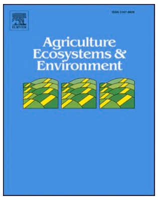
Agriculture, Ecosystems and Environment 397 (2026) 110060

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

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



Restoration of ecological interactions: The influence of site and landscape factors

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ARTICLE INFO

Keywords:
Grassland
Plant-herbivore
Plant-pollinator
Woodlands

ABSTRACT

Restoration has been extensively used in agricultural landscapes as a mitigation measure to reduce biodiversity loss in response to historic habitat destruction. Trophic interactions between insects and plants underpin key ecosystem processes and contribute to system robustness, which is a critical outcome for habitat restoration. We evaluate how restoration age, site size and landscape proximity to similar habitats impact the re-establishment of trophic linkages between empirically measured grassland plant-pollinator (60 sites; 1–76 years) and woodland plant-herbivore networks (60 sites; 13–67 years). In each case, sites were selected along a chronosequence with the goal of maximising variation along these temporal and spatial gradients. For both grassland and woodlands, older and larger sites typically support higher levels of connectance, nestedness and generality of the networks. In contrast, landscape proximity promotes these metrics for woodland webs but has the reverse effect for grassland webs. The similarities show common characteristics of community trophic re-establishment in response to local environmental drivers for these different ecosystems. Focusing on interactions rather than species identity highlights opportunities for targeted policies to restore ecosystem function in wider agricultural landscapes; for example, through increasing site size as well as the need for continuity of older sites.

1. Introduction

Ecosystem restoration provides an opportunity to reverse the loss of important natural habitats with the goals of enhancing biodiversity and maintaining critical ecosystem processes in intensively managed agricultural landscapes (Rey Benayas et al., 2009; Bullock et al., 2011; Cadotte et al., 2011; Bryan et al., 2018; Bullock et al., 2022). More widely, this approach has been used to re-establish lost or degraded habitats in terrestrial, marine and aquatic systems (Rey Benayas et al., 2009; Bullock et al., 2011). It also represents the practical outcome of national and international initiatives, including the Bonn Challenge (Verdone and Seidl, 2017), United Nations Decade on Ecosystem Restoration (Pimm et al., 2021) and large-scale restoration policies across China (Bryan et al., 2018). In the UK, widescale governmental programs have been instigated to promote reforestation and grassland restoration in agricultural systems in response to losses of historic loss of cover (Watts, 2006; Fuentes-Montemayor et al., 2017; Ridding et al., 2020; Woodcock et al., 2021; Larkin and Stanley, 2023). Restoration of these habitats provides an opportunity to understand the processes that underpin community reconstruction in response to environmental drivers across diverse habitat types.

The success of habitat restoration is often measured using reference communities considered representative of rare or threatened habitats (Hilderbrand et al., 2005; Gann et al., 2019). Measuring restoration success using pre-defined target assemblages (e.g. ancient chalk grasslands or woodlands) likely fails to capture the dynamic and heterogeneous characteristics of natural systems (Woodcock et al., 2012; Bullock et al., 2022; Pettorelli and Bullock, 2023). The use of target communities also implies an underlying assumption of a succession to a pre-determined end point that ignores the stochastic component of

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https://doi.org/10.1016/j.agee.2025.110060
Received 25 June 2025; Received in revised form 29 October 2025; Accepted 30 October 2025

species establishment (Young et al., 2005; Pettorelli and Bullock, 2023). Perhaps more problematic is that the choice of these targets has more to do with conservationists' perceptions of what 'natural' or 'native' (sensu Gann et al., 2019) should look like, which is hard to verify (Bullock et al., 2022). While replicating specific communities is likely to remain the core of restoration programs, a pure focus on target assemblages may be to the detriment of wider system integrity and functionality in the face of immediate (e.g. land-use change or diffuse pollution) or longer term (e.g. climate change) environmental pressures (Oliver et al., 2015; Bullock et al., 2022; Braun et al., 2023).

System complexity provides an alternative approach that moves the focus towards outcomes that have theoretical and empirical support for system integrity, as well as potentially contributing to other desirable aspect such as ecosystem functionality and resilience (Tscharntke et al., 2012; Landi et al., 2018; Bullock et al., 2022). Here we follow Bullock et al. (2022) in defining complexity as the number of components and the connections between them within a system. Maximising system complexity is not incompatible with conventional habitat- or species-targeted approaches, with many such habitats representing complex communities (Hilderbrand et al., 2005; Rey Benayas et al., 2009; Pimm et al., 2021). However, it provides a more generalisable framework for system restoration that avoids a regional or biome-specific focus in terms of what represents the 'right' communities. By moving the emphasis from highly variable indicator species to fundamental structural and trophic facets of communities, restoration may improve long-term recovery and maintenance of biodiversity and ecosystem processes (Bullock et al., 2022). If generalizable these provide opportunities to develop rules to understand how system complexity re-establishes across diverse biomes and habitat types, thus providing a common conceptual framework for successful restoration.

Where common environmental drivers act to influence the re-establishment of aspects of system complexity such as trophic interactions, these might be manipulated through targeted management or policy to fast-track restoration success. This has important applied implications. Almost all approaches to restoration can be characterised by three key factors. The first is *time* - specifically how long the restoration has been in progress. The age of restorations has been linked to the stochastic probability of species colonisations and restoration of required niche space, e.g. food plants for specialist herbivores (Grimbacher and Catterall, 2007; Verdone and Seidl, 2017; Woodcock et al., 2021). The second is *site size*. Most restoration efforts are confined to defined areas with distinct boundaries, often resulting in edge effects and challenges in meeting the minimum area requirements for population persistence (Grimbacher and Catterall, 2007; Gieselman et al., 2013; García-Romero et al., 2019). The third is the *landscape context* within which the restoration occurs, which affects not just colonising species pools but also the potential for dispersal and metapopulation persistence (van Swaay, 2002; Grimbacher and Catterall, 2007; Piqueray and Mahy, 2010; Woodcock et al., 2010). While many other factors are likely to alter restoration on site-by-site basis, these three represent underlying constraints common to restoration across a diversity of habitat types.

Here we assess the establishment of trophic feeding interactions between species – which represent a fundamental aspect of system complexity – across 60 grassland and 60 woodland restoration sites in Great Britain. These feeding relationships represent energy pathways that are the product of antagonistic (plant-herbivore) and mutualistic (plant-pollinator) relationships whose links represent an emergent property of individual species' ecological, behavioural and colonisation characteristics during habitat restoration (Dunne et al., 2002; Tylianakis et al., 2007; Thébault and Fontaine, 2010; Vanbergen et al., 2017; Larkin and Stanley, 2023). The web of trophic interactions between species therefore provides an indicator with which to understand drivers of overall system complexity (Dunne et al., 2002; Heleno et al., 2012; Landi et al., 2018). We apply simulation methods to model how the complexity of empirically measured trophic interactions develop during restoration of these habitats and how habitat age, size and landscape proximity to similar habitats influence these processes (Fig. 1). We hypothesise that networks of older, larger and more connected sites (e.g. high proximity to species rich grassland or woodlands) will be characterised by trophic interactions of greater complexity as defined by a range of standard metrics.

2. Materials and methods

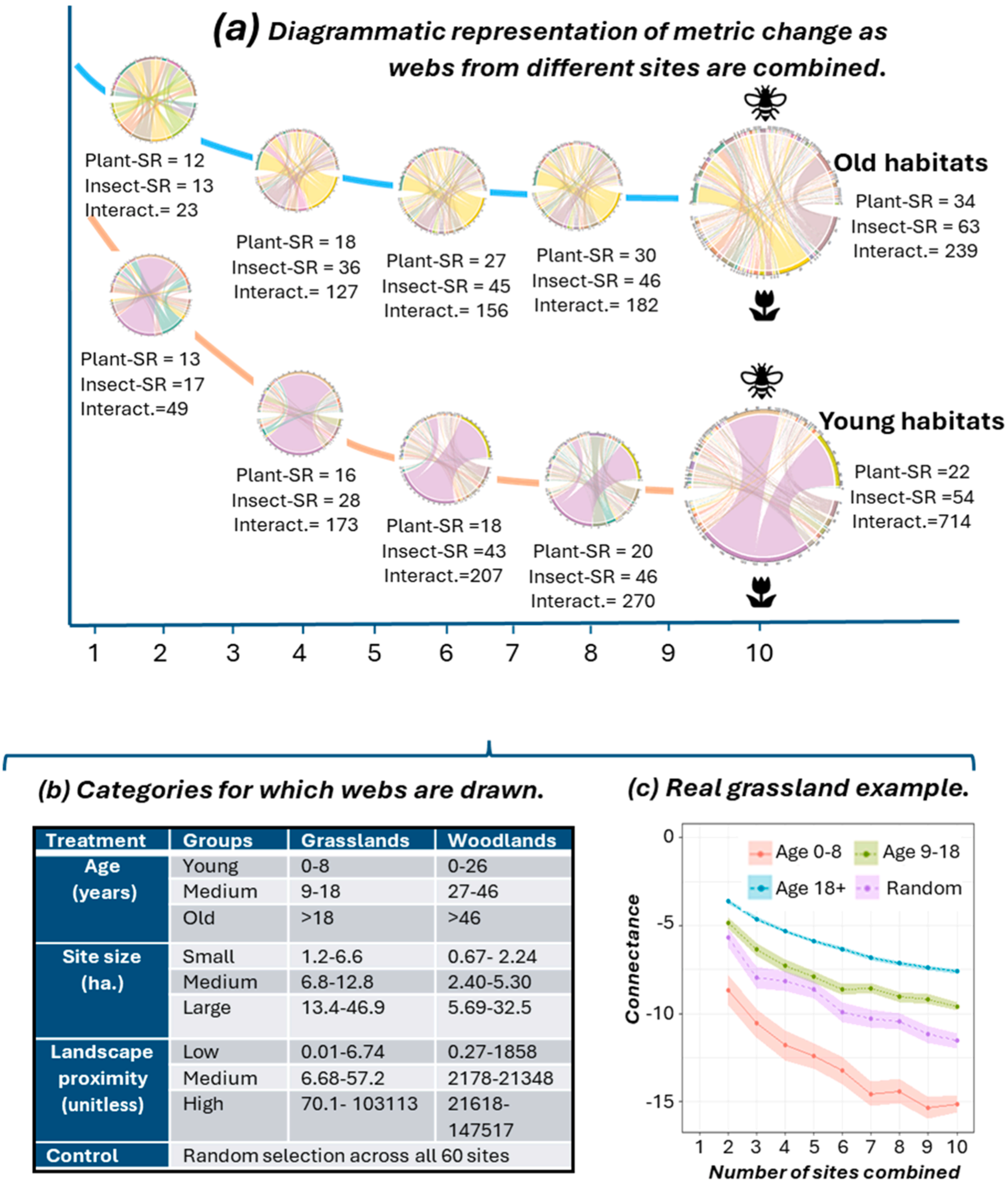
2.1. Restoration sites

In 2021 and 2022 we undertook surveys of plant-insect interactions in 60 calcareous grassland restoration sites in Southern England (Lat. 51.07, Long. −1.97–51.83, −0.59) and 60 deciduous woodland restoration sites in the English Midlands and Central Scotland (52.19, 0.22–56.53, −4.67). While located in geographically different parts of GB they more fundamentally represent to different endpoints of restoration. In the following analysis we look at how common drivers of age, site size and landscape act to structure plant-insect trophic interactions in common ways independent of these differences. These sites were undergoing restoration to re-establish those habitats on land previously used for either arable (grassland and woodland) or industrial mining (woodland only) land uses. Grassland restoration was typically promoted by seed sowing (n = 54), with the remainder of sites established by natural regeneration. Woodland establishment was achieved by direct planting of trees. Grasslands are open ecosystems that must be continually managed by grazing or cutting to prevent domination by scrub and trees. Woodlands were either unmanaged or occasionally trees were thinned.

Selection of the 60 sites of each habitat was undertaken to maximise variation in habitat age (since restoration was initiated), size and the proximity (defined in Supplementary Methods) of similar habitat to the restoration site within the surrounding landscape, within the variation offered by sites in the regions. We directly assessed the influence of these factors on the establishment of trophic interactions by splitting the sites of each habitat into equally sized treatment groups of 20 sites for habitat age, site size and site proximity to the same habitat type. Table S1 shows the range in values for these three factors for the grasslands and woodland sites. There was some evidence of covariance between the different treatment groups although this was relatively minor (Supplementary Material, Table S2).

2.2. Monitoring trophic interactions between insects and plants

We monitored plant-pollinator interactions in the grasslands in 2021 and plant-insect herbivore interactions in the woodlands (Scotland 2021, England 2022). Detailed descriptions of the sampling of these trophic interactions are provided in the Supplementary Methods. In overview, plant-pollinator interactions were assessed using transect walks to quantify insects' foraging relationships with flowers. Each transect was visited for a total of three occasions from May-August. Bees, hoverflies, butterflies, moths and most flies were identified moths and most flies to the lowest taxonomic level feasible, typically to species or genus. For the woodland each site was sampled twice from June to September for plant-insect herbivore interactions. For each site, ten trees were selected in proportion to prevalence of each species within the woodland. Each tree was individually surveyed using beating trays where collected phytophagous insects were assumed to be feeding on the tree they were sampled from (see Supplementary Methods for caveats). Insects were identified to the highest practical taxonomic resolution, again typically to species or genus. While herbivore and pollinator interactions are fundamentally different, here we use them as an indicator of system complexity in response to environmental drivers during restoration.



Treatment	Groups	Grasslands	Woodlands
Age (years)	Young	0-8	0-26
	Medium	9-18	27-46
	Old	>18	>46
Site size (ha.)	Small	1.2-6.6	0.67- 2.24
	Medium	6.8-12.8	2.40-5.30
	Large	13.4-46.9	5.69-32.5
Landscape proximity (unitless)	Low	0.01-6.74	0.27-1858
	Medium	6.68-57.2	2178-21348
	High	70.1- 103113	21618-147517
Control	Random selection across all 60 sites		

Fig. 1. We simulated how bipartite web metrics (connectance, nestedness and generality) for grassland plant-insect pollinator (60 sites) and woodland tree-insect herbivores (60 sites) accumulate or decline as the webs of randomly selected individual sites are combined. These were derived for different treatment groups (typically composed of 20 sites, with Fig. 1a representing an example of the process) representing sites with low, medium or high values of habitat age, size, or landscape proximity to similar habitat (Fig. 1b). As a control we also derived accumulation/decline curves across all sites (60 webs for either grassland or woodland) ignoring any these groupings (Fig. 1b). This process or random selection of webs with groups for combination was repeated 500 times, allowing derivation of mean and 95 % confidence intervals for each additional site added (Fig. 1c; with all decline/accumulation curves in Supplementary Information Figs S4-S6).

2.3. *Structural measures of plant-insect trophic interactions*

Bipartite webs were used to describe the quantitative frequency of either mutualistic (grassland plant-pollinator) or antagonistic (woodland plant-herbivore) relationships. For each web, we derived: 1) weighted connectance representing the marginal total weighted diversity of interactions per species divided by the number of species in the network (Dormann et al., 2009). Linked to community robustness mediated in part through greater redundancy of trophic links (Dunne et al., 2002; Thébault and Fontaine, 2010; Lever et al., 2014); 2) Nestedness metric based on Overlap and decreasing Fill (NODF) which represents the extent to which specialists (pollinators or herbivores foraging on a restricted number of plant species) interact with subsets of plant species that the generalists interact with (Dormann et al., 2009). Nestedness has been shown to contribute to the stability of the overall network (Bascompte et al., 2003; Bastolla et al., 2009; Thébault and Fontaine, 2010; Lever et al., 2014); 3) Generality is the effective number of plant species fed upon or pollinated per insect weighted by the marginal totals (Tylianakis et al., 2007). Provides an indication of the number of trophic links between species providing inferences and resilience to loss of plant species through environmental change. All webs were derived using the Bipartite package in R version 4.4 (Dormann et al., 2008; R Core Development Team, 2023). It is common for measures of network structure to be sensitive to the size of the network, e.g. number of plant and pollinator species. To account for this issue, each of these metrics were z-score standardised by comparing its value to a null model that held fundamental aspects of network structure constant but otherwise randomised the interactions (Almeida-Neto et al., 2008; see Supplementary Methods for details).

2.4. Simulation modelling of accumulating measures of network structure with network size

Empirically measured bipartite interaction webs have the potential to be under sampled (Chacoff et al., 2012). This is particularly likely when sampling many sites given practical limitations of traveling between them within a limited period. To account for this issue, we simulated how web metrics (connectance, nestedness and generality) would accumulate or decline as clusters of restoration sites sharing similar properties (habitat age, size or proximity) were combined (Fig. 1). This approach has similarities to species accumulation curves although it focuses on the accumulation of network structure metrics with the addition of sites as a measure of sampling effort. This approach allowed us to project the potential web metrics achievable across large numbers of restoration sites that share certain characteristics, i.e. age, size or landscape context. As such this can be seen as analogous to gamma diversity and represents a measure of potential web structure achievable should restoration focus on maximising that characteristic across sites. In addition, the shape of the accumulation or decline curve provides insights into how similar or dissimilar the species and the types of trophic links are between sites. Where sites show high levels of similarity in both their species and types of trophic interactions the accumulation/decline curve would be expected to rapidly plateau because when new sites are added to the networks, they bring little novelty in terms of species or interactions.

The web metric accumulation algorithm was applied by randomly selecting between one to ten bipartite webs from the pool of monitored sites. This was done separately for the grassland plant-pollinator and woodland plant-herbivore webs. These multiple webs and their trophic interactions were then directly combined and from this combined single interaction web, connectance, nestedness and generality metrics were derived. This process was repeated to a maximum of ten combined sites to calculate how these metrics accumulated or declined with more sites. This process was then repeated 500 times, allowing derivation of mean and 95 % confidence intervals for each additional site added. The accumulation/decline curves were derived for each of the treatment groups (n = 20 sites) representing sites with low, medium or high values of habitat age, size or landscape proximity. As a control we also derived accumulation/decline curves across all sites (i.e. the 60 webs for each habitat) ignoring any of these groupings for habitat age, size or proximity. This approach was also applied to understand the accumulation of plant and insect species richness within the networks which is presented in the supplementary material (Fig S1-2).

2.5. Data analysis

The simulation modelling produced accumulation or decline curves for metrics of web architecture as networks of trophic interactions from one to ten sites were added. These curves were derived separately for each treatment (i.e. habitat age, size or proximity) from the high, medium and low grouping of sites within them (Table S2). Comparisons between treatment group means at the point where ten networks were combined were undertaken based on overlap in the 95 % confidence intervals. We also derived Cohen's d effect sizes to compare the mean web metric score for each treatment group to that of the control, i.e. where the predicted web metrics were drawn from all 60 sites independent of age, size or proximity groupings. Cohen's d was defined a:

$$d = \frac{(T - C)}{s_p}$$

Where T is the mean predicted web metric where ten networks were combined within a treatment group (e.g. sites of large size), C is the same but for the control group, and s_p is the pooled sample variance.

We also fitted exponential or linear regression models depending on the shape of the web metric accumulation/decline curves. These were fitted non-linear least squares implemented in the Stat package in R version 4.4 (R Core Development Team, 2023). In the case of web connectance this showed a consistent pattern of non-linear decline as additional networks were combined; we therefore fitted an exponential decay model:

$$Connectance = a + b.e^{-c \times No\ Sites}$$

Where: a = asymptote value for connectance where the number of sites (*No Sites*) from which the combined networks were derived approached infinity, b = the predicted difference between the initial value and the asymptote, and c = rate of decay in connectance with increasing numbers of sites. For this exponential decay model this equation was solved using fitted values to determine the number of sites in the landscape required to achieve 99 % of the predicted asymptote for connectance. We also tested whether the exponential decay model was a better fit to the data than a simple linear regression of:

$$Connectance = a + b.No\ sites$$

Where: a=intercept and b=slope of trend. This model was fitted using non-linear least squares method to facilitate a comparison using likelihood ratio tests. For nestedness and generality this approach was repeated, however, the accumulation of metrics values as site network were combined was typically linear, either with a positive or negative trend. Simple linear regressions were in all cases compared to a null intercept only model using likelihood ratio tests.

3. Results

From the grasslands 2866 insects from 152 taxonomic groupings (species, generic, family and order classifications) were recorded, while 1199 insect herbivores from 40 taxonomic groupings were recorded from the woodlands. As additional networks from individual sites were combined (see Fig. 1 for an example), both plant and insect species richness increased for both the grasslands and woodlands (Fig. S1 & S2).

3.1. Grassland plant-pollinator networks

The architecture of trophic interactions changed as plant-pollinator networks from different sites were combined (Fig. 1 for visualisation of the process, Fig. S3 for example networks; Fig S4-6 for accumulation of web metrics with new site networks). For the grasslands connectance, nestedness and generality were highest across 10 combined networks when they were drawn from older (Fig. 2a, Fig1 S4-5, Table S3) and larger (Fig. 2b, Fig S4–5, Table S3) restoration sites, or those from landscapes with low proximity to other species-rich grassland (Fig. 2c, Fig S6, Table S3). As networks from different sites were combined, connectance decayed exponentially to an asymptote (a in Table 1, Fig S4-6) that was highest where sites were drawn from older or larger sites, or from landscapes with low proximity to species-rich grassland. The number of sites required to reach 99 % of the exponential asymptote for connectance was lowest where networks were selected from high proximity landscapes (17.9 sites) or the medium to large sizes (14.7–15.7 sites) (Table 1). However, for the habitat age treatment it was the mid-aged sites that plateaued first. For this age group only 13.8

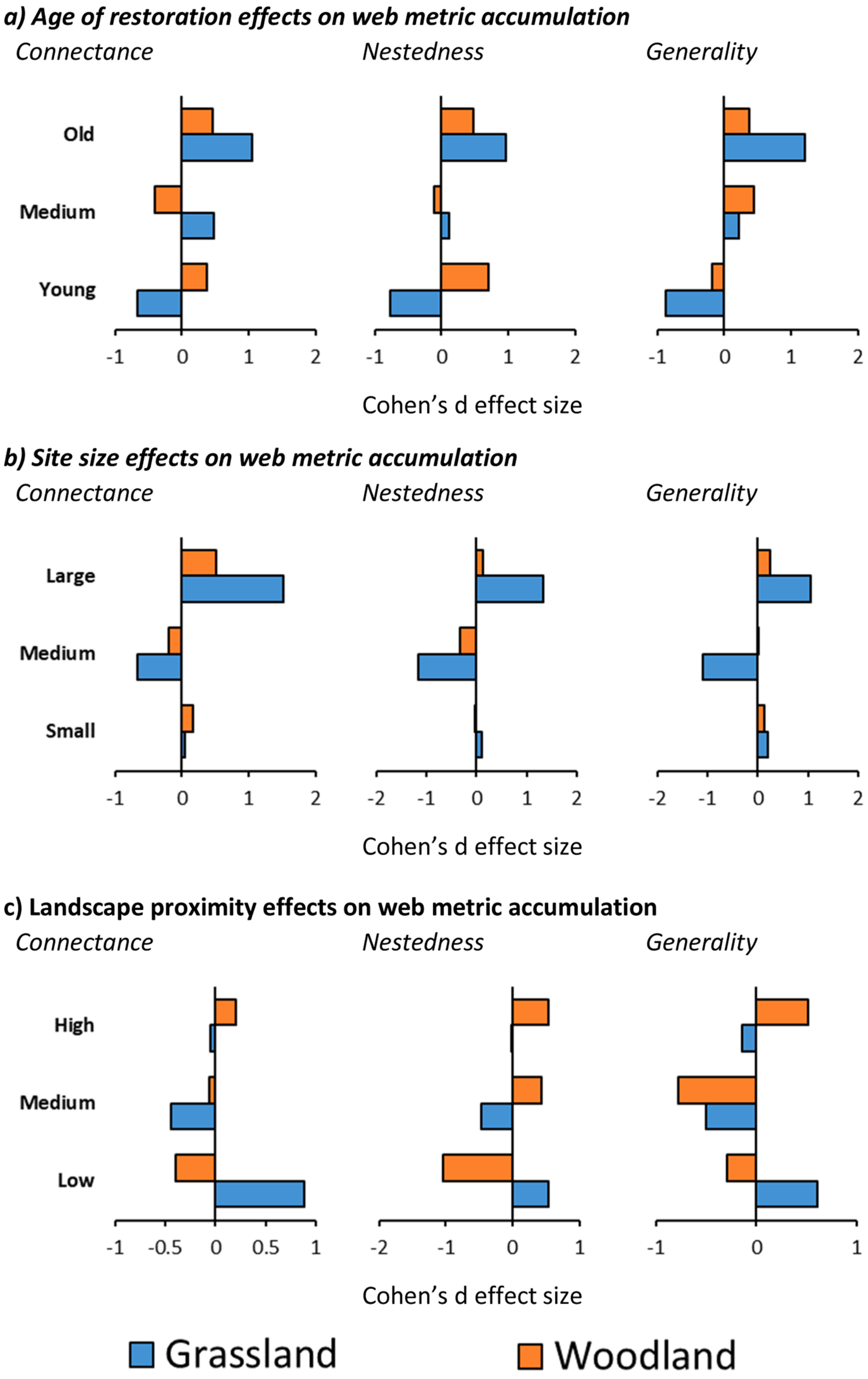


Fig. 2. Accumulation of bipartite web metrics according to whether sites were drawn from groupings based on age (young, middle or old), size (small, medium or large) or landscape proximity to similar habitat types (low, medium or high). In each case, the predicted web metric was based on 500 randomised draws of ten sites from each of these groups. Effect size (Cohen's d) was used to compare these values to a control where the randomised draws were made from the total pool of 60 grasslands or 60 woodland sites, i.e. independent of the age, size or proximity groupings. Full accumulation trends for web metric in response to additional sites are given in full in Fig. S3-5.

Table 1

Parameter estimates for the predicted exponential decay in web connectance as additional restoration sites are added to restoration groups. Connectance is z-score corrected relative to a null model and derived for the plant-insect pollinator (grassland) and plant-insect herbivore (woodland) networks. The exponential decay models show relative differences in how connectance changes with the addition of sites within groups defined by habitat age, size and landscape proximity to similar habitat types. Where: a = asymptote value of connectance where the number of sites from which the combined bipartite web approaches infinity, b = is the predicted difference between the initial value and the asymptote, and c = rate of decay in connectance with increasing numbers of sites. The predicted number of sites required for connectance to decay to 99 % of the asymptote has been derived. The significance of the exponential decay model relative to a simple linear model is shown.

		a	*b*	*c*	*Sites at 99 % plateau*	*Significance relative to linear model*
Grasslands - connectance						
Age	***Young***	−16.4	12.4	0.23	19.3	$X_1^2 = 15.4$, $p < 0.001$
	Middle	−9.78	9.41	0.33	13.8	$X_1^2 = 24.0$, $p < 0.001$
	Old	−8.55	7.04	0.20	22.3	$X_1^2 = 39.0$, $p < 0.001$
Size	***Small***	−12.1	9.84	0.22	21.3	$X_1^2 = 25.9$, $p < 0.001$
	Medium	−15.6	15.6	0.31	14.7	$X_1^2 = 25.2$, $p < 0.001$
	Large	−5.83	5.08	0.29	15.7	$X_1^2 = 27.9$, $p < 0.001$
Proximity	***Low***	−8.93	7.33	0.21	22.19	$X_1^2 = 24.2$, $p < 0.001$
	Medium	−16.8	14.3	0.21	21.6	$X_1^2 = 11.7$, $p < 0.01$
	High	−12.73	12.28	0.26	17.90	$X_1^2 = 26.1$, $p < 0.001$
Woodlands connectance						
Age	***Young***	−3.15	4.34	0.94	4.89	$X_1^2 = 33.6$, $p < 0.001$
	Middle	−4.55	2.93	0.31	14.4	$X_1^2 = 9.54$, $p = 0.002$
	Old	−2.99	2.11	0.44	10.3	$X_1^2 = 26.5$, $p < 0.001$
Size	***Small***	−3.46	2.48	0.51	8.92	$X_1^2 = 33.7$, $p < 0.001$
	Medium	−4.00	3.89	0.54	8.51	$X_1^2 = 19.2$, $p < 0.001$
	Large	−3.04	3.91	1.03	4.44	$X_1^2 = 31.4$, $p < 0.001$
Proximity	***Low***	−4.33	3.45	0.37	12.3	$X_1^2 = 19.6$, $p < 0.001$
	Medium	−3.97	2.51	0.24	18.9	$X_1^2 = 7.45$, $p < 0.01$
	High	−3.42	3.14	0.71	6.44	$X_1^2 = 34.4$, $p < 0.001$

sites were required to reach the 99 % plateau, although groups of younger sites plateaued before older groups (19.3 and 22.3 sites, respectively; Table 1)). As one to ten networks were combined, nestedness and generality showed linear declines with each site network added. The rate of this decline was lowest for both metrics where sites were drawn from older or larger groups, or those from higher proximity landscapes (β in Table 2; Fig S4 & S5).

3.2. Woodland plant-herbivore interactions

There were similarities in the response of woodland networks to those of the grassland networks for site size and age. Where networks were drawn from larger sites, we found that connectance, nestedness and generality were highest (Fig. 2a, S4-S6; Table S3b). The effect of habitat age as a predictor of plant-herbivore network structure was more complex, but again had parallels to the pollinators in that older sites tended to support the highest values of connectance and generality (Fig. 2b & S4–6; Table S3a). The trend for nestedness of trophic interactions deviated somewhat from what was seen for the pollinators, as the youngest sites had the highest values although the effect size was similar to that of older sites (Fig. 1). The major difference from grassland pollinators was that connectance, nestedness and generality of the plant-herbivore interactions were consistently higher in woodland sites originating from high proximity landscapes (Fig. 2c & S4–6, Table S3c).

The highest asymptotes for the decay in connectance were found where networks were combined from older or larger groups. This was comparable to the pattern seen for the grassland pollinators (a in Table 1). The number of sites required to reach 99 % of the connectance asymptote was lowest where networks were drawn from either the youngest or largest restorations, or those with the highest landscape proximity to other woodlands (Table 1). This was very similar to the pattern seen for the pollinators. The trend by which plant-herbivore nestedness changed with the addition of restoration sites was linear although had more variability in its direction than was seen for the grassland pollinators (Fig S5). The rate of increase in nestedness when additional site networks were combined was highest for younger sites or those located in high proximity landscapes (Table 2). The response of nestedness to site size was more complex, as nestedness did not change in response to increasing numbers of sites drawn from either large or small site groupings, although there was a negative trend for the mid-sized site group (Table 2). Generality linearly increased as networks from different sites were combined (Fig S6). The slope describing this rate of increase was highest where these were drawn from older or larger restoration sites, or those from high proximity landscapes (Table 2).

4. Discussion

In this study we have considered how the accumulation of complexity in trophic interactions changes as the networks of multiple restoration sites with similar characteristics are combined. This gamma diversity analogy for understanding the landscape scale potential for supporting trophic interactions is highly relevant to the emerging landscape scale aspirations of restoration programs within agricultural systems intended to mitigate biodiversity loss (e.g. the English nature recovery network; Isaac et al., 2018). Indeed, Bullock et al. (2022) argued for the complexity concept to be applied to restoration at the landscape as well as the site scale. Within this context we have demonstrated common patterns in how temporal and spatial environmental factors structure the complexity of trophic interactions during restoration across different habitats and for both mutualistic and antagonistic feeding relationships. Habitat age and size act in a broadly consistent manner to structure network connectance, nestedness and generality for both types of networks. These findings have implications not just for how trophic interactions establish during restoration, but also provide opportunities for developing strategies for restoration that emphasise system complexity as an outcome for restoration success.

4.1. Habitat age and size effects on trophic complexity

There is strong evidence that robustness to environmental drivers is promoted where the complexity of trophic interactions is characterised by high levels of connectance (Dunne et al., 2002; Thébault and Fontaine, 2010; Lever et al., 2014; Keyes et al., 2024). It is for this fundamental measure of complexity that the drivers of age and site size have the most consistent effects on both pollinator grassland and herbivore woodland networks. Larger and older sites were consistently associated with higher connectance both where ten networks were combined and as a projected asymptote. These sites also supported higher levels of nestedness and generality across both habitats and types of feeding relationship, although this trend showed greater variability. As for connectance, nestedness can increase the stability of the network to

Table 2

Parameter estimates for the predicted linear response of web nestedness or generality to additional restoration sites added to landscapes. Web metrics are z-score corrected relative to a null model and derived for plant-insect pollinator (grassland) and plant-insect herbivore (woodland) networks. The regression models show relative change in web metrics with the addition of sites within groups defined by habitat age, size and landscape proximity to similar habitat types.

		Nestedness			***Generality of insects***		
Grasslands		***α***	***β***	***Significance***	***α***	***B***	***Significance***
Age	***Young***	−1.10	−0.51	$F_{1,6}$= 1299, $p < 0.001$	−0.51	−0.60	$F_{1,8}$= 349.6, $p < 0.001$
	Middle	−0.61	−0.35	$F_{1,7}$= 1064, $p < 0.001$	−0.04	−0.31	$F_{1,7}$= 3725, $p < 0.001$
	Old	−0.91	−0.19	$F_{1,6}$= 240.8, $p < 0.001$	−0.77	−0.02	$F_{1,7}$= 13.4, $p < 0.001$
Size	***Small***	−1.24	−0.31	F_{16}= 204.8, $p < 0.001$	−0.54	−0.24	$F_{1,8}$= 640.4, $p < 0.001$
	Medium	−0.08	−0.72	$F_{1,6}$= 897.1, $p < 0.001$	−0.17	−0.56	$F_{1,8}$= 372.5, $p < 0.001$
	Large	−0.40	−0.16	$F_{1,6}$= 234.4, $p < 0.001$	−0.50	−0.06	$F_{1,7}$= 17.2, $p < 0.001$
Proximity	***Low***	*−0.47*	*−0.31*	$F_{1,7}$= 521.7, $p < 0.001$	*−0.43*	*−0.17*	$F_{1,7}$= 286.9, $p < 0.001$
	Medium	*−0.04*	*−0.56*	$F_{1,6}$= 1534, $p < 0.001$	*0.01*	*−0.55*	$F_{1,7}$= 448.7, $p < 0.001$
	High	*−0.99*	*−0.37*	$F_{1,6}$= 276.2, $p < 0.001$	−0.28	−0.37	$F_{1,8}$= 647.8, $p < 0.001$
Woodlands		***α***	***β***	***Significance***	***α***	***B***	***Significance***
Age	***Young***	−0.60	0.03	$F_{1,8}$= 33.8, $p < 0.001$	−0.60	0.02	$F_{1,8}$= 33.8, $p < 0.0001$
	Middle	−0.55	−0.05	$F_{1,7}$= 44.7, $p < 0.001$	−0.32	0.10	$F_{1,7}$= 101.1, $p < 0.001$
	Old	−0.59	ns	$F_{1,8}$= 0.35, $p = 0.51$	−0.43	0.10	$F_{1,8}$= 66.2, $p < 0.001$
Size	***Small***	−0.79	ns	$F_{1,7}$= 0.47, $p = 0.51$	−0.42	0.09	$F_{1,8}$= 69.3, $p < 0.001$
	Medium	−0.35	−0.08	$F_{1,7}$= 160.2, $p < 0.001$	−0.22	0.05	$F_{1,7}$= 183.3, $p < 0.001$
	Large	−0.68	ns	$F_{1,8}$= 0.74, $p < =0.41$	−0.60	0.11	$F_{1,8}$= 321.4, $p < 0.001$[*]
Proximity	***Low***	−0.94	−0.08	$F_{1,7}$= 42.8, $p < 0.001$	−0.56	0.07	$F_{1,8}$= 183.7, $p < 0.001$
	Medium	−0.32	ns	$F_{1,7}$= 3.37, $p = 0.10$	−0.21	ns	$F_{1,7}$= 2.68, $p = 0.18$
	High	−0.53	0.03	$F_{1,8}$= 58.7, $p < 0.0011$	−0.35	0.10	$F_{1,8}$= 129.7, $p < 0.001$

[*] This fit of this trend was improved by fitting this data to an exponential model (χ^2_1=14.9, $p < 0.001$).

perturbations (Bascompte et al., 2003; Bastolla et al., 2009; Thébault and Fontaine, 2010; Lever et al., 2014) while generality may insulate networks against cascading effects of species loss (Waser et al., 1996; Redhead et al., 2020; Becoche-Mosquera et al., 2023). The role of habitat age and size in driving these metrics of trophic structure is likely attributable to their association with colonisation and subsequent persistence of species. Older sites, exposed to more episodes of insect dispersal, will likely have led to more opportunities for species to colonise. Indeed, it appears that this stochastic process of colonisation means that while older sites may accumulate networks with higher connectance, it takes far more sites for this to plateau. Older sites may also contain habitat features required by colonising species that may take many years to develop (Watts, 2006; Grimbacher and Catterall, 2007; Woodcock et al., 2012; Waddell et al., 2024). As species colonise, competition may also drive an increasingly comprehensive use of niche space, promoting novel trophic links and increasing connectance (Behmer and Joern, 2008; Augustyn et al., 2016). This effect on connectance may be independent of the rate of accumulation of species. However, for woodland insect herbivores, younger sites accumulated more species as networks were combined, suggesting that the fewer species of older sites contribute more to the complexity of tropic interactions (Fig. S2). These results may to some extent be an artefact of the tray beating sampling method whereby younger sites with smaller trees may have a disproportionate amount of their canopy sampled than in older sites.

The higher levels of connectance, nestedness and generality in older and larger sites may be driven by multiple interacting factors. Generalist insect species may be selected for where greater spatial complexity (e.g. clustering) of plant resources found in larger and older sites favours species that can make use of more of these sub-habitats, reducing energetically costly foraging distances (Waser et al., 1996). Even so, larger sites may still be beneficial for habitat specialists, whose interactions become nested within those of generalists, due to requirements for minimum viable population sizes or sensitivity to edge effects (Krauss et al., 2003; Ewers et al., 2007; Fahrig, 2017). The greater opportunity for colonisation events in older sites may result in more species driving exploitation of novel resources promoting increased network complexity (Behmer and Joern, 2008; Augustyn et al., 2016). Interestingly, in the case of grasslands more pollinators were associated with smaller restoration sites although this did not result in greater connectance once corrected for web size (see Supplementary Methods). This higher species richness accumulated across smaller sites reflects the scale of foraging by many pollinators who exploit resources at landscape scales such that smaller sites may be more prone to infiltration of non-resident pollinators (Steffan-Dewenter et al., 2002; Jauker et al., 2009). However, environmental filtering within smaller sites does seem to be acting to limit establishment of species critical to system connectance, nestedness and generality, with potential negative implications for community stability (Heleno et al., 2012).

While restoration age and size had similar effects there were exceptions to this pattern. Woodland plant-herbivore networks were in general more variable. This may reflect unaccounted for secondary drivers acting to structure trophic interactions. These may include predation of largely low mobility herbivores, a risk that may be of less importance for highly mobile pollinators (Vidal and Murphy, 2018). For the woodland networks, the effect of age showed deviations from the pattern seen for the grassland plant-pollinators, whereby nestedness was high for both older and younger restorations (being lowest for intermediate aged restorations). While connectance increased with habitat age as species with novel trophic interactions colonised, nestedness, as a description of how specialist herbivore interactions sit within those of generalists, would not necessarily be subject to the same drivers. The multi-peaked response may instead be a product of shifts in the communities of plants, insects and their associated interactions over time (Aparicio-Jimenez et al., 2024; Fonseca-González et al., 2024). The transitional period between young and old woodland restorations may also be associated with the loss of early-successional insect species as woodlands undergo pronounced architectural structure changes with age (Sober et al., 2024; Waddell et al., 2024). In contrast, grassland structural changes are far more limited (van Swaay, 2002).

4.2. Landscape effects on trophic complexity

The role of landscape configuration as a predictor of the establishment of complex trophic interactions during restoration is clearly important, but the directionality of this process is dependent on ecological characteristics of the species within the network (Krauss et al., 2003; Tscharntke et al., 2012). Network connectance, nestedness and generality were all highest for the woodland plant-herbivores in sites with high proximity to other woodlands. This contrasted with the response of the grassland plant-pollinator networks for which all three metrics were highest where there was low proximity to other grasslands.

Interestingly, it appears that the asymptote plateau for connectance is achieved with the smallest number of sites for both grasslands and woodlands. This suggests that restoration in sites with high proximity to other habitat patches facilitates movement and colonisation even if that colonisation is not necessarily associated with species that drive high connectance. Divergence in the effects of landscape on the structure of plant-pollinator and plant-herbivore networks has been reported previously (Shinohara et al., 2019).

Why grassland plant-pollinator network structures were in general lower for the considered metrics may be linked to differences in how the observed insects are responding to and utilising the landscape. Species presence within a restoration site is a product of not just reproductive dispersal, but also where species are exploiting foraging resources in a transient manner at a landscape scale (Young et al., 2005; Jauker et al., 2009). Many pollinators exploit foraging resources as such scales (Steffan-Dewenter et al., 2002; Jauker et al., 2009). Species found on flowering plants within grasslands may be breeding in other habitats, for example *Eristalis* spp. hoverflies have aquatic detritivore larvae. Even for those species breeding in grasslands, their ability to forage over large distances may mean that their contribution to plant-pollinator interactions need not require that location to provide a breeding habitat (Steffan-Dewenter et al., 2002; Jauker et al., 2009). In contrast, species within woodland plant-herbivore networks were dominated by low mobility species, either larvae or adults unlikely to be foraging over large spatial scales. For these, their occurrence was likely dependent on reproduction by previous generations, rather than transient resource exploitation by mobile adults. For the more sessile insects in the woodland, their presence likely implies a breeding population. It is worth noting that for both grasslands and woodlands the accumulation of insect species was highest for sites with high proximity to the same habitat type (Fig S2). This may suggest that while more pollinator species may be present in grasslands with high proximity to other grasslands, their contribution to the network structural complexity was relatively low.

5. Conclusions

During restoration, the fundamental characteristics of habitat age, size and its location within complex landscapes act as environmental filters on species establishment and persistence, leading to emergent consequences for the development of complex trophic interactions. While these processes did not always operate in a consistent direction between the two habitats and types of web, there is enough consistency to suggest that similar processes are in operation in the structuring of these interactions for multiple habitats and types of feeding relationships. Considering complexity as a criterion for restoration success is applied here *a posteriori* and does not reflect the original goals (if indeed stated) by which the success of these restorations was to be quantified. However, as these trophic structure metrics are associated with system robustness, this has important implications for the long-term viability of habitat creation under future environmental change scenarios within agricultural landscapes (Bastolla et al., 2009; Heleno et al., 2012; Vanbergen et al., 2017; Shinohara et al., 2019).

The consistencies between grasslands and woodlands in how complexity re-established during restoration provide potential criteria for supporting site selection based on site size or could act as a basis for policy decisions that emphasise the need to ensure continuity of older restoration sites. Even so, a more nuanced effect of landscape on establishing complex trophic interactions means that the species typical of different sub-compartments of the overall community network respond differently. While such differences are likely a product of unique dispersal characteristics of certain species, it highlights the need for a whole system quantification of trophic interactions to elucidate landscape effects on the re-establishment of system complexity during restoration. Overall, we suggest that the application of measures of system complexity may provide a critical benchmark for management decision that could be integrated into both policy decision and applied management guidelines intended to promote agri-biodiversity, even where the types of trophic interactions used as indicators of complexity vary between habitat types.

CRediT authorship contribution statement

B.A. Woodcock: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **E. Waddell**: Conceptualization, Data curation, Investigation, Methodology, Writing – review & editing. **M.G. Weites**: Data curation, Investigation, Methodology, Writing – review & editing. **M. Guy**: Formal analysis, Writing – review & editing. **M. Freeman**: Data curation, Investigation, Writing – review & editing. **K. Park**: Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **E. Fuentes-Montemayor**: Conceptualization, Funding acquisition. **K. Watts**: Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **R.J. Barnett:** Data curation, Investigation, Methodology, Writing – review & editing. **S. l. Rogerson**: Investigation, Methodology, Writing – review & editing. **A. Opris**: Data curation, Investigation, Writing – review & editing. **J. Harris**: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **J.M. Bullock:** Conceptualization, Funding acquisition, Methodology, Project administration, Methodology, Project administration, Supervision, Writing – review & editing.

Funding

The research was funded under the NERC consortium award ‘Restoring Resilient Ecosystems’. Grants were NE/V006525/1 to JMB and BAW, NE/V006444/1 to JH and RC, NE/V006460/1 to EFM, KP and KW.

Declaration of generative AI and AI-assisted technologies in the writing process

No AI and AI-assisted technologies in the writing process.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ben Alex Woodcock reports financial support was provided by UK Research and Innovation Natural Environment Research Council. Editorial Advisory Board member of the journal Agriculture, Ecosystems & Environment If there are other authors, they 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 wish to thank landowners for generously granting access to sites, although for data protection reasons we do not name the directly. Thanks also to Robin Walls, Andrew Branson, Jon Crewe, Carolyn Steele, Tom Smith and Jean Smith who were involved in field work but not data collection directly used in this paper. Data and code to reproduce anlyses are avaliable at DOI 10.5281/zenodo.17477385.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.110060.

Data availability

Data and code are avaliable on github with a link provided in the data statement. If accepted we will transfer this to Zenodod for a fixed DOI

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