae> of Britain. Biological Records Centre, Institute of Terrestrial Ecology, Monks Wood Experimental Station.

Luff, M. L. (with Royal Entomological Society). (2007). Handbooks for the identification of British insects. Vol. 4, Pt. 2: The Carabidae (ground beetles) of Britain and Ireland (2. ed, Vol. 4). Royal Entomological Society.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14 (11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1.

Neumann, J.L., Holloway, G.J., Hoodless, A., Griffiths, G.H., 2017. The legacy of 20th century landscape change on today's woodland carabid communities. Divers. Distrib. 23 (12), 1447–1458. https://doi.org/10.1111/ddi.12652.

Ng, K., Barton, P.S., Blanchard, W., Evans, M.J., Lindenmayer, D.B., Macfadyen, S., McIntyre, S., Driscoll, D.A., 2018. Disentangling the effects of farmland use, habitat edges, and vegetation structure on ground beetle morphological traits. Oecologia 188 (3), 645–657. https://doi.org/10.1007/s00442-018-4180-9.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., Favila, M.E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biol. Conserv. 141 (6), 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011.

Noordijk, J., Schaffers, A.P., Heijerman, T., Sýkora, K.V., 2011. Using movement and habitat corridors to improve the connectivity for heathland carabid beetles. J. Nat. Conserv. 19 (5), 276–284. https://doi.org/10.1016/j.jnc.2011.05.001.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., … Weedon, J. (2024). *vegan: Community Ecology Package* (Version 2.6-8) [Computer software]. 〈https://cran.r-project.org/web/packages/vegan/index.html〉.

Olden, J.D., 2006. Biotic homogenization: A new research agenda for conservation biogeography. J. Biogeogr. 33 (12), 2027–2039. https://doi.org/10.1111/j.1365-2699.2006.01572.x.

Oliver, C.D., Larson, B.C., 1996. *Forest stand dynamics* (Update ed). Wiley.

Parisi, F., Innangi, M., Tognetti, R., Lombardi, F., Chirici, G., Marchetti, M., 2021. Forest stand structure and coarse woody debris determine the biodiversity of beetle communities in Mediterranean mountain beech forests. Glob. Ecol. Conserv. 28, e01637. https://doi.org/10.1016/j.gecco.2021.e01637.

Pearce, J.L., Venier, L.A., 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. Ecol. Indic. 6 (4), 780–793. https://doi.org/10.1016/j.ecolind.2005.03.005.

Pebesma, E., 2018. Simple Features for R: Standardized Support for Spatial Vector Data. R. J. 10 (1), 439–446.

Petit, S., 1994. Diffusion of forest carabid beetles in hedgerow network landscapes. In: Desender, In.K., Dufrêne, M., Loreau, M., Luff, M.L., Maelfait, J.-P. (Eds.), Carabid Beetles: Ecology and Evolution. Springer Netherlands, pp. 337–341. https://doi.org/10.1007/978-94-017-0968-2_51.

Petit, S., Usher, M.B., 1998. Biodiversity in agricultural landscapes: the ground beetle communities of woody uncultivated habitats. Biodivers. Conserv. 7 (12), 1549–1561. https://doi.org/10.1023/A:1008875403868.

R Core Team (2021). *R: A language and environment for statistical computing v4.2.1* [Computer software]. 〈https://www.R-project.org/〉.

R Core Team (2023). *R: A language and environment for statistical computing v4.3.2* [Computer software]. 〈https://www.R-project.org/〉.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39 (1), 157–176. https://doi.org/10.1046/j.1365-2664.2002.00695.x.

Rowland, C.S., Morton, R.D., Carrasco, L., McShane, G., O'Neil, A.W., Wood, C.M., 2017. *Land Cover Map 2015 (25m raster, GB)* [Image/tiff TIFF]. NERC Environmental Information Data Centre. https://doi.org/10.5285/BB15E200-9349–403 C-BDA9-B430093807C7.

RStudio Team, 2023. *RStudio: Integrated Development for R* (Version 2023.12.1+402) [Computer software] RStudio, PBC. 〈http://www.rstudio.com/〉 (Version 2023.12.1+402) [Computer software].

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574 (7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3.

Sverdrup-Thygeson, A., Skarpaas, O., Blumentrath, S., Birkemoe, T., Evju, M., 2017. Habitat connectivity affects specialist species richness more than generalists in veteran trees. For. Ecol. Manag. 403, 96–102. https://doi.org/10.1016/j.foreco.2017.08.003.

Taboada, A., Kotze, D.J., Tárrega, R., Salgado, J.M., 2006. Traditional forest management: do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? For. Ecol. Manag. 237 (1), 436–449. https://doi.org/10.1016/j.foreco.2006.09.077.

Tiede, J., Iuliano, B., Gratton, C., 2022. Agriculturally intensified landscapes are associated with reduced body condition of lady beetles. Landsc. Ecol. 37 (7), 1921–1936. https://doi.org/10.1007/s10980-022-01458-0.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes—Eight hypotheses. Biol. Rev. 87 (3), 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Vodka, S., Konvicka, M., Cizek, L., 2009. Habitat preferences of oak-feeding xylophagous beetles in a temperate woodland: implications for forest history and management. J. Insect Conserv. 13 (5), 553–562. https://doi.org/10.1007/s10841-008-9202-1.

Waddell, E.H., Fuentes-Montemayor, E., Park, K.J., Carey, P., Guy, M., Macgregor, N.A., Watts, K., 2024. Larger and structurally complex woodland creation sites provide greater benefits for woodland plants. Ecol. Solut. Evid. 5 (2), e12339. https://doi.org/10.1002/2688-8319.12339.

Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peredo-Alvarez, V., Ferryman, M., Bellamy, C., Brown, N., Park, K.J., 2016. Using historical woodland creation to construct a long-term, large-scale natural experiment: The WrEN project. Ecol. Evol. 6 (9), 3012–3025. https://doi.org/10.1002/ece3.2066.

Watts, K., Handley, P., 2010. Developing a functional connectivity indicator to detect change in fragmented landscapes. Ecol. Indic. 10 (2), 552–557. https://doi.org/10.1016/j.ecolind.2009.07.009.

Watts, K., Whytock, R.C., Park, K.J., Fuentes-Montemayor, E., Macgregor, N.A., Duffield, S., McGowan, P.J.K., 2020. Ecological time lags and the journey towards conservation success. Nat. Ecol. Evol. 4 (3), 304–311. https://doi.org/10.1038/s41559-019-1087-8.

Webb, J., Heaver, D., Lott, D., Dean, H.J., Van Breda, J., Curson, J., Harvey, M.C., Gurney, M., Roy, D.B., Van Breda, A., Drake, M., Alexander, K.N.A., Foster, G., 2017. The Pantheon database: Habitat related traits, conservation status and taxa associations for invertebrates in England [Text/csv Comma-separated values (CSV)]. NERC Environ. Inf. Data Cent. https://doi.org/10.5285/2A353D2D-C1B9-4BF7-8702-9E78910844BC.

Winqvist, C., Bengtsson, J., Öckinger, E., Aavik, T., Berendse, F., Clement, L.W., Fischer, C., Flohre, A., Geiger, F., Liira, J., Thies, C., Tscharntke, T., Weisser, W.W., Bommarco, R., 2014. Species' traits influence ground beetle responses to farm and landscape level agricultural intensification in Europe. J. Insect Conserv. 18 (5), 837–846. https://doi.org/10.1007/s10841-014-9690-0.

Woodcock, B.A., Bullock, J.M., Mortimer, S.R., Pywell, R.F., 2012. Limiting factors in the restoration of UK grassland beetle assemblages. Biol. Conserv. 146 (1), 136–143. https://doi.org/10.1016/j.biocon.2011.11.033.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D., Coomes, D., 2019. Advances in microclimate ecology arising from remote sensing. Trends Ecol. Evol. 34 (4), 327–341. https://doi.org/10.1016/j.tree.2018.12.012.