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RESEARCH ARTICLE

Drivers of complexity in ecosystem restoration

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Abstract

1. Ecological complexity is linked to emergent properties, such as ecosystem processes and resilience. Enhancing complexity may therefore be a more effective goal for ecosystem restoration than the traditional focus of replicating reference communities, especially under global environmental change. However, ecological complexity is rarely empirically studied in real-world systems, so the potential applications of complexity and the relationships between different aspects of complexity are poorly understood.
2. Here, we examine complexity in the context of restoration within two contrasting ecosystems, 54 calcareous grasslands and 60 broadleaved woodlands. We derive 'ecological complexity' indices for multiple ecosystem attributes, including soil bacteria, soil fungi, habitat structure, plants, invertebrates and species networks. Using Structural Equation Models, we quantify the effect of key drivers (including site age and size, amount of grassland/woodland in surrounding landscape, former land-use, establishment method and ongoing management) on complexity and the strength of associations among different aspects of complexity.
3. We find that decisions made at the onset of restoration have a large role in the subsequent development of complexity, including grassland establishment method and former land-use for woodlands.
4. High structural complexity was identified as a positive driver of invertebrate complexity in both habitats, but in general we observed limited relationships between the different complexity aspects.

5. *Policy implications*. This study shows that ecological complexity is empirically measurable, and its development in restoration can be influenced by key variables, which have mechanistic underpinnings. The foundational role of structural complexity driving other aspects of complexity could guide management efforts to enhance ecological complexity. Our results suggest, however, that ecological complexity is multi-faceted and cannot be reduced to a few simple indicators. Thus, to gain a holistic understanding of how complex an ecosystem is, one needs to measure multiple aspects rather than focusing on, for example, taxonomic diversity of a few taxa. One approach is to consider a syndrome-focussed framework, whereby a set of complexity measures provides a good indication of ecosystems status and resilience.

KEYWORDS
ecological complexity, ecosystem restoration, habitat structural complexity, restoration ecology, soil microbial diversity, species interaction networks, structural equation modelling

1 | INTRODUCTION

The global crises of biodiversity loss and climate change have created an urgent need to restore degraded ecosystems and landscapes (Pörtner et al., 2023). As a consequence, numerous global initiatives have been launched, including the UN Decade on Ecosystem Restoration (2021–2030) and the 2011 Bonn Challenge (Dave et al., 2017). However, implementing restoration is fraught with conceptual and technical challenges (Palomo et al., 2025), and determining the best methods to achieve successful restoration at the necessary scale remains a major challenge in ecology (Maes et al., 2024).

Restoration, to date, has generally focussed on re-establishing plant communities and assessing success in terms of species inventories, with 'reference' natural or semi-natural communities as targets (Evju et al., 2020; Gann et al., 2019). The concept underpinning these goals has its roots in traditional paradigms of species and habitat conservation (Young, 2000). But using specific (semi-) natural ecosystems to define endpoints is increasingly contested (Bullock et al., 2022; Higgs et al., 2018). Firstly, defining a reference community relies on assumptions about the 'natural' state of an ecosystem, which may be misleading in regions where human have intensively modified the environment over multiple centuries (Higgs et al., 2014). Even if reference systems can be defined, attempting to recreate these target communities, which developed historically under different environmental and climatic conditions, may be neither realistic in the face of ongoing environmental change, nor desirable in the context of the ecosystem services desired from that habitat. Secondly, there is uncertainty as to what extent such historical reference communities can sustain themselves under global environmental change (Harris & van Diggelen, 2006; Thomas et al., 2022). It may become increasingly important to restore ecosystems that are resilient to future pressures in order to provide vital ecosystem functions and services (Bullock et al., 2022; Gardner & Bullock, 2021; Higgs et al., 2018). Thus, there is a need for a systems-based approach to restoration that places a greater emphasis on the maintenance of complex self-sustaining ecosystems that have high functioning and resilience (Gardner & Bullock, 2021). One potential approach gaining traction in recent years is to focus on ecological complexity as a goal for restoration (Bullock et al., 2022; Moreno-Mateos et al., 2020).

Ecological complexity has a substantial theoretical and conceptual literature base, linking it to the support of multiple functions and services, resilience and stability (Allesina & Tang, 2012; Duffy et al., 2007; Pimm, 1984). While there has been a steady increase in the mention of 'ecological complexity' in recent decades there is no universally accepted definition (Riva et al., 2023). More generally, complex systems are characterised by multiple interacting parts, diversity, heterogeneity, non-linearity, the emergence of higher-level properties and path dependence during development (Elliott-Graves, 2023). In the context of restoration, Bullock et al. (2022) provide a pragmatic (i.e. empirically measurable) definition of ecological complexity as 'the number of components in a system and the number of connections among them'. Because not all components (e.g. species richness, functional groups and structural features) and connections can be measured directly, they emphasise the importance of measuring multiple aspects of complexity in unison, capturing both ecological components and their connections (i.e. interactions among them), to gain a holistic view of ecosystem-level complexity. Interactions, or connections, between components, such as the structure of trophic networks or the functional connectivity of landscapes (Anand et al., 2010; Bullock et al., 2022; Moreno-Mateos et al., 2020; Parrott, 2010), are more challenging to measure empirically. However, they provide deeper insights into complexity than simpler metrics, such as species richness (Albrecht et al., 2007; Moreno-Mateos et al., 2020; Tylianakis et al., 2007). The link between complexity, multifunctionality and resilience offers a way to understand restoration as a process that helps the system self-organise into a more complex state (Bullock et al., 2022). In practice, this might be considered as restoration towards systems that show diversity at multiple trophic levels, that support a multiplicity of ecosystem functions, and which are resilient to perturbations and adaptable to environmental change.

The application of complexity as a target for restoration remains largely unstudied in real-world systems, although calls for its investigation go back some time (McQuillan, 1998). Of critical interest is the extent to which interventions designed to restore reference communities under the existing paradigm might limit or promote the establishment of complex ecosystems. For example, species colonisation and establishment into newly created habitats is likely to increase over time (Broughton et al., 2021; Brunet, 2007; Bullock et al., 2002; Waddell et al., 2024), leading to greater community diversity and stronger biotic interactions that underpin ecosystem complexity. However, this relationship will not necessarily be linear, and other factors will likely affect the development of complexity, such as the initial state of the system (e.g. the former land-use), the size of the restoration area, proximity to sources of species, restoration method used and ongoing management (Watts et al., 2020). Colonisation and establishment into isolated and highly degraded sites are slower for a range of taxa than in better connected, less degraded areas (Broughton et al., 2022; Brunet et al., 2021; Hughes et al., 2023; Woodcock et al., 2010). One would also expect aspects of complexity to influence others (Bullock et al., 2022); for example, as a range of taxa establish, the network of interactions among them is likely to diversify and intensify over time (Morriën et al., 2017). Increased habitat structural complexity, in particular, is known to enhance the establishment of a range of taxa by increasing niche space and resources (Fuller et al., 2018; Minor et al., 2021; Waddell et al., 2024; Woodcock & Pywell, 2010). This association among different aspects of complexity is linked to self-reorganisation and self-regulation, fundamental characteristics of a complex system (Cadenasso et al., 2006; Ochoa-Hueso et al., 2021). However, there is a knowledge gap concerning the extent to which complexity in one part of an ecosystem influences or reinforces complexity in others, and the key drivers underlying these dynamics.

Here, we examine the development of ecological complexity in the context of restoration, within two habitats that represent major targets for restoration and conservation efforts in temperate regions, calcareous grasslands and broadleaved woodlands. Following the definition of complexity in Bullock et al. (2022) (i.e. 'the number of components in a system and the number of connections among them'), collected data and calculated metrics describing multiple ecological components (soil fungi, soil bacteria, plants, invertebrates and habitat structure) and their connections (species interaction networks), to gain a holistic view of ecosystem complexity at 114 restoration sites. We then used structural equation modelling (SEM) to test how these different aspects of complexity were linked, assessing both the drivers of complexity and the relationships among its aspects during restoration. We hypothesised that site age (i.e. time since restoration was initiated) will be a critical predictor of all aspects of ecological complexity and that site size and the amount of habitat in the surrounding landscape (a measure of isolation) will have a positive effect on complexity in both grasslands and woodlands. We expect that complexity of habitat structure and lower trophic levels (bacteria, fungi and plants) will be critical for driving increases in the complexity of higher trophic levels. We also expect that former land use and restoration decisions, including establishment methods and management will mediate the development of complexity.

2 | METHODS

2.1 | Site selection

We used existing restoration sites to design a natural experiment, taking advantage of pre-existing variation in site age, size and landscape context (Watts et al., 2016). Sites were selected to maximise variation across these key environmental and temporal gradients (see Supporting Information Appendix 1 for an expanded version of all methods in this study). We selected 54 grassland restoration sites (Figure S1) across Southern England with the aim of maximising variation in time since initiation of restoration (hereafter site age) and the amount of calcareous grassland in the surrounding landscape. Grassland site age ranged from 1 to 35 years (median = 11) with the percentage cover of calcareous grassland in the surrounding landscape (1 km buffer; UKCEH 2019 Land Cover Map; Morton et al., 2022) ranging from <1 to 72.1% (mean = 15.6%, SE = 1.8). All sites were established on former arable land, with seeds sown into bare soil. We distinguish two types of establishment management: (1) simple seed mixes of fewer than 10 species, often composed of commercially available plant varieties; and (2) complex seed mixes comprising either species-rich, commercially available seed mixes or from hay spreading or brush harvested seeds collected from existing species-rich grasslands. All sites were grazed by sheep but differed in whether cattle were also present.

For woodlands, sites were selected along similar gradients to those used for grasslands: site age and amount of woodland in the surrounding landscape (Figure S2). We selected 60 broadleaved or mixed planted woodland sites in lowland, predominantly agricultural landscapes; 30 in central Scotland and 30 in the midlands of England (Figure S1), with 15 sites on former agricultural land and 15 sites on former industrial land within each region. As broadleaved woodland is found throughout Great Britain, the regions were selected to increase geographic coverage and make results more generalisable across Great Britain. Former land use and site age were determined using a combination of Land Cover Maps (Fuller et al., 2002; Morton et al., 2014; Rowland et al., 2020), historical georeferenced maps (National Library of Scotland, 2024) and woodland creation grant contract start dates (Forestry Commission, 2024). The age of the woodlands ranged 13–67 years (median = 36). Landscape woodland extent raster was used to guide site selection. Landscape metrics were subsequently recalculated for each woodland (see below).

2.2 | Measuring complexity

Ecological sampling of grasslands and woodlands requires different approaches in terms of sampling design and tailoring methods to the habitat. Data were collected on habitat structure, vascular plants, invertebrates and soil across two field campaigns May–November 2021 (grasslands and Scottish woodlands) and May–September 2022 (English woodlands). For grassland fieldwork, data collection was conducted in line with UK Centre for Ecology & Hydrology ethical policy. For woodland fieldwork, data collection was approved by the University of Stirling (AWERB 2021 2551 1956). Landowner permissions were granted for all surveys, including permits for six woodland sites from Forestry and Land Scotland (Ref SUR53), Forestry England (Ref 08), Leicestershire and Rutland Wildlife Trust and Natural England.

In grasslands, sampling was focused within a 60×60m area in the centre of each field. In May–June 13, quadrats (0.5×0.5m) were placed at equal distances along a 'W-shaped' sampling transect. Within these quadrats the presence of vascular plant species (forbs, ferns and graminoids) was recorded to provide an overall probability of detection from these 13 quadrats. The average percentage cover of bare ground across all quadrats was estimated. Sward height was measured to indicate structural complexity using a drop disc (Stewart et al., 2001) at 40 locations along each arm of the sampling 'W'. From these data, means and standard deviations were calculated per site. Sward-active invertebrates were sampled using a Vortis suction sampler (Burkard Ltd., UK) on two occasions approximately 8 weeks apart (May–August). In each grassland, 60 suctions each of 10s duration were undertaken along the length of the 'W'. To provide a measure of species network complexity, insect-flower foraging interactions were assessed 1m either side of a 50m transect across the 'W' any insect seen in contact with, or feeding on, any flower was identified, along with the flower species.

In woodlands, similar data were collected within five circular plots (10m radius; 0.03ha), with the location of each randomly determined. Within each 10m radius plot, we measured diameter-at-breast height (DBH; 1.3m) for all stems ≥7cm dbh, while all small trees ≥4 <7cm dbh were measured within a sub-plot of 3m radius. From these data, we calculated structural metrics per site: number of tree stems, mean and standard deviation of dbh (a measure of structural heterogeneity) and basal area per hectare. Vascular ground plants (forbs, ferns and graminoids) were recorded and identified to species (May–July) in two 2×2m quadrats located 5m from each plot centre along two randomly generated bearings (10 quadrats per site). We sampled the invertebrate communities in trees (>1.5m in height) using beating trays (0.11×0.86m tray and 10s beating) at two points per plot (10 per site), on two occasions approximately 8 weeks apart (May–September). The beating survey method targeted individual trees to enable us to associate phytophagous larvae with host plants and create trophic webs (see species networks section below).

For invertebrates collected in both grasslands and woodlands, we identified all individuals (adults & larvae) within well-represented Orders (Coleoptera, Dermaptera, Hemiptera, Lepidoptera, Neuroptera, Araneae and Opiliones, excluding aphids in woodlands) to the finest taxonomic resolution that was practical.

2.3 | Soil microbial metagenomics

To sample the soil microbial community, 10 soil cores (to a 10cm depth with a 100mm×17mm soil corer) were taken and amalgamated at each of five locations per site. For grasslands, the five sampling locations were spaced out using the 'W' sampling design and in woodlands, samples were taken in the five plots. All soil samples were stored in airtight bags at 4°C, before a subsample was sieved to 2mm and stored at −20°C for DNA extraction. The remainder of the soil was sieved to 2mm and stored at 4°C for measures of total carbon, total nitrogen and pH. Soil was dried at 105°C before total carbon and total nitrogen were measured.

DNA from each sample was extracted using the DNeasy® PowerSoil® kit (Qiagen Cat. No./ID: 47014) with modified procedure for highly calcareous grassland soil samples (see Supporting Information). The DNA was sent to Novogene (www.novogene.com) where it was amplified with internal barcodes using in-house protocols. Amplicon sequencing was carried out using a 250bp paired-end Illumina Novoseq 6000 platform with established primers. For bacteria, the 16S gene V3-V4 region was amplified, for fungi the internal transcribed spacer ITS1-1F. The sequenced reads were imported into the QIIME2 v2022.11 (Bolyen et al., 2019) environment where they were cleaned, filtered and processed. Relative abundance feature tables were then generated for amplicon sequence variants (ASVs) using DADA2 (Callahan et al., 2016).

2.4 | Diversity metrics

For each taxonomic group (plants, invertebrates, soil bacteria and soil fungi), we computed four related measures of alpha diversity: taxonomic diversity, functional diversity, phylogenetic diversity (PD; plants and soil bacteria only) and abundance per site (invertebrates only). We used the same methods for both grasslands and woodlands. Analyses were carried out using relevant packages in R Statistical Software v4.4.1 (R Core Team, 2024) unless stated otherwise.

For plants, the total number of ground flora species recorded per site was the measure of taxonomic diversity. For plant functional diversity, 14 traits were collated for each species found (Table S1), following a broad definition of traits as inherent species characteristics influencing ecological strategies and performance. We calculated functional richness (*FR*; the amount of niche space filled by all species in the community; Villéger et al., 2008) using the '*FD*' R package (Laliberté et al., 2014). We calculated Faith's *PD* (the total sum of phylogenetic branch lengths between species found in the community; Faith, 1992) using the '*U.PhyloMaker*' R package (Jin & Qian, 2023). We used the 'GBOTB.extended.WP megatree' (Jin &

Qian, 2022; Smith & Brown, 2018; Zanne et al., 2014), which we pruned to our plant species data (grasslands and woodlands pruned separately). From the resulting pruned phylogenies, *PD* was calculated using the '*picante*' R package (Kembel et al., 2010). The proportion of quadrats a species was found in (out of 13 for grasslands or 10 for woodlands) was used as a measure of individual species frequency in calculations for both functional and PD metrics.

For invertebrates, we used the total number of genera recorded per site as the measure of taxonomic diversity. This allowed us to retain as much of our dataset as possible while also maintaining a high taxonomic resolution (woodlands = 58.9% of individuals identified to species or genus; grasslands = 36.11%; this lower level of for grasslands is because of large numbers of Hemipteran nymphs [25.8%] and aphids [16.3%]). We used the total number of individuals within our focal orders as our measure of invertebrate abundance. Total biomass (mg) per site was an additional measure of abundance. For functional diversity, we followed the same methods used for plants, with the exception that *FR* was calculated at Genus-level for invertebrates using five genus-specific traits (Table S2). PD of our invertebrate communities could not be calculated due to the lack of a published invertebrate supertree.

For soil bacteria and fungi, diversity metrics were calculated using QIIME2 plugins, PICRUSt2 (for bacteria) and FUNGuild (for fungi). For taxonomic diversity of bacteria and fungi, Shannon entropy (Shannon, 1948) was estimated from the relative abundance tables using the standard QIIME2 functions. Functional diversity (*FD*) of soil bacteria was estimated using the output of the PICRUSt2 QIIME2 plugin v2023.2 (Douglas et al., 2020) followed by the calculating Chao1 index (Chao, 1984). In a similar way, the fungi functional diversity was estimated using FUNGuild v1.1 (Nguyen et al., 2016), and the output used for Chao1 index calculation in QIIME2. PD of soil bacteria was evaluated using Faith *PD* (Faith, 1992). First, an alignment of the ASVs sequences was performed using MAFFT (Katoh & Standley, 2013) (via qiime2-alignment function); then, a phylogenetic tree was created from the alignment using FastTree (Price et al., 2010) (via q2-phylogeny function, rooted tree by maximum-likelihood approximation). Finally, Faith's *PD* was calculated using QIIME2-diversity function from the bacteria feature table and rooted tree. *PD* was not calculated for soil fungi due to known issues with aligning distantly related fungal ITS amplicons (Tedersoo et al., 2015) without additional paired 18S sequencing. For both soil bacteria and fungi, no measure of absolute abundance per site was calculated, as this is not available from the amplicon sequencing.

2.5 | Species networks

We calculated bipartite feeding webs describing quantitative trophic interactions between plants and insects. For grasslands, plant–insect pollinator interactions were quantified from directly observed visits of insects to flowering plants summed at the level of an individual site. For woodlands, trophic interactions were based on antagonistic plant–insect herbivore feeding interactions. Feeding associations were assumed based on the direct collection of larval or juvenile herbivorous insects sampled from individual tree species within each woodland using the beating trays. We focused on larval/juvenile stages as these have low mobility and so were unlikely to be present on a tree as a temporary refuge. The identified feeding associations were validated against the relevant published feeding relationships (Ward et al., 2019).

For each of the 54 grassland and 60 woodland insect–plant bipartite webs we derived connectance, nestedness, generality and vulnerability using the Bipartite package (Dormann et al., 2008). Weighted connectance represents the marginal totals-weighted diversity of interactions per species divided by the number of species in the network. Nestedness describes the extent to which specialists (pollinators or herbivores foraging on only a few plant species) interact with subsets of the plant species with which the generalist pollinators interact. Generality defines the effective number of plant species per pollinator or herbivore weighted by the marginal totals. Vulnerability is the reverse of generality, focusing on the number of insects per plant species.

2.6 | Spatial metrics

For each site, we calculated site area and the amount of habitat in the surrounding landscape. Grassland area was the area of the field in which sampling occurred, and for woodlands it was the contiguous woodland habitat surrounding our sampling plots. The amount of habitat in the surrounding landscape was the percentage cover of all calcareous grassland in the 2019 Land Cover Map (Morton et al., 2022) or all broadleaved woodland in the National Forest Inventory 2021 (Forestry Commission, 2023a, 2023b) within a 2 km buffer of the site.

2.7 | Datasets

An overview of the datasets and key variables used in the analyses is provided in Table S3. All data supporting this study are deposited in the NERC Environmental Information Data Centre (EIDC): raw grassland data (Woodcock et al., 2024), raw woodland data (Waddell et al., 2025) and derived soil metrics (Hibdige et al., 2026a, 2026b).

2.8 | Deriving indices of complexity

We computed an 'index of complexity' for each of the four taxa (plants, invertebrates, soil bacteria and soil fungi) as well as for the structural components of these habitats. We also computed a 'network complexity index' for species networks, which captures the connection part of our definition of ecological complexity. This approach allowed us to test the effect of drivers (age, size, habitat in landscape, former land-use, establishment method and grazing) on broad aspects of ecosystem complexity (each composed of multiple collinear sub-metrics, similar to a composite variable) as well as how they interact with each other during restoration.

To compute our complexity indices, we undertook dimension reduction using principal component analysis (PCA) to combine the multiple metrics of each aspect of complexity. The metrics included within each PCA were the measures of diversity for the taxonomic groups (Table S4). For both structure and species networks, we selected metrics that capture different elements of each (Table S4). We then extracted the first principal component (PC1) to use as our complexity index for each aspect. The variance explained across six complexity indices (i.e. explained by the PC1s) was high and ranged over 38–85% for grasslands (mean = 61.2%) and 40–84% for woodlands (mean = 68.6%; Table S4). Three grassland indices (structural, bacteria and plants) were multiplied by minus 1 to ensure that high values of the index reflected high complexity.

2.9 | Structural equation modelling

We analysed the relative influences of our key drivers on our indices of ecological complexity and the relationship among different complexity indices using SEM. SEM is a multivariate statistical framework that tests whether hypothesised direct and indirect causal relationships between variables are supported by the observed data. We used existing ecological knowledge to construct two broadly similar metamodels: for grasslands (Figure 1a) and for woodlands (Figure 1b; see Table S5 for details on rationale behind each hypothesised relationship in our metamodels). For grasslands, the drivers were site age, site size, amount of grassland in surrounding landscape, establishment method and grazing. For woodlands, the drivers were site age, site size, amount of woodland in surrounding landscape and former land-use. The three categorical variables, establishment method, grazing and former land-use, each had just two categories and were therefore turned into binary variables. For establishment method, this was seed mix with >15 species (1) and seed mix with <10 species (0). For grazing, this was cattle and sheep present (1) and sheep only present (0), and for former land-use, this was former industrial (1) and former agriculture (0).

SEMs were implemented using the 'piecewiseSEM' R package (Lefcheck, 2016). We favoured piecewiseSEM due to its ability to analyse complex models, the flexibility of including different types of models within the same SEM framework (e.g. generalised linear models and mixed-effects models) and its ability to highlight potentially missing paths. SEM fit was evaluated using Fisher's C and chi-squared statistics, with a $p > 0.05$ indicating a good model fit (i.e. that the hypothesised model is consistent with the observed data). Missing paths were incorporated in the models where a causal relationship was deemed ecologically plausible, otherwise they were allowed to freely covary within the SEM as correlated errors.

The best model approach for all sub-models in both the grassland and woodland SEMs was a linear model. In the woodland SEM, region (binary variable: Scotland (1) or England (0)) was added as a fixed effect in all sub-models to control for regional differences. Region was not a variable of interest and is not displayed in the

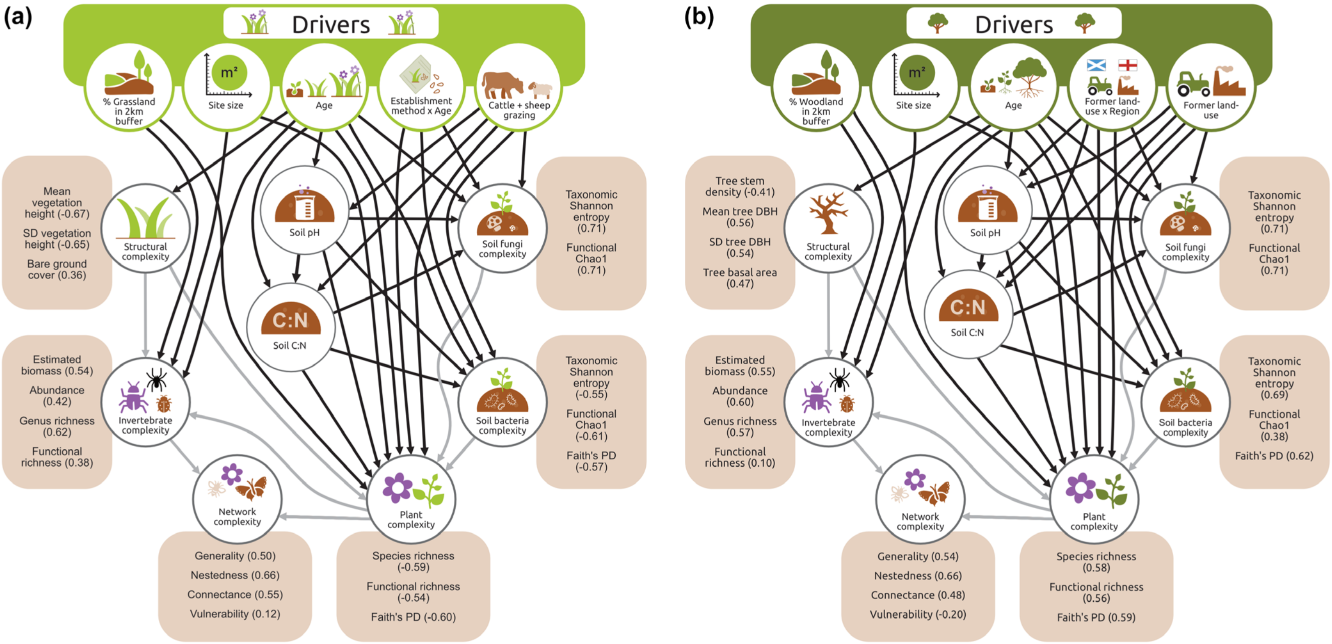

FIGURE 1 Structural equation metamodels showing hypothesised drivers of 'ecological complexity' within restoring (a) calcareous grasslands and (b) broadleaved woodlands. Six complexity indices (black circles) were calculated using a principal component analysis (PCA) approach and the first principal component (PC1) extracted. Loadings for each metric within each PC1 are included within the boxes. The black lines indicate the hypothesised relationships from drivers to complexity indices and grey lines are hypothesised relationships between indices of complexity. See main text and Supporting Information Appendix 1 for details on calculations, and Table S5 for justification of each hypothesised relationship included in these metamodels.

metamodel or result figures (see Table S6). However, preliminary analysis showed a potentially influential interaction between region and former land-use; therefore, this interaction was added to each model which contained both variables (Figure 1b). A link from site size to species network complexity was not included in the grassland metamodel as a priori relationship but was added as a relationship after being flagged as a missing path. In woodlands, both former land-use and the interaction between former land-use and region were added as relationships to structural complexity after being flagged (see Table S6 for details of additional correlated errors included in both SEMs).

Model residual fits for all sub-models within each SEM were assessed using the 'DHARMa' package (Hartig & Hartig, 2017), which tests for model misfit, overdispersion and spatial autocorrelation. To improve model fit, a further interaction between establishment method and age in the grassland plant sub-model was added. Where spatial autocorrelation was detected by Morans I testing, we tested multiple models, including single, interaction and polynomial combinations of latitude and longitude coordinates (i.e. X, Y, X^2, Y^2 and X*Y) as fixed effects. From these, we selected models that removed evidence of spatial autocorrelation.

3 | RESULTS

Across both habitats, we recorded 306 plant species (178 in grasslands and 210 in woodlands) and a total of 49,487 individual invertebrates (32,640 in grasslands and 16,847 in woodlands) representing 529 genera (309 in grasslands and 309 in woodlands). In woodlands, we measured 11,597 tree stems from 28 genera to calculate habitat structure metrics.

There was strong evidence in support of our fitted SEMs in terms of the global goodness-of-fit (Figure 2a,b). The grassland SEM explained 0.05–0.57 of the variation across the different aspects of complexity (Figure 2a). For the woodland SEM, the variation explained was 0.22–0.79 (Figure 2b) and was notably higher than grasslands for soil bacteria, soil fungi and structural complexity, but lower for plant complexity ($R^2=0.22$ in woodlands cf. $R^2=0.57$ in grasslands).

3.1 | Drivers of complexity

In woodlands, restoration site age had a strong direct positive effect on structural complexity (Figure 2b, Table S6; $p<0.001$) and a direct positive effect on soil bacteria complexity (Figure 2b, Table S6; $p<0.01$). Age also had an indirect positive effect on invertebrate complexity (mediated by structural complexity; Figure 1b, Tables S5 and S6), and a weak indirect negative effect on species network complexity (mediated by structural complexity -> invertebrate complexity; Figure 2b, Tables S6 and S7). In grassland sites, we found an interaction between age and establishment method with a strong direct effect on plant complexity (Figure 2a, Table S6; $p<0.05$); meaning that plant complexity

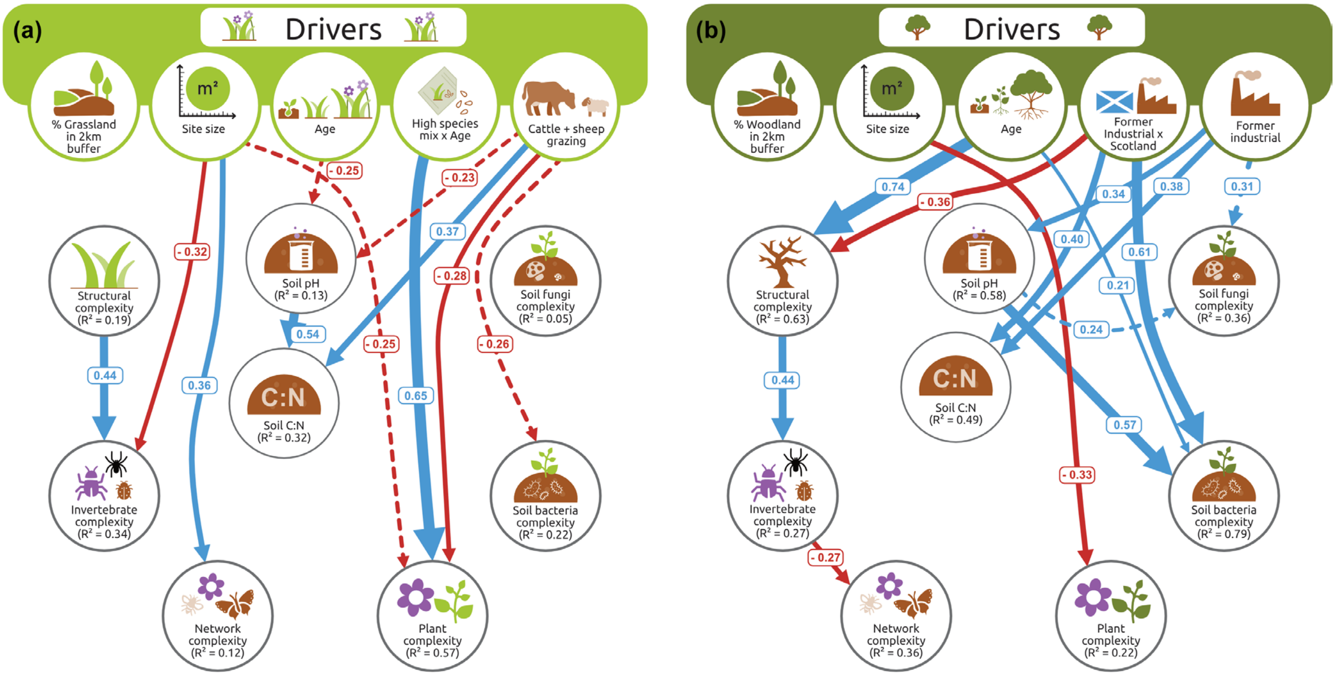

FIGURE 2 Structural equation model showing the supported drivers of ecological complexity within restoring (a) calcareous grasslands and (b) broadleaved woodlands. Model test statistics for grasslands: Fisher's $C=60.97$; $p=0.94$; $df=80$, and woodlands: Fisher's $C=77$; $p=0.57$; $df=80$. Positive relationships are shown with blue lines, and negative relationships with red. Significant relationships ($p<0.05$) are solid lines and marginally significant ($p<0.1$) are dashed lines. Numbers are the standardised path coefficients from the SEM, which are also reflected in the line width. R^2 values are shown for each endogenous variable in the SEM.

developed faster in grasslands sown with a rich seed mix (i.e. comprising >15 species).

Site size had a direct negative effect on plant complexity in both habitats, although this was marginal ($p < 0.1$) in grasslands (Figure 2a,b, Table S6; grasslands: $p = 0.051$; woodlands: $p < 0.05$). In grasslands, size also had a direct negative effect on invertebrate complexity (Figure 2a, Table S6; $p < 0.05$), as well as a direct positive effect on species network complexity ($p < 0.05$). Interestingly, we found no significant effect of the amount of habitat in the surrounding landscape on any aspect of complexity in either habitat.

In woodlands, former land-use was a key driver of complexity. There was an interaction between former land-use and region; that is formerly industrial and Scotland had a direct negative effect on structural complexity (Figure 2b, Table S6; $p < 0.05$), but a strong positive effect on soil bacteria complexity ($p < 0.001$). There was a small indirect negative effect of this interaction on invertebrate complexity (Table S7) and small indirect positive effect on species network complexity (Table S7) mediated through structural complexity. Former land-use alone had a marginal direct (Figure 2b, Table S6; $p = 0.072$) and marginal indirect (mediated by soil pH; $p = 0.053$) positive effect on soil fungi complexity, and an indirect positive effect on soil bacteria, also mediated by soil pH (Table S7).

In grasslands, grazing with cattle and sheep rather than sheep alone (a form of grassland management) had a direct negative effect on plant complexity (Figure 2a, Table S6; $p < 0.05$) and a marginal direct negative effect on soil bacteria complexity ($p = 0.095$). Establishment method alone had no effect on any complexity index in grasslands, although it was significant in an interaction with age (see above).

3.2 | Associations between aspects of complexity

Overall, we found very few associations between the different aspects of complexity. For both grasslands and woodlands, invertebrate complexity increased with higher structural complexity (Figure 2a,b; grasslands: $p < 0.001$; woodlands: $p < 0.01$). In woodlands, species network complexity decreased with higher invertebrate complexity (Figure 2b; $p < 0.01$).

4 | DISCUSSION

Prioritising the establishment of complex ecosystems refocuses the goals of restoration to emphasise system functionality and resilience. We addressed this paradigm empirically by assessing multiple aspects of complexity in restoring grasslands and woodlands, including above and below ground biodiversity, species networks and habitat structure. Interestingly, our results show that decisions made at the onset of restoration (e.g. grassland establishment method and former land-use prior to woodland creation) have a large role in the subsequent development of complexity. Unexpectedly, few hypothesised causal links among these different aspects of complexity were supported by our data, suggesting that increasing complexity in one aspect of an ecosystem does not necessarily drive wider system complexity; that is complexity is multi-faceted.

We found parallels between grasslands and woodlands in how system complexity developed. These similarities between different habitat types suggest fundamental processes that could inform restoration programmes. In particular, the starting context of a restoration played a key role in the development of system complexity. In grasslands, increasing the number of species added to the seed mix speeded up development of complexity for plants. In woodlands, former Scottish industrial sites had higher soil microbial complexity and lower structural and invertebrate complexity (although the two land-uses showed no differences in England).

The similarities observed between grasslands and woodlands also suggest that this approach may be applicable beyond the habitat types studied here. Many of the variables used to characterise complexity, such as biodiversity across trophic levels, habitat structure and species interaction networks, are readily measurable in other terrestrial systems, including heathlands and tropical forests. While the specific drivers of complexity are likely to differ among ecosystems and regions, the underlying principle of integrating multiple biotic and abiotic dimensions should be broadly transferable where comparable data are available. Extending this approach to aquatic, wetland, or marine systems would be an interesting and important direction for future work and would provide a useful test of how broadly applicable it is across ecosystems.

We anticipated that age would be a key driver of system complexity (as argued by, e.g. Moreno-Mateos et al., 2020). Yet, in grassland we did not see any direct effect of age, and in woodlands there was only a direct positive effect on soil bacteria and habitat structural complexity (also an indirect effect on invertebrate complexity). However, we acknowledge that these woodlands, with a median age of 36 years, are in the early stages of their development process (Fuentes-Montemayor, Watts, et al., 2022). Although our study captures temporal dynamics indirectly, future work would benefit from explicitly quantifying changes in complexity over time. Revisiting sites or integrating long-term monitoring data would allow trajectories of different complexity components to be assessed more directly and strengthen inference on ecosystem development during restoration.

Complexity was greatly influenced by management in grasslands, with lower plant and soil bacteria complexity in sites grazed with cattle in addition to sheep, which is an interesting result given that cattle grazing tends to have a more positive effect of grassland plant diversity than does sheep grazing (Su et al., 2023). This annual disturbance regime had an overriding effect on grassland system complexity. While anthropogenic in origin, livestock grazing replicates missing megafauna and so acts to maintain grasslands as a distinct stable state from woodlands with analogies to natural systems like savannas (Malhi et al., 2016). However, this may suggest that where habitat state is dependent on the effects of dominant ecosystem engineers, like large grazers, their impact may consistently act as a key predictor of system complexity across all types of restoration.

The lack of responses to landscape context (i.e. amount of habitat) and the unexpected negative effects of site size on our complexity indices could have been caused by the establishment of species that are not typical of these habitats (e.g. grassland species in woodlands; Tscharntke et al., 2005; Woodcock & Pywell, 2010). This is an interesting conjecture as it supports the idea that complexity may take a different trajectory than metrics based on community identity (Bullock et al., 2022).

At the community level, the biotic and abiotic components of an ecosystem are often closely connected through trophic links—herbivory, predation, symbiosis, decomposition and parasitism (e.g. soil–plants–invertebrates; Ochoa-Hueso et al., 2021), with attendant feedbacks and interdependencies. We expected to find links between different aspects of complexity reflecting these connections, for example between habitat structure and soil microbial communities and plants, invertebrates and species networks. Instead, we observed that different biotic components of complexity seem to establish independently of each other at ecosystem scale. Thus, complexity is multidimensional and not reducible to a simple metric or two. To gain a holistic understanding of how complex a system is, one needs to measure multiple aspects rather than, for example focusing on taxonomic diversity of a few taxa (Bullock et al., 2022). This finding accords with definitions of complexity in terms of the amount of information needed to describe a system (e.g. Moreno-Mateos et al., 2020).

Despite this general independence among complexity components, we nevertheless found evidence that restoration actions can influence both component complexity (e.g. biodiversity and structure) and aspects of connection complexity (e.g. species networks). One association we found in both habitats was the positive influence of high structural complexity, describing the physical environment of the sites and its effect, on invertebrate complexity. In woodlands, this effect also propagated indirectly to species interaction network complexity, although a similar effect was not seen for the grasslands. Habitat structural complexity has long been associated with high diversity across taxa (August, 1983; Stein et al., 2014; Torres-Pulliza et al., 2020; Waddell et al., 2024). These studies and our findings suggest a role of structural complexity in driving other aspects of complexity, and that there may be some more 'foundational' aspects of complexity that underpin other aspects. This insight could guide management efforts to address complexity in restoration projects.

The negative relationship observed between woodland invertebrate complexity and species interaction network complexity suggests that increases in diversity do not necessarily translate into more complex interaction networks. We found that species network complexity (PC1) was most strongly associated with nestedness and generality. As invertebrate complexity increased, the mean number of tree species fed upon by invertebrate herbivores tended to decline, while fewer specialist herbivores would interact with subsets of tree species that the generalists would. This indicates that changes in network complexity primarily reflect reorganisation of interaction structure rather than simple increases in interaction number. One potential factor affecting this may be density dependence in plant–herbivore interactions, specifically where increasing plant and invertebrate diversity reduces the dominance of individual herbivore species and overall herbivory pressure (Agrawal & Maron, 2022; Hambäck et al., 2014; Kaplan & Denno, 2007).

While we take one approach to defining and measuring complexity (following Bullock et al., 2022), we recognise that there are other approaches that may yield different results. For example, Moreno-Mateos et al. (2020) define complexity as 'the amount of ecological information required to describe a metric or attribute of an ecosystem', with species interaction networks 'accumulating the largest amount of information'. However, our definition focuses on multiple aspects, including species interaction networks, and gives a clear explanation of how to empirically measure it. One key part of our approach is that we are not concerned by species identity (e.g. whether a species is native or non-native, or a specialist of a particular habitat); if we had been, we might have found different responses to these drivers (Fuentes-Montemayor, Park, et al., 2022; Waddell et al., 2024; Whytock et al., 2018; Woodcock et al., 2010). Traditional restoration often focuses on indicator species considered as typical of the target habitat, but the inclusion of all species may create a far more complex assemblage, driving greater overall ecosystem complexity. The rationale behind this is the idea that high complexity is linked to increased resilience through functional redundancy, although further work linking our complexity indices to the ecosystem multifunctionality would be needed to provide empirical evidence for this. As definitions of ecological complexity continue to evolve (Gann et al., 2019), our study provides an initial empirical advance towards applying this concept within restoration ecology, offering a foundation for future refinement and testing across systems.

What do these findings mean for future restoration that seeks to target complexity? Hilderbrand et al. (2005) famously observed that ecological restoration has been framed around a set of approaches and paradigms, which have been widely employed in policy and practice, but are rarely examined critically. As we have argued, complexity provides an approach more suited to a changing world than reference habitat-based prescriptions. We demonstrate in this study that complexity is measurable and appears to be influenced by key variables consistent with underlying ecological mechanisms. The complex, multi-faceted nature of complexity suggests we cannot rely on a small set of complexity metrics; just as the use of overly simplistic biodiversity metrics in conservation has been criticised (Marshall et al., 2020). Rather we might consider a syndrome-focussed framework, whereby a set of complexity measures provides a good indication of ecosystems status and resilience, analogous to syndromes as used in medical practice (Hassan et al., 2021; Nugent et al., 2023). Such an approach could complement policy initiatives aimed at restoring or enhancing ecosystem resilience (e.g. biodiversity gain, nature recovery and rewilding), providing a practical, evidence-based means to evaluate ecological outcomes beyond traditional species-based targets.

AUTHOR CONTRIBUTIONS

Emily H. Waddell, Ben Woodcock, Jim Harris, Kirsty J. Park, Elisa Fuentes-Montemayor, Kevin Watts, Mark Pawlett, Alexey Larionov, Matt Guy and James Bullock conceptualised the research. Emily H. Waddell, Matt Guy, Samuel P. Rogerson, Ross J. Barnett, Maico G. Weites, Melanie Shears, Samuel Hibdige, Oscar Aguinaga, Lynne Roxbee Cox, Emma Feeley, Andrada D. Opris, Anna Gee and Cecilia De Sanctis collected the data. Emily H. Waddell analysed the data. Samuel P. Rogerson made the figures in the main text. Emily H. Waddell led the writing of the manuscript with assisted from Ben Woodcock, Jim Harris, Kirsty J. Park, Elisa Fuentes-Montemayor, Kevin Watts, Mark Pawlett, Alexey Larionov, Matt Guy, Samuel Hibdige, Lynne Roxbee Cox, Emma Feeley and James Bullock. All authors contributed critically to the final draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Elisa Fuentes-Montemayor is an Associate Editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

All data supporting this study are deposited in the NERC Environmental Information Data Centre (EIDC), including raw grassland data: https://doi.org/10.5285/552977d4-b9aa-4932-a055-5ea3bdf16d56 (Woodcock et al., 2024), raw woodland data: https://doi.org/10.5285/8c997943-1f90-4897-87b3-491eaef534ec (Waddell et al., 2025) and derived soil metrics in grasslands: https://doi.org/10.5285/8c8a836c-2117-4a36-bc1b-214b40e66feb (Hibdige et al., 2026a) and in woodlands: https://doi.org/10.5285/a21b8ed1-124b-4b2a-adb4-c3fdcc9f95a2 (Hibdige et al., 2026b).

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SUPPORTING INFORMATION

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

Appendix 1: Extended methods.

Figure S1. Map of 60 woodlands (yellow circles), 54 grasslands (blue squares).

Figure S2. Scatterplot of 114 sites in this study, showing the spread in the three key variables of interest: time since restoration, amount of habitat in the surrounding landscape and former land-use.

Table S1. List of plant traits collected for calculation of functional diversity.

Table S2. List of invertebrate traits collected for calculation of functional diversity.

Table S3. Description of site-level metrics used to quantify hypothesised drivers and ecosystem complexity metrics (component and connection aspects) across 54 restoring calcareous grasslands and 60 restoring broadleaved woodlands.

Table S4. Summary of variables included within our six 'complexity indices' computed using Principal Component Analysis, including the variance captured in PC1, split by grasslands and woodlands.

Table S5. Summary of hypothesised direct relationships within the grassland and woodland metamodel.

Table S6. Model output from SEM testing drivers of and associations between aspects of ecological complexity within restoring calcareous grasslands and broadleaved woodlands.

Table S7. Total effect of predictors on all response variables in SEM testing drivers of and associations between aspects of ecological complexity within restoring calcareous grasslands and broadleaved woodlands.

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