

Moth community responses to woodland creation: The influence of woodland age, patch characteristics and landscape attributes

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Abstract

Aim: Large-scale habitat creation is crucial to mitigate the current ecological crisis, but scientific evidence on its effects on biodiversity is scarce. Here, we assess how assemblages of a biodiverse group (moths) develop over time in habitat creation sites. We use temperate woodlands as a case study, and compare species assemblages in restored and mature habitat patches. We also identify local- and landscape-level attributes associated with high species richness and abundance.

Location: Central Scotland, United Kingdom.

Methods: We surveyed moths in a chronosequence of 79 temperate woodland patches encompassing woodland creation sites (20–160 years old) and mature “ancient” woodlands (250+ years old). We used structural equation models, generalized linear models and ordination techniques to quantify moth community responses to woodland creation, and degree of similarity to moth assemblages in ancient woodlands.

Results: Woodland creation sites harboured large numbers of moth species (212), were dominated by woodland generalists and had high species turnover. Moth abundance and diversity increased with woodland connectivity. Macromoths were more abundant and diverse in younger woodlands; micromoth specialists occurred more frequently in older woodland creation sites. Ancient woodlands had similar moth abundance/richness than woodland creation sites (except for fewer macromoth woodland specialist species), but their species composition was somewhat different. Patterns of beta diversity (low nestedness) indicated that moth species in woodland creation sites are not simply subsets of species in ancient woodlands.

Main conclusions: To benefit moth communities, woodland creation sites should be structurally diverse and in close proximity to other woodlands. At the landscape scale, a mosaic of woodland patches of different ages is likely to increase moth beta (and consequently gamma) diversity. Ancient woodlands and woodland creation sites each host substantial proportions of “unique” species; individual woodland patches contain

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distinctive moth assemblages and should be protected and valued for their contribution to regional moth diversity.

KEYWORDS

afforestation, Lepidoptera, moths, reforestation, restoration, tree planting, woodland creation, woodland expansion, WrEN project

1 | INTRODUCTION

Habitat loss is amongst the leading causes of global biodiversity declines (Díaz et al., 2019). Additionally, habitat fragmentation (i.e. the division of habitat into smaller fragments separated by a matrix of human-transformed land cover) can also lead to changes in the habitat structure of remaining fragments and severe disruption of ecological processes (Haddad et al., 2015), although its impacts on biodiversity continue to be debated (e.g. Fahrig, 2017; Fletcher et al., 2018). Conserving remnant natural and semi-natural habitats is therefore of paramount importance to prevent further ecological degradation. In addition, large-scale landscape restoration (e.g. through re-creating and re-connecting semi-natural habitats) is increasingly recognized as a crucial strategy to mitigate the current ecological crisis (Strassburg et al., 2020). For example, several global initiatives have recently been launched to accelerate and scale up ecosystem restoration actions, including the Bonn Challenge (aiming to restore 350 million ha of degraded and deforested land by 2030) and the UN's Decade on Ecosystem Restoration 2021–2030 (FAO, 2020a).

However, much of the scientific evidence currently used to underpin landscape restoration strategies comes from studies of habitat loss and fragmentation, and it is unclear whether the resulting ecological principles are applicable to habitat creation and restoration processes (e.g. Naaf & Kolk, 2015). This is because some species, who will ultimately go extinct, might persist in remnant patches for some time after fragmentation has occurred (a process known as “extinction debt”; Semper-Pascual et al., 2018). Conversely, it can take a long time for species to start colonizing and capitalizing on resources in new habitat patches (“colonization credit”; Lira et al., 2019). These lags in species' responses could mask important factors influencing colonization and establishment events in new habitat patches (Jackson & Sax, 2010). Studying landscape restoration over sufficiently long, ecologically realistic time-scales is thus crucial to adequately understand its ecological consequences, and the potential biodiversity benefits accrued over time (Watts et al., 2020). However, these investigations are challenging, particularly for habitats with slow development rates (e.g. temperate woodlands) where ecological time-lags can be more pronounced. This, in addition to the inherent challenges of studying ecological processes over sufficiently large spatial scales at which landscape restoration takes place, has resulted in a lack of empirical studies to underpin landscape restoration strategies (Haddad, 2012). As a consequence, there are numerous ongoing debates in the scientific and

conservation communities on how to prioritize actions (e.g. increasing habitat quality vs. amount vs. connectivity) aimed at rebuilding resilient networks of habitats, restoring species and regaining ecosystem functions and services (Isaac et al., 2018).

Woodland is one of the most biodiverse biomes on Earth and harbours more than 80% of terrestrial species (UNEP, 2009). However, long-term large-scale deforestation has resulted in ca. 50% reduction in woodland cover over the last three centuries, and the majority of remaining woodland is highly fragmented and degraded (Haddad et al., 2015; Ramankutty & Foley, 1999). More recently, tree planting has led to a global increase of 123 million ha of woodland since 1990 (although nearly half of this consists of commercial production forests; FAO, 2020b); this expansion is likely to continue at an accelerated rate with many countries having ambitious woodland expansion targets. For example, in the United Kingdom (UK), tree planting has contributed to increasing woodland cover from a historic low of 5% in the early 1900s (down from a post-glacial of ca. 70%) to the current figure of 13% (Watts, 2006; Forestry Commission, 2020). Increasing woodland extent further is at the forefront of the UK's environmental policy agenda, with the UK Government pledging to plant 180,000 ha in England over a 25-year period (2018–2042; Defra, 2018) and the Scottish Government having a current target of planting 12,000 ha of trees per year, increasing to 15,000 ha from 2024 (Scottish Government, 2018). While large-scale woodland creation programmes can successfully increase woodland extent (and sometimes connectivity; Quine & Watts, 2009), their effectiveness in restoring biodiversity and ecosystem processes over time is largely unknown (Brancalion & Holl, 2020; Di Sacco et al., 2021; Holl & Brancalion, 2020). Furthermore, despite the overall increase in woodland area over recent decades in the UK, many species (particularly those strongly associated with native semi-natural woodland) continue to undergo severe population declines (Reid et al., 2021). Although these trends may be partly driven by other factors (e.g. climate change, biological invasions and pollution; Wagner et al., 2021) outweighing the positive effects of increasing habitat amount, the apparent mismatch between restoration efforts and biodiversity trends highlights the urgent need to understand the factors that facilitate species colonization and capitalisation of new resources in woodland creation sites, and the timeframes over which these processes take place.

Moths are a biologically diverse group with many species occurring regularly in woodlands (e.g. about two-thirds of British macromoths; Waring & Townsend, 2003). Many moth species have undergone significant population declines over recent decades (e.g.

a 33% decline in total abundance from 1968 to 2017 in Britain; Fox et al., 2021), and some are considered priority species for conservation action (e.g. have been included in the UK Biodiversity Action Plan and/or the Scottish Biodiversity List; NatureScot, 2020). Habitat loss and degradation have been identified as amongst the key factors driving moth population declines (Conrad et al., 2004; Wagner et al., 2021), with changes in the structure, management and spatial configuration of woodlands also being linked to declines of certain species (e.g. Broome et al., 2011). Moths play crucial ecological roles (e.g. pollination; MacGregor et al., 2015), are an important food source for many taxa (e.g. bats and birds; Vaughan et al., 1997; Wilson et al., 1999) and a sensitive indicator group for forest quality (Kitching et al., 2000).

The impacts of woodland loss and fragmentation on moth communities have been relatively well-studied. In general, moth abundance and species richness are higher in larger woodland fragments of compact shapes and well-connected to other woodlands (Fuentes-Montemayor et al., 2012; Slade et al., 2013). Local woodland characteristics also influence moth assemblages, with woodlands with high tree species richness and large tree basal areas often hosting more abundant and diverse moth communities (Summerville & Crist, 2003, 2004). Woodland amount in the surrounding landscape is another important factor influencing moth abundance and species richness in woodland fragments, with the scale-of-effect mostly ranging from 160m to 500m (although woodland specialist macromoths are influenced by larger spatial scales up to 1500m; Summerville & Crist, 2004; Fuentes-Montemayor et al., 2012; Merckx et al., 2019).

Conversely, moth responses to woodland creation have received much less attention. Moths have been shown to respond quickly to the creation of other habitat types (e.g. grasslands; Alison et al., 2017) and to land management changes that involve habitat improvements in agricultural landscapes (e.g. the implementation of agri-environment schemes; Fuentes-Montemayor et al., 2011; Merckx, Feber, Dulieu, et al., 2009; Froidevaux et al., 2019). For woodlands, a study comparing the vegetation attributes of young (<30 years) woodland creation sites to those of more mature (>60 years) semi-natural woodlands suggested that moth abundance and diversity are likely to be lower in the younger than in the older woodlands, and that woodland creation sites in early development stages are more likely to benefit generalist and highly mobile moth species (Fuentes-Montemayor et al., 2015). Another study of farm woodlands "known or suspected to have been planted in the previous 30 to 90 years" identified herbaceous plant species richness and woodland patch area, shape and isolation as key drivers of moth diversity (Usher & Keiller, 1998). However, these few studies have investigated moth responses to woodland creation over relatively short temporal scales; this can potentially under- or overestimate the longer-term effects of habitat creation, for example if the habitat becomes gradually "better" for some species as it matures, or if species associated with early-successional habitats "lose out" over time (e.g. Dantas de Miranda et al., 2019). Temperate woodland creation sites develop slowly (e.g. it can take between 80 and 160 years

for them to acquire certain vegetation attributes similar to those of mature ancient woodlands; Fuentes-Montemayor et al., 2021). It is therefore crucial to investigate biodiversity responses to woodland creation and development over accordingly relevant time-scales. Assessing the long-term effects of woodland creation on biodiversity is one of the aims of the Woodland Creation and Ecological Networks (WrEN) project, a large-scale natural experiment designed to study the ecological consequences of 160 years of woodland creation in UK landscapes (Watts et al., 2016).

Here, we surveyed a chronosequence of 79 temperate woodland patches encompassing woodland creation sites (planted on former agricultural land between 20 and 160 years ago; part of the WrEN project) and mature "ancient" woodlands (continuously wooded for at least 250 years) in central Scotland. Our overall aim was to assess how moth abundance, species richness and community composition develop over time in woodland creation sites, and how they compare to moth assemblages in mature ancient woodlands (usually regarded as higher quality habitats for many taxa than woodlands in earlier successional stages). In addition, we aimed to identify local- (e.g. patch age and vegetation structure) and landscape-level (e.g. amount of surrounding woodland and degree of connectivity) attributes of woodland creation sites associated with high moth abundance and species richness.

Different moth species (or species groups) vary in their response to local- and landscape-level habitat characteristics, due partly to differences in their habitat specificity (e.g. woodland specialists displaying stronger associations with local woodland character than generalist species; Summerville & Crist, 2008; Fuentes-Montemayor et al., 2012) and dispersal abilities (e.g. micromoths usually being less mobile and therefore more strongly influenced by local habitat, and by patch isolation, than larger macromoths; Nieminen et al., 1999; Merckx et al., 2010). Therefore, we expected moth responses to woodland creation and development, and to local- and landscape-level woodland attributes, to vary according to species mobility (micro- vs. macromoths) and degree of habitat specialization (woodland specialists vs. generalists). We also expected differences in moth community composition across a gradient of woodland age, with generalists and relatively mobile species quickly colonizing younger woodlands, and then a gradual turnover towards specialists and lower-mobility species dominating more mature woodlands.

2 | METHODS

2.1 | Site selection and study design

Our study sites were located in a ca. 4000 km² area of central Scotland dominated (>70%) by agricultural land, representing a fairly typical lowland landscape in this country. We used a systematic site selection protocol to minimize variation in topography, climate and soil types across sites, and the National Forest Inventory (NFI; Forestry Commission, 2012) to identify 64 broadleaved woodland patches created over the past 160 years on former agricultural land

(see Watts et al., 2016 for further details on site selection). We used the Ordnance Survey historic maps collection (EDINA, 2013) to determine the approximate date when each woodland was created (i.e. the time period when each woodland patch *appeared* in maps). Woodland creation sites ranged in approximate age (20–160 years old), size (0.5–5 ha), amount of surrounding broadleaved woodland (0–22% of area within 1 km from the perimeter of each focal patch) and proximity to nearest broadleaved woodland (10–1130 m). In addition, we used the Ancient Woodland Inventory (a spatial dataset of sites which have been continuously wooded since at least 1750 in Scotland; Spencer & Kirby, 1992; Forestry Commission, 2011) to select 15 mature woodlands with longer ecological continuity. Ancient woodlands were selected with similar characteristics (e.g. patch sizes) and located in the same landscapes as the woodland creation sites (Figure S1). Study sites were >1 km from each other (in most cases >3 km). While many moth species are capable of dispersing over these distances, we consider unlikely that the same individuals would be sampled at more than one site.

2.2 | Characterization of woodland sites and surrounding landscapes

We conducted field surveys during the summers of 2013 and 2014 to characterize the vegetation structure of all woodland sites using the point-centred quarter method along an edge-to-interior transect (see Fuentes-Montemayor et al., 2021 for a detailed description). We obtained metrics of tree species richness, tree diameter at breast height (DBH), tree density and amount of understorey cover. For tree DBH, we used mean as a metric of tree size, and standard deviation (SD) as an index of vegetation structural heterogeneity. We also recorded on-site presence of livestock (or signs of, e.g. prints, dung or wool).

We used Geographic Information Systems software (ArcGIS 10.2; ESRI) and NFI data to measure the area and shape (patch perimeter divided by the minimum perimeter possible for a maximally compact patch of the same area; McGarigal & Cushman, 2002) of each woodland. In addition, we calculated the proportion of woodland edge adjacent to agricultural areas (i.e. arable land or agriculturally improved grassland based on Land Cover Map [LCM] 2007 data; Morton et al., 2011). At the landscape scale, we used LCM data to quantify the proportion of semi-natural habitats (e.g. rough grassland and scrub but excluding woodland), and NFI data for the proportion of broadleaved woodland within a 500 m buffer around the perimeter of each study site and the Euclidean distance to the nearest broadleaved woodland (as a metric of connectivity). These UK-wide spatial datasets consist of vector land parcels with attributes describing land cover derived from thematic classification of satellite image data with high spatial resolution (minimum mappable unit of 0.5 ha) and provide categorical data of land cover types which have been shown to influence moth communities in agricultural landscapes (e.g. Fuentes-Montemayor et al., 2012; Slade

et al., 2013). A spatial scale of 500 m was selected for landscape metrics because it encompasses the scale-of-effect previously detected for most woodland moths in the study area (Fuentes-Montemayor et al., 2012) while minimizing the overlap between nearby buffers (there was no overlap between nearby buffers, apart from two pairs of sites which buffers overlapped by 7% and 2%, respectively). We also counted the number of hedgerows (manually mapped using satellite imagery from Google Earth Pro; Google Inc., 2017) physically connected to each study site.

2.3 | Moth surveys

Moths surveys were conducted from June to September 2017 using portable 6 W Heath light traps (Watkins & Doncaster) powered with 12V batteries. Traps were activated 15 min after sunset and switched off 15 min before sunrise using automated timers (sourcingmap model CN101A). During each survey session (one night), two traps were set up in each woodland patch (one in the interior and one in the edge) typically ≥ 100 m apart to prevent the lights from interfering with each other (Merckx, Feber, Dulieu, et al., 2009; Merckx, Feber, Riordan, et al., 2009); if the woodland was too small for this distance between traps, we ensured trees/shrubs interrupted visibility between lights (shortest distance between traps ca. 50 m). The majority of woodland creation sites were surveyed twice (46 sites \times 2 traps \times 2 nights), with the exception of three sites that had only one full survey session due to trap malfunction (3 sites \times 2 traps \times 1 night); a subset of 15 sites were surveyed three times (15 sites \times 2 traps \times 3 nights; total = 280 trap-nights) and used in the comparison with ancient woodlands (see Section 2.4.3); trapping sessions were spaced at least two weeks apart. In addition, 15 ancient woodlands were surveyed three times over the season ($n = 5$ –6 trap-nights per site \times 15 sites = 93 trap-nights). We recognize that 2–3 visits to each site provide a fairly coarse description of local moth assemblages and that rare species may have been missed at some sites. We adopted this approach to maximize the number/range of sites surveyed, and because previous work has indicated that it can successfully identify influential habitat characteristics (e.g. Froidevaux et al., 2019; Fuentes-Montemayor et al., 2012). Traps were checked shortly after sunrise when moths were identified in the field and released at the site of capture; photographs were taken and specimens collected for further examination when identification in the field was not possible. Moth species were categorized into macro- and micromoths and into habitat specialization groups following Sterling et al. (2012) and Waring and Townsend (2003). Species for which woodland is listed as the main habitat where species occurs and/or for which the larval food is a woody plant were classed as “woodland specialists”; species for which woodland is listed as one of the habitats where species occurs were classed as “woodland generalists”; all other species were classed as “non-woodland species” and excluded from further analyses.

2.4 | Data analyses

All statistical analyses were conducted in R v3.6 within Rstudio v1.2.1335 (R Core Team, 2019; RStudio Team, 2019).

2.4.1 | Moth abundance and richness in woodland creation sites

We used structural equation models (SEMs) to quantify the relative importance of local- and landscape-level attributes on moth abundance and species richness. SEMs are a multivariate technique that can be used to test whether a priori hypothesised direct and indirect causal relationships between variables are supported by observed data, and to compare relative effect sizes of predictor variables (Grace et al., 2010). We used ecological theory to guide the construction of our global conceptual model (Figure S2) which incorporated landscape-level attributes (likely to influence species colonization and dispersal processes) and local-level attributes (likely to determine habitat suitability and influence species establishment). Data from all traps and survey sessions were pooled per site. The total number of trap-nights per site was included in the model as an offset for moth abundance to account for differences in sampling effort (alternative models without an offset are presented in Figure S3). We ran separate models for macro- and micromoths, and for woodland generalists and specialists. Moth abundance and richness data were log-transformed and modelled with a Gaussian error distribution in all cases, except for micromoth woodland specialists for which abundance was too low and species occurrence data were modelled using a Binomial error distribution instead. Continuous predictor variables were mean centred and scaled by 1 SD, and a binary predictor variable (i.e. presence/absence of grazing) was transformed to have values of -1 and 1 , so that its effect size was directly comparable with those of continuous predictors. SEMs were performed using the “psem” function in the “piecewiseSEM” R package (Lefcheck, 2016). Shipley's test of directed separation (Fisher's C) was used to evaluate global SEM fit, where values of $p > .05$ indicated the model was supported by the observed data.

2.4.2 | Moth β diversity and species composition in woodland creation sites

To assess differences in moth species composition between sites, we calculated an incidence-based metric of beta diversity (Sorensen pairwise dissimilarity), and partitioned this into its nestedness (i.e. differences due to subsets of species communities between sites) and turnover (i.e. differences due to replacement of species between sites) components; we also calculated the proportion of species shared between pairs of sites (all possible combinations) using the “betapart.core” function within the “betapart”

R package (Baselga et al., 2013). In addition, we visually assessed differences in moth species composition between sites using non-metric multidimensional scaling (NMDS; “metaMDS” function in the “vegan” R package; Oksanen et al., 2020) with an abundance-based dissimilarity index (Bray–Curtis). We then used the “envfit” function (with a $p < .05$ threshold and 999 permutations) to examine whether differences in moth species composition between sites as shown in the NMDS ordination were driven by the local- and landscape-level attributes outlined in Section 2.2. We ran these analyses separately for macro- and micromoths. To minimize the influence of seasonal effects (e.g. differences in peak flight seasons of individual moth species) on beta diversity and species composition, we restricted these analyses to a subset of data which included moth survey sessions 1 and 2 only (i.e. we excluded data from survey session 3 for sites where this was conducted, and removed three sites from the dataset which only had one full survey session; $n = 4$ trap-nights per site \times 61 sites = 244 trap-nights).

2.4.3 | Comparison of moth assemblages in woodland creation sites vs. mature ancient woodlands

We compared moth abundance, species richness and community composition in a subset of 15 woodland creation sites vs. 15 ancient woodlands. All sites used for this comparison were surveyed three times, with the exception of one ancient and two woodland creation sites where one of the traps malfunctioned on one occasion ($n = 5$ – 6 trap-nights per site \times 30 sites = 177 trap-nights). Data from all traps and survey sessions were pooled per site.

Differences in moth abundance and species richness (log-transformed and modelled with a Gaussian error distribution) were assessed using linear models with “woodland age” as a categorical variable (i.e. “woodland creation” vs. “ancient” sites) and the number of trap-nights per site was included as an offset.

To quantify the degree of similarity between woodland creation and ancient sites (in terms of moth species composition), we calculated the proportion of species shared between pairs of sites (all possible combinations) using the “betapart.core” function in the “betapart” R package (Baselga et al., 2013). We also calculated overall incidence-based metrics of beta diversity partitioned into nestedness and turnover components (see Section 2.4.2). In addition, we used an NMDS ordination to visually assess differences between sites driven by moth species composition and the “envfit” function (see Section 2.4.2) to test whether woodland age category (or vegetation characteristics influenced by woodland age) were driving dissimilarities between sites. Other local (e.g. patch size) and landscape variables were not included as potential predictors to avoid overfitting and because variation in these variables was minimized during the selection of the subset of sites used for this comparison (Figure S1).

3 | RESULTS

3.1 | Effects of patch age, management and landscape context on the attributes of woodland creation sites

Woodland age had a significant effect on some vegetation attributes; specifically, older woodlands had lower tree density, larger trees and higher structural heterogeneity (quantified as standard deviation in tree diameter). Structural heterogeneity was also influenced (positively) by tree species richness. Understorey cover was not influenced by woodland age, but it was marginally lower in sites where grazing stock was present. At the landscape scale, distance to the nearest broadleaved woodland was negatively associated with the amount of surrounding broadleaved woodland (Figure 1).

3.2 | Moth communities in woodland creation sites

After 280 trap-nights in 64 secondary woodlands, we recorded a total of 8643 moths belonging to 254 species (77 micromoths and 177 macromoths, including aggregate species groups). Of these, 79 species were classed as woodland specialists, 133 as woodland generalists and 42 as non-woodland species (Table 1). Twenty of these species are included in the Scottish Biodiversity List because they

are of special conservation concern. A list of woodland-associated species is presented in Table S1.

3.2.1 | Moth species richness and abundance in woodland creation sites

As expected, moth abundance and species richness were strongly associated (positively) in all cases (Figure 1). However, for macromoth woodland generalists, abundance was not the only direct driver of species richness; we detected direct effects of woodland age (negative) and structural heterogeneity (positive, marginal effect) on this group's species richness, and negative effects of distance to nearest broadleaved woodland on their abundance (Figure 1a). Macromoth woodland specialists were more abundant (and hence species rich) in woodland patches located close to other broadleaved woodlands, of compact shapes and with higher tree densities (marginal effect; Figure 1b). Micromoth woodland generalists were more abundant and species rich in woodlands located close to other woodlands and with relatively low proportions of semi-natural habitats in the surrounding landscape (Figure 1c). The probability of occurrence of micromoth woodland specialists was marginally higher in older woodlands (direct effect) with relatively low proportions of adjacent agricultural land (Figure 1d). The direction of the effects presented in Figure 1 did not change when analyses were re-run without "number

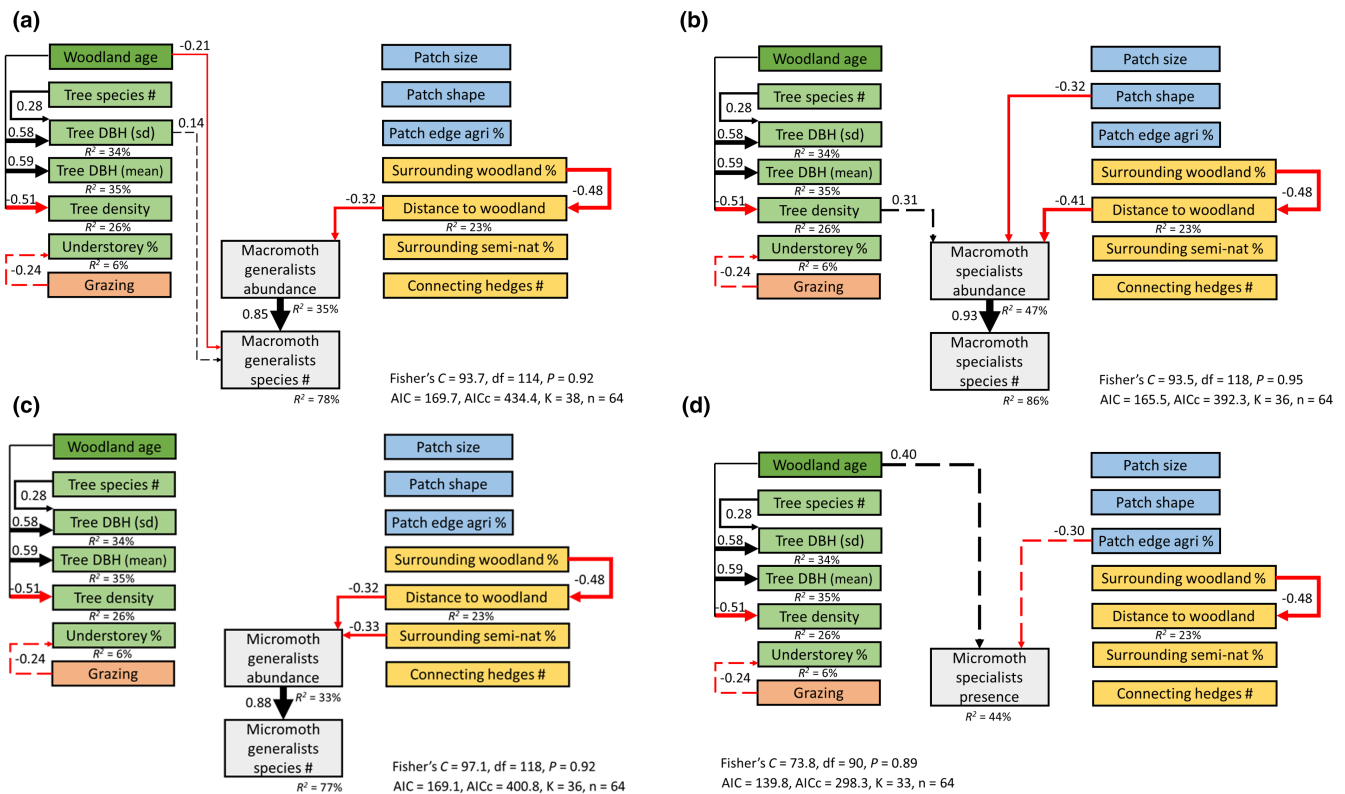


FIGURE 1 Results of piecewiseSEM showing local- and landscape-level factors influencing the abundance and species richness of (a) macromoth generalists, (b) macromoth specialists and (c) micromoth generalists, and (d) micromoth specialists presence in woodland creation sites

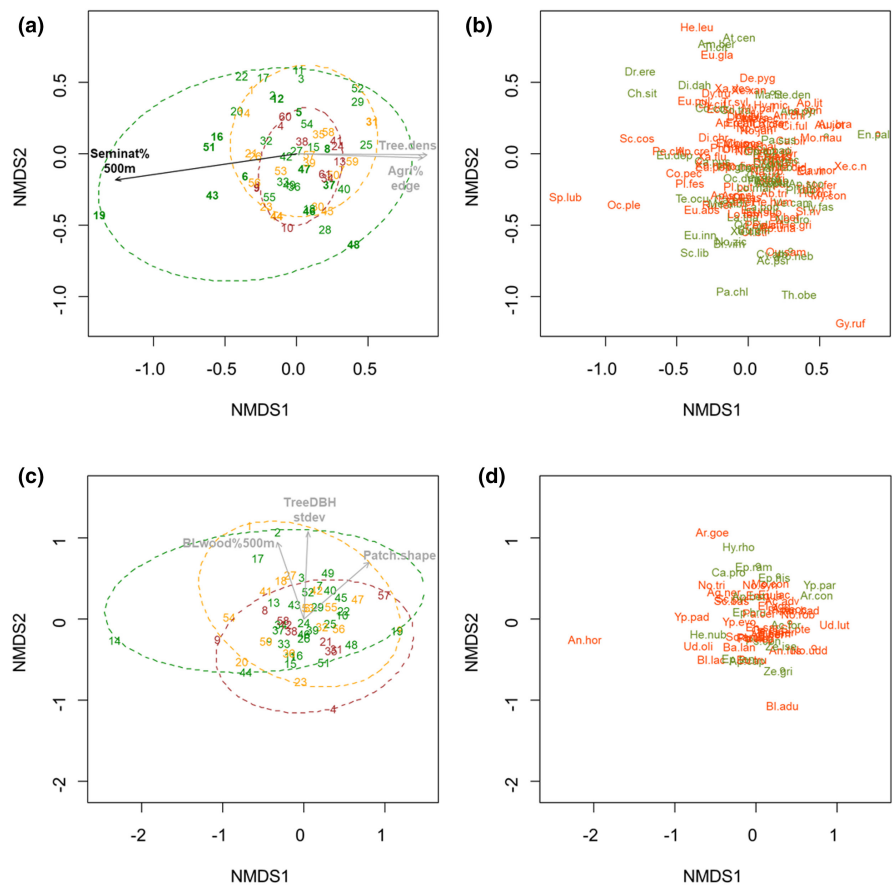
TABLE 1 Moth species recorded in 64 woodland creation sites

	Micromoth species richness ^a	Macromoth species richness ^a	Total moth species richness ^a	Micromoth abundance ^b	Macromoth abundance ^b	Total moth abundance ^b
Woodland specialists	18	61	79	73	945	1018
Woodland generalists	41	92	133	815	5629	6444
Non-woodland species	18	24	42	138	893	1031
Unidentified	-	-	-	150	0	150
Total	77	177	254	1176	7467	8643

^aIncludes aggregate species groups.

^bIncludes aggregate species groups and unidentified specimens.

FIGURE 2 NMDS ordination biplots showing dissimilarities between woodland creation sites driven by macro- (a and b) and micromoth (c and d) species composition. Coloured numbers in (a and c) represent woodland sites in different age categories: Red ≤30 years; orange = 31–80 years; green = 81–160 years since planting. Species abbreviations in (b and d) are colour-coded to represent woodland generalists (orange) and specialists (green). Full species names are presented in Table S1. Arrows represent predictor variables driving dissimilarities between sites/species (black arrows $p < .05$; grey arrows $p < .1$). In (a) sites in bold represent presence of grazing stock



of trap-nights” as an offset on a subset of sites with equal sampling effort (Figure S3).

3.2.2 | Moth species composition in woodland creation sites

Overall, beta diversity across sites was high (Sorensen dissimilarity = 0.95; on a 0–1 scale), with low nestedness (0.02) and high turnover (0.93). Pairs of sites shared on average 20.3% of species, with a minimum of 0% and a maximum of 48.5% shared species between

the two most similar sites (in terms of moth species composition). This average proportion of shared species was higher for macro (22.7%, range 0–50%) than for micromoths (8.7%, range 0–53.3%).

Macromoth species composition in woodland creation sites was significantly influenced by the proportion of semi-natural habitat in the surrounding landscape ($p < .01$), in-site grazing ($p < .05$), and marginally by woodland tree density and the proportion of agricultural land at the woodland edge (both $p < 0.1$). Micromoth species composition in woodland creation sites was not significantly influenced by any of the examined woodland attributes (although amount of broadleaved woodland within 500m, variation in tree DBH and

patch shape were marginally significant predictors). Woodland age did not significantly drive moth species composition in a particular direction; however, visual inspection of the ordination plots showed that species composition was fairly constrained in young woodlands, and then gradually diverged in more mature woodlands, particularly for macromoths (Figures 2a,c).

Further examination of moth species composition in relation to degree of habitat specialization revealed that assemblages were dominated by woodland generalists; macromoth woodland specialists represented only 39% of macromoth woodland species, while micromoth woodland specialists represented just 31%. Overall, woodland generalists occurred more frequently than woodland specialists in woodland creation sites (Figure 3); this trend was more marked for micromoths (e.g. most common woodland specialist *Hedya nubiferana* occurring in 8% of sites; Figure 3b) than for macromoths (e.g. *Campaea margaritaria* occurring in 57% of sites; Figure 3a). We found no clear patterns in the ordination plots in relation to species habitat specialization, neither for macro nor micromoths (Figures 2b,d).

3.3 | Comparison of woodland creation sites vs. mature ancient woodlands

After 93 trap-nights in 15 ancient woodlands, we recorded a total of 2646 moths belonging to 179 species (49 micromoths and 130 macromoths, including aggregate species groups). Of these, 45 species were classed as woodland specialists, 108 as woodland generalists and 26 as non-woodland species (Table 2). Seventeen species are included in the Scottish Biodiversity List because they are of special conservation concern. A list of woodland-associated species recorded in ancient woodlands and a subset of woodland creation sites used for comparison is presented in Table S2.

3.3.1 | Differences in moth abundance and species richness

Moth abundance and species richness in ancient woodlands were similar to those found in a subset of woodland creation sites (Table 2); we found no statistical differences in moth abundance or species richness between these two woodland types, except for a higher number of macromoth woodland specialist species in woodland creation than in ancient sites (average \pm SE of 9.6 ± 1.1 and 6.5 ± 1.1 species per site, respectively; Figure S4).

3.3.2 | Differences in moth species composition

Beta diversity across the subset of 15 ancient and 15 woodland creation sites was high (Sorensen dissimilarity = 0.91), with low nestedness (0.04) and high turnover (0.87). Pairwise comparisons between sites showed that the average proportion of shared species was

relatively low (24.4%, range 3.7–48.1%), higher for macro (27.3%, range 4–53.1%) than for micromoths (12.2%, range 0–50%) and similar within and between age categories (Figure S5). Overall, 27 species (representing 14.7% of total species) were unique to ancient woodlands, 34 (18.5%) to woodland creation sites, and 123 (66.8%) were present in both. Woodland age (ancient vs. creation sites) was not a direct factor driving differences in species composition between sites for either macro- or micromoths. However, age indirectly influenced site dissimilarities for macromoths through age-driven changes in average tree size (DBH, $p < .014$); most woodland creation sites (with smaller trees on average than ancient woodlands) were clustered in the left half of the ordination plot, while sites on the right quadrats were mostly ancient woodlands and one relatively old (i.e. 120 years) woodland creation site with large trees (Figure 4a). Variation in tree size marginally influenced micromoth community composition ($p < .1$).

In terms of degree of habitat specialization, both micro- and macromoth assemblages were strongly dominated by woodland generalists in woodland creation sites and ancient woodlands (Figure 5). For micromoths, woodland specialists represented 24% of species in ancient woodlands, and 26% in woodland creation sites; for macromoths, this proportion was slightly higher (30% of species in ancient and 36% in creation woodlands). Occupancy rates of individual woodland specialist species were particularly low for micromoths, with the most common woodland specialist *Hedya nubiferana* occupying only 13% of ancient woodlands and 20% of woodland creation sites (Figure 5a,b); the most common woodland specialist macromoths occupied 67% of ancient woodlands (*Diarsia dahlia*) and 67% of woodland creation sites (*Campaea margaritaria*; Figure 5c,d). In the ordination plot for macromoths, woodland specialists were slightly shifted towards the left of the graph (characterized by sites with smaller trees) and woodland generalists towards the right (sites with larger trees; Figure 4b). No clear patterns were observed in the ordination plot for micromoth species (Figure 4d).

4 | DISCUSSION

Woodland is the focus of many landscape-scale restoration projects partly because of its potential to reverse biodiversity declines and mitigate climate change. However, the effectiveness of woodland creation in restoring biodiversity over ecologically realistic time-scales is still largely unknown (e.g. Brancalion & Holl, 2020; Watts et al., 2020). The distribution and population trends of UK moths have been well-studied for decades (e.g. woodland-associated moths have expanded their distributions by ca. 12% in the UK since 1980, although population trends of individual species have been mixed; Fox et al., 2021). However, it is unclear how these trends relate to woodland creation rates, or to changes in the management and spatial configuration of woodlands, making it difficult to identify the ecological principles needed to underpin and target effective woodland creation and restoration strategies that have the greatest potential to benefit biodiversity. Here, we examined the response

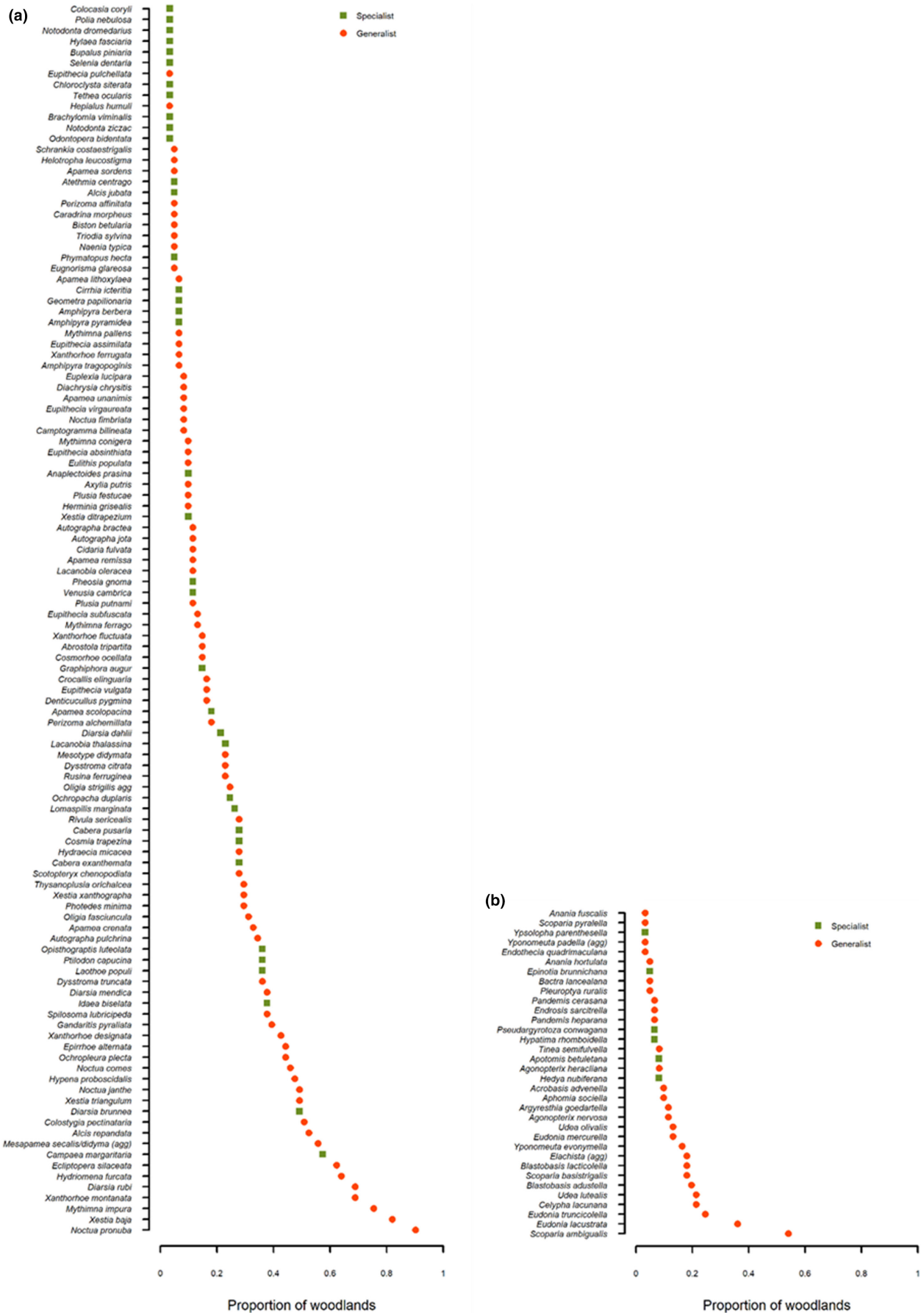


FIGURE 3 Proportion of woodland creation sites occupied by (a) macromoth and (b) micromoth species. Symbol colours denote species habitat specialism (green = woodland specialists, orange = woodland generalists). Species present in <2 sites are not shown

TABLE 2 Moth species richness and abundance in ancient woodlands (n = 15 sites, 93 night-traps) and woodland creation sites (n = 15 sites, 89 night-traps)

		Micromoth species richness ^a	Macromoth species richness ^a	Total moth species richness ^a	Micromoth abundance ^b	Macromoth abundance ^b	Total moth abundance ^b
Ancient	Woodland specialists	10	35	45	24	267	291
	Woodland generalists	29	79	108	268	1742	2010
	Non-woodland species	10	16	26	64	281	345
	Unidentified	-	-	-	36	0	36
	Total	49	130	179	392	2290	2682
Woodland creation sites	Woodland specialists	9	43	52	27	293	320
	Woodland generalists	28	76	104	408	1765	2173
	Non-woodland species	9	18	27	55	248	303
	Unidentified	-	-	-	34	0	34
	Total	46	137	183	490	2306	2830

^aIncludes aggregate species groups.

^bIncludes aggregate species groups and unidentified specimens.

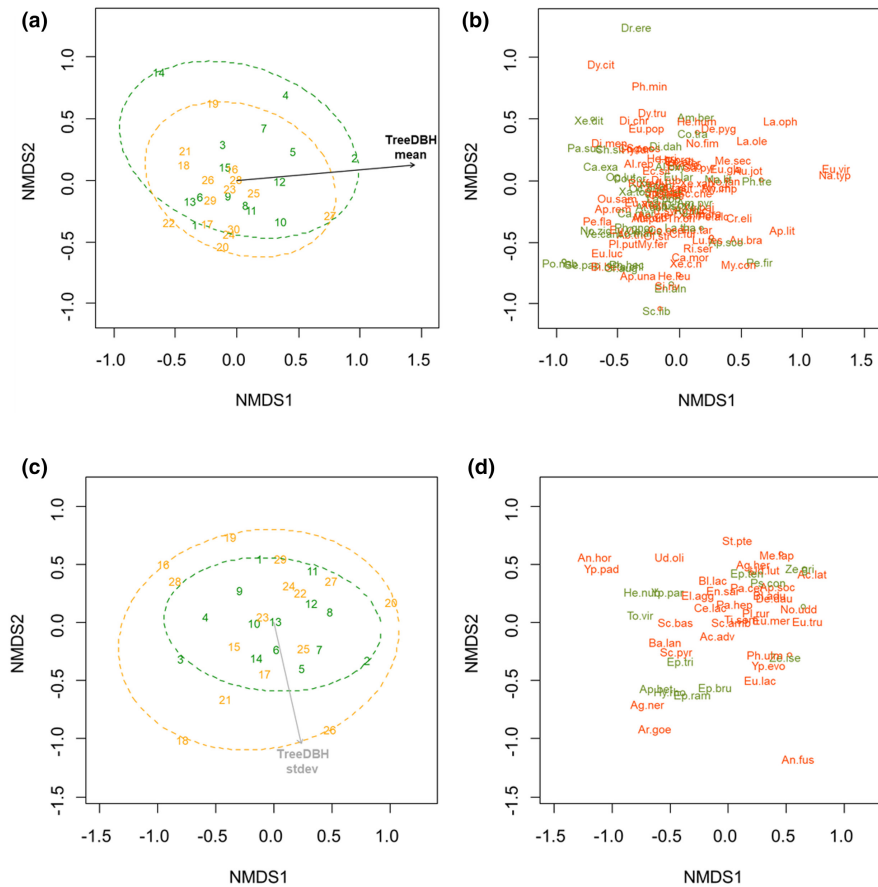


FIGURE 4 NMDS ordination biplots showing dissimilarities between ancient woodlands and woodland creation sites driven by macro- (a and b) and micromoth (c and d) species composition. Coloured numbers in (a and c) represent woodland sites in different age categories: Green = ancient woodlands; orange = woodland creation sites. Species abbreviations in (b and d) are colour-coded to represent woodland generalists (orange) and specialists (green). Full species names are presented in Table S1. Arrows represent predictor variables driving dissimilarities between sites/species (black arrows $p < .05$; grey arrows $p < .1$)

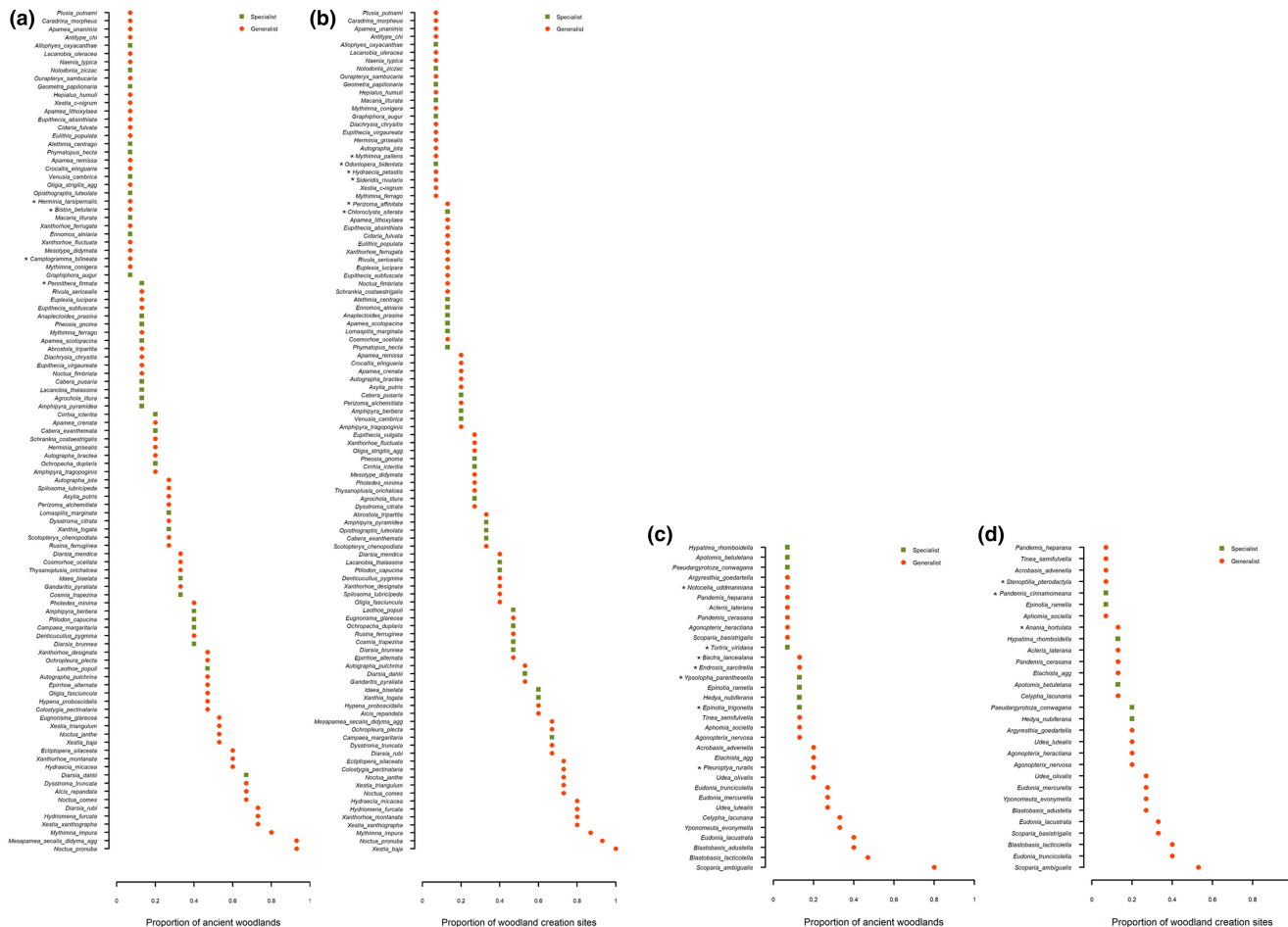


FIGURE 5 Proportion of ancient woodlands and woodland creation sites occupied by macromoth (a and b) and micromoth (c and d) species. Symbol colours denote species habitat specialism (green = woodland specialists, orange = woodland generalists). Species “unique” to either ancient or woodland creation sites are indicated with a star preceding their name. Species present in <2 sites are not shown

of moth communities to long-term woodland creation and identified local- and landscape-level attributes associated with high moth abundance and species richness. We also assessed the degree of similarity between moth assemblages in woodland creation sites and in mature “ancient” woodland sites (usually regarded as higher quality habitat for many species).

4.1 | Moth assemblages in woodland creation sites

Moth assemblages in woodland creation sites were strongly dominated by woodland generalists. The low ratio of woodland specialists to generalists may initially appear to indicate that many woodland specialist species have not been able to colonize/establish in these sites so far, even after more than a century since woodland creation. This pattern was especially marked for micromoths (ca. 31% woodland specialists), possibly because their lower mobility hinders their ability to colonize new habitat patches. However, at least for macro-moths, the proportion of woodland specialists present in our sites (ca. 39% vs. 61% woodland generalists) closely mirrors that of wider Scotland, where 165 of the 437 species listed as using woodland to

breed, exclusively breed in this habitat (i.e. are woodland specialists; Cook et al., 2021). Most moth species groups were influenced by distance to nearest woodland (abundance and richness markedly decreased in woodlands >400m from their nearest patch), suggesting that dispersal ability is an important factor mediating the colonization of woodland creation sites. In addition, the high beta diversity and species turnover across sites may indicate that colonization is somewhat stochastic (Cardoso et al., 2015), opportunistic and constrained by the pool of species within each landscape. However, we acknowledge that differences in the timing of survey sessions across sites and imperfect sampling of moth communities (leading to an underestimation of species richness) may have partly affected the beta diversity patterns we observed; incomplete sampling is likely to be more pronounced for micromoths, for which low-wattage light traps are probably less efficient than for macromoths. Therefore, we recommend caution in the interpretation of beta diversity patterns, especially for micromoths. Other landscape-level attributes, such as the amount of semi-natural habitats in the surrounding landscape, also influenced some species groups (i.e. micro- and macromoth woodland generalists). In the case of macromoths, generalist species such as *Spilosoma lubricipeda*, *Ochropleura plecta*

and *Schrankia costaestrigalis* were characteristic of sites surrounded by large amounts of semi-natural habitats. Contrastingly, micromoth woodland generalists were less abundant/diverse in woodlands with larger amounts of semi-natural habitats in the landscape.

Patch-level attributes (more likely to determine habitat suitability and influence species establishment) also influenced moth abundance, species richness and composition in woodland creation sites. For example, micromoth woodland specialists were (marginally) more likely to occur in woodlands with relatively low proportion of their edge adjacent to agricultural land, while macromoth woodland specialists were more abundant/diverse in patches of compact shapes (in agreement with findings from Usher & Keiller, 1998; Fuentes-Montemayor et al., 2012); this suggests high importance of “core” woodland areas. Contrary to previous findings (e.g. Fuentes-Montemayor et al., 2012), we did not detect any negative effects of in-site grazing on moth abundance or species richness; however, the presence of grazing stock did influence the composition of macromoth assemblages; this may be because some species are more resilient to (or able to recolonise sites affected by) this disturbance.

4.2 | Effects of woodland age on moth assemblages in woodland creation sites

Woodland age, and vegetation variables driven by woodland age, also influenced moth assemblages in woodland creation sites. Macromoth generalist species richness was higher in younger woodlands (direct negative effect of woodland age), suggesting that these species are relatively quick to colonize newly created woodland patches, and can capitalize on early-successional habitats. However, there was also an indirect positive effect of woodland age (albeit smaller than the direct effect of age and only marginally significant) indicating higher moth species richness in woodlands with higher structural heterogeneity (i.e. in older woodlands and in those with higher tree species richness). Macromoth woodland specialists were also (marginally) more abundant in younger woodlands with higher tree densities (indirect negative effect of woodland age). This is in agreement with previous findings of higher abundance of macromoth woodland specialists in woodlands with high tree densities and relatively small trees (Fuentes-Montemayor et al., 2012, 2015). Although macromoth species composition did not significantly change according to woodland age, moth assemblages in younger woodlands appeared more similar to each other (i.e. were closer in the ordination space) than more mature woodlands. However, this was not reflected in the degree of habitat specialization of species in the assemblage, and there was no clear divide in the proportion of specialists vs. generalists in woodlands of different ages. It is possible that other life history traits (e.g. voltinism, phenology and host plant specificity) are more important drivers of moth community assemblage than habitat specificity (e.g. Wagner et al., 2021). It is also possible that the larger degree of dissimilarity amongst

older woodlands is an artefact of the larger number of sites in this “81–160 years since planting” category ($n = 33$, compared to 10 sites of 0–30 years and 18 sites of 31–80 years) or of this category encompassing more years than the other two categories.

Micromoth specialist species occurred (marginally) more frequently in older woodlands (direct positive effect of woodland age), possibly because the longer ecological continuity of these sites has allowed for the accumulation of these relatively low mobility species over time. The abundance and species richness of micromoth generalists were not influenced by woodland age, or by vegetation attributes related to woodland age, and micromoth species composition did not change according to woodland age either.

4.3 | Comparison of moth communities in woodland creation sites vs. more mature “ancient” woodlands

Moth abundance and species richness in ancient woodlands were similar to those found in a subset of woodland creation sites, except for a higher number of macromoth woodland specialist species in woodland creation than in ancient sites. While a higher abundance of woodland specialists has been reported at younger than “mature” sites before (e.g. Fuentes-Montemayor et al., 2012, 2015), the lower number of species in ancient woodland was somewhat surprising. In addition, for macromoths, there was a moderate degree of dissimilarity in the species composition of ancient versus creation sites, driven by differences in average tree size (generally larger in ancient woodlands); sites with larger trees tended to be dominated by generalist species such as *Eupithecia virgaureata* and *Naenia typica*, whereas woodland specialists were more abundant in sites with smaller trees (similar to previous findings, e.g. Fuentes-Montemayor et al., 2012). For micromoths, no patterns were observed in terms of species composition, suggesting that the abundance and diversity of this group (typically more limited by dispersal than macromoths) are more constrained by the regional species pool, rather than by site characteristics.

In general, the low nestedness and high turnover components of moth beta diversity observed suggest that moth species in woodland creation sites are not simply subsets of species in ancient woodlands; instead, a substantial proportion of species was unique to each woodland type. Both woodland types should be seen as complementary habitats and important contributors to the moth gamma diversity of rural landscapes. However, both ancient and woodland creation sites were dominated by woodland generalist species. The sites studied here are fairly small patches (<5 ha) immersed in an agricultural matrix, some of them heavily overgrazed and with a lack of natural regeneration affecting the three-dimensional structure of the woodland (Fuentes-Montemayor et al., 2021). They are characteristic of British woodlands (including ancient semi-natural woodlands of which ca. 70% are <5 ha; Reid et al., 2021). It is thus likely that moth assemblages at these sites have undergone “environmental filtering” with relatively few woodland specialists able to

persist (Wöfling et al., 2020). At woodland creation sites, this may manifest as colonization credits not being fully realized, while the long history of disturbance at ancient woodlands (Peterken, 1996; Rackham, 1980) has probably resulted in an extinction debt having already been paid. Larger ancient woodlands managed for conservation purposes are likely to be of higher biodiversity value than the sites we studied here.

4.4 | Implications for landscape-scale restoration and woodland management

Both local and landscape-level attributes influenced moth assemblages in woodland creation sites. In particular, woodland connectivity was one of the main predictors of moth abundance and diversity. Other factors related to patch geometry (e.g. shape and proportion of edge adjacent to agricultural land) were important too, as were vegetation characteristics related to woodland age. Based on these findings, we recommend that, to benefit moth communities, woodland creation sites should be:

1. Located in close proximity (<400m) to other woodlands to facilitate colonization, including by species more limited by dispersal such as micromoths.
2. Of compact shapes, and with “buffer areas” to minimize the proportion of woodland edge adjacent to agricultural land.
3. Structurally diverse (e.g. with high variation in tree sizes within the woodland).

At the landscape scale, a combination of woodland patches of different ages is likely to increase moth beta (and consequently gamma) diversity. Young woodlands with high tree densities and small trees will be particularly beneficial for macromoths (both generalists and specialists), while older woodlands with long ecological continuity are more likely to be occupied by micromoth woodland specialists. Given that moth assemblages within each woodland patch are fairly distinctive (i.e. contribute to high spatial turnover and beta diversity) and that ancient woodlands and woodland creation sites both host substantial proportions of “unique” species, individual woodland patches should be protected and valued for their contribution to regional moth diversity.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data supporting the results are available from DataSTORRE: Stirling Online Repository for Research Data: <http://hdl.handle.net/11667/198>.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13599>.

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BIOSKETCH

EFM is an applied ecologist and conservation biologist investigating how human activities impact biological communities and ecosystem functioning, with a focus on assessing the effectiveness of actions to conserve and restore biodiversity in human-modified landscapes. Her main areas of expertise include animal ecology, woodland ecology, restoration ecology and spatial ecology. Alongside KP and KW, she co-leads the Woodland Creation and Ecological Networks project (WrEN; www.wren-project.com), a large-scale natural experiment designed to assess the long-term effects of past woodland creation on current biodiversity and ecosystem functioning to inform future landscape restoration strategies.

Author contributions: E.F.M., K.P. and K.W. designed the study; P.S. and W.S. collected the data; E.F.M. conducted the statistical analyses and wrote the first draft of the manuscript; all authors contributed to manuscript revisions.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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