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RESEARCH ARTICLE

Drivers of invertebrate community assembly during ecosystem restoration

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Abstract

Introduction: Ecosystems are complex multi-trophic systems, and successful restoration needs to consider the mechanisms that underpin the reestablishment of biotic interactions. Critical to supporting this is improved understanding of the ecological processes that govern community assembly. Here, we investigate invertebrate community assembly within restoring calcareous grasslands and broadleaved woodlands, two habitats that represent major targets for restoration efforts.

Objectives: This study investigates how top-down and bottom-up trophic interactions structure arthropod communities in restoring grasslands and woodlands.

Methods: We surveyed arthropod predators and herbivores across 53 grasslands and 59 woodlands undergoing restoration. Using Structural Equation Modeling, we assessed how community structure responds to local (site age, size, habitat structure, plant species richness, starting conditions, and ongoing management) and landscape drivers (amount of habitat in the surrounding landscape).

Results: Top-down processes were stronger drivers of community assembly, with large predatory arthropods shaping species richness in both habitats and abundance in grasslands. Interactions among arthropod guilds were always positive, suggesting facilitation rather than competition. Large predators were less diverse in larger grasslands but more abundant in larger woodlands. Vegetation structure was a critical factor in structuring arthropod communities in both habitats; only in woodlands did landscape composition have an effect.

Conclusions: Predator-mediated coexistence plays an underappreciated role in restoration, with vegetation complexity acting as a critical mechanism through which habitats mediate trophic interactions. Recognizing complex community processes like species interactions will improve the effectiveness of management strategies for creating functionally diverse habitats.

Implications for Practice: Restoration practice largely focuses on facilitating species recovery through resource provisioning and habitat connectivity, with less attention to how trophic interactions structure assembling communities. Our findings suggest that managing for predator establishment could be particularly effective during early restoration, when simplified food webs may amplify top-down control. Vegetation structure emerges as the key mechanism through which habitat mediates these trophic interactions, and its role in facilitating predator-mediated coexistence may be underappreciated in restoration contexts. We suggest simple measures to increase structural complexity: planting mixed tree species and selectively thinning in woodlands, and encouraging taller, more heterogenous swards in grasslands through reduced mowing or grazing intensity.

Key words: arthropod communities, broadleaf woodland, calcareous grassland, predator-mediated coexistence, species interactions, structural complexity, top-down control, trophic interactions

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Introduction

Ecological restoration has become a global priority for addressing the interlinked biodiversity and climate crises, as habitat loss and degradation continue at unprecedented rates. The United Nations Decade on Ecosystem Restoration represents a concerted global effort to prevent, halt, and reverse ecosystem degradation (United Nations Environment Programme 2021), aligning with ambitious targets to restore 350 million ha of degraded landscapes and 30% of degraded ecosystems globally by 2030 (FAO 2020). Restoration is particularly urgent for invertebrates, which face severe population declines, with some regions experiencing over a 75% decline in flying insect biomass since the 1980s (Hallmann et al. 2017). Globally, terrestrial insect abundance has declined by approximately 9% every decade (van Klink et al. 2020). As restoration efforts accelerate worldwide, understanding the ecological processes that govern invertebrate recovery is becoming increasingly vital to ensure successful outcomes (Strassburg et al. 2020; Contos et al. 2021).

Restoration presents unique challenges for understanding recovery dynamics because communities are generally assembling from simplified states rather than maintaining established equilibria, such as in protected sites (Young et al. 2005). This dynamic process of community assembly complicates both how we define restoration success and how we measure the drivers of biodiversity recovery (Maes et al. 2024). In restoration contexts, habitat development typically occurs through human intervention rather than solely through natural succession. This is because early restoration attempts identified plant dispersal limitation as a major hurdle preventing rapid habitat creation (Bakker & Berendse 1999; Holl 1999). Doing so, however, potentially alters assembly dynamics compared to natural colonization processes (Young et al. 2005; Crouzeilles et al. 2017). The sequential arrival of different species and functional groups during community assembly creates dynamic conditions that may influence long-term community structure (Schrama et al. 2012). While many restoration studies examine biodiversity across different taxonomic groups, few studies explicitly examine how community assembly processes differ across trophic levels and how these processes interact to shape overall recovery trajectories (Ruiz-Jaen & Mitchell Aide 2005). Understanding how trophic structure and species interactions develop in response to environmental drivers is particularly critical for understanding species coexistence (Ruiz-Jaen & Mitchell Aide 2005). With their short generation times, variable colonization rates, and sensitivity to environmental change, invertebrates provide excellent study systems for investigating how communities assemble in restoring habitats (Bond et al. 2006; Westveer et al. 2018).

In addressing the issues for restoration, an important question in ecology concerns whether "top-down" or "bottom-up" processes primarily shape community assembly (Hunter & Price 1992). Bottom-up processes are driven by primary producers, which form the foundation upon which higher trophic levels depend, with resource availability and plant diversity cascading upward to shape herbivore and predator communities (Hunter & Price 1992). Bottom-up regulation can also occur across consumer trophic levels, in which herbivore abundance and diversity influence predator establishment and diversity (Lu et al. 2022). Conversely, top-down processes occur through predation and behavioral interactions that increase community diversity by preventing competitive exclusion among herbivores (Borer et al. 2005). In established ecosystems, apex predators often exert strong top-down control over species at lower trophic levels (Ritchie & Johnson 2009). The relative importance of top-down versus bottom-up processes varies across different stages of community development and ecosystem types (Shurin et al. 2002; Schmitz 2003; Finke & Denno 2004). This balance may be further altered where high spatial and temporal variation, common to restoration, results in more dynamic environments than in mature ecosystems (Young et al. 2005; Schrama et al. 2012). These processes are likely to further interact with secondary factors such as dispersal, habitat suitability, and interspecific interactions, which may operate differently in habitats undergoing restoration (Palmer et al. 1997). Site-specific (local) variables such as age, area, and habitat structure may also determine both resource availability for lower trophic levels and the suitability for predator establishment (Perring et al. 2015). Landscape context, such as the amount and proximity of similar habitat in the surrounding area, may further mediate these local factors by influencing colonization dynamics and species pool availability (Rösch et al. 2013). Understanding these context-dependent relationships is essential for developing restoration strategies that can be tailored to specific site conditions and landscape settings (Perring et al. 2015).

In this study, we investigate invertebrate community assembly across different trophic levels, examining interactions between large and small predators and specialist and generalist herbivores. Our study focuses on two contrasting habitats that represent major targets for restoration and conservation efforts in temperate regions, calcareous grasslands and broadleaved woodlands. We use a large space-for-time approach, comparing sites across a restoration age gradient of 1–35 years in grasslands, and 13–67 years in woodlands, to understand the long-term process of community assembly. Specifically, we ask: (1) To what extent do top-down versus bottom-up forces drive community assembly patterns in restoring habitats? (2) Do these mechanisms differ between abundance and species richness, and habitat (grassland vs. woodland)? (3) What is the relative influence of habitat-specific local (e.g. site age and size) and landscape variables (e.g. amount of habitat in the surrounding landscape) in mediating trophic community assembly during ecological restoration?

Methods

Site Attributes

We selected 53 grassland restoration sites (Fig. S1) across southern England with the aim of maximizing 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 = 12) with the percentage cover of calcareous grassland in the surrounding landscape

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(1 km buffer; UK Centre for Ecology and Hydrology 2019 Land Cover Map; Morton et al. 2022) ranging from less than 1% to 87% (median = 13%). Site area was the area of the field in which sampling occurred, which ranged from 1.4–47 ha (median = 8.5 ha). All sites were established on former arable land, with seeds sown into bare soil. We distinguish two types of starting seed mix: (1) simple seed mixes of fewer than 10 species, often composed of commercially available plant varieties ($n = 20$ grasslands); and (2) complex seed mixes comprising either species-rich (>15 species), commercially available seed mixes or from hay spreading or brush harvested seeds collected from existing species-rich grasslands ($n = 33$ grasslands). For grasslands, we had a measure of "management intensity," which integrated the number of management operations (cutting, cattle grazing, and sheep grazing) with the change in sward height across the sampling season. Sward height was measured using a drop disk (Stewart et al. 2001) in June–July and again in August, with 40 measurements per field. The composite index was calculated as the product of operation number (0–3) and sward height change, capturing both the diversity of management practices and their cumulative effect on sward structure (Crofts & Jefferson 1999; Woodcock et al. 2007).

Woodland sites were also selected based on site age (years since planting) and amount of woodland in the surrounding landscape (Fig. S1). We selected 59 broadleaved or mixed woodland sites in lowland, predominantly agricultural landscapes; 30 in central Scotland and 29 in the midlands of England, with 15 sites on former agricultural land within each region and 15 and 14 sites on former industrial land in Scotland and England, respectively. Former land use and site age were determined using a combination of Land Cover Maps (Fuller et al. 2002; Rowland et al. 2020; Morton et al. 2022), historical georeferenced maps (National Library Scotland 2024) and woodland creation grant contract start dates (Forestry Commission 2025). Woodland age ranged from 13 to 67 years (median = 36). The percentage cover of broadleaf woodland in the surrounding landscape (1 km buffer; Forestry Commission 2021b, 2023) ranged from 0.4 to 23% (median = 7%). Site area was the area of contiguous woodland habitat surrounding our sampling plots, within a 500 m buffer, which ranged from 0.7–47 ha (median = 5.4 ha).

Invertebrate and Habitat Sampling

The ecological sampling of grasslands and woodlands required different approaches in terms of sampling design and tailoring methods to the habitat, but in each site, data were collected on invertebrates, habitat structure, and plants (forbs in grasslands and trees in woodlands). Data were collected across two field campaigns, May–November 2021 (grasslands and Scottish woodlands) and May–September 2022 (English woodlands). In grasslands, sampling was focused within a 60 × 60 m area in the center of each field. Sward-active invertebrates were sampled using a Vortis suction sampler (Burkard Ltd., U.K.) on two occasions, approximately 8 weeks apart (May–August). At each site, 60 suctions each of 10 seconds duration were undertaken along the length of a "W-shaped" sampling transect. In May–June, 13 quadrats (0.5 × 0.5 m) were placed at equal distances along the "W." Within these quadrats, the presence of forb plant species were recorded to provide an overall species list per site. Sward height was measured using a drop disc (Stewart et al. 2001) at 40 locations along each arm of the sampling "W." From these data, mean vegetation height was calculated per site.

In woodlands, similar data were collected within five circular plots (10 m radius; 0.03 ha), with the location of each randomly determined. We sampled the invertebrate communities in trees (>1.5 m in height) using beating trays (110 × 86 cm tray and 10 seconds beating) at two points per plot (10 per site), on two occasions approximately 8 weeks apart (May–September). Trees were identified to the lowest taxonomic rank possible (species for most but oak, willow and birch to genus due to uncertainty in species id) and calculated the genera richness per site. Within each 10 m radius plot, we measured diameter-at-breast height (DBH; 1.3 m) for all stems ≥7 cm DBH, while all small trees ≥4 < 7 cm DBH were measured within a subplot of 3 m radius. From these data, we calculated the following structural metrics per plot: number of tree stems, mean and standard deviation of DBH (a measure of structural heterogeneity) and basal area per hectare. These four metrics were combined using a Principal Component Analysis, with the first principal component extracted (77% of the variance captured by PC1) and used as an index of "woodland structural complexity."

Trophic Guild Assignment

We identified all individuals (adults and larvae) within well-represented arthropod Orders (Coleoptera, Dermaptera, Hemiptera, Lepidoptera, Neuroptera, Araneae, and Opiliones excluding aphids in woodlands) to the finest taxonomic resolution that was practical. For each arthropod identified to species or genus, we collated trait information on broad adult trophic group (herbivore, predator, omnivore, or detritivore; Roberts 1995; Webb & Lott 2006; Woodcock et al. 2021; Woodcock & Pywell 2010), adult diet breadth (monophagous, oligophagous—genus, oligophagous—family and polyphagous; Ward et al. 2019) and body size (mm; measurements from this study; Gossner et al. 2015; Pekár et al. 2021). Using body size measurements, we estimated biomass (mg) for each species using the calculation: $body\ mass = 0.0305 \times body\ length^{2.62}$ following Rogers et al. (1976). For Araneae and Opiliones (not included in Rogers et al. 1976 study), we used average values calculated by Ruiz-Lupión et al. (2020), which resulted in $body\ mass = 0.055173118 \times body\ length^{2.760290323}$.

From these data we categorized species into predators (including omnivores) and herbivores; detritivores were excluded due to low abundance (approximately 5.3%). Predator body mass is inherently continuous; however, for the purposes of the modeling framework, predators were grouped into functional size classes (guilds). Species were therefore classified as large or small predators using habitat-specific median body mass values, with species above the median categorized as large predators and those at or below the median categorized as small

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predators. This led to an approximately even split between large and small predators in both habitats (grasslands: large predators = 52% species, small predators = 48% species; woodlands: large predators = 45% species, small predators = 55% species; Tables S1 & S2). Herbivores were categorized as specialists and generalists using adult diet breadth. Species that specialize on a single species (monophagous), genus, or family (oligophagous) were classified as specialist herbivores, and species with no apparent specialism (i.e. polyphagous) were classified as generalist herbivores.

Structural Equation Modeling

We analyzed the relationship among our four different trophic guilds and the relative influences of local and landscape factors on these guilds using Structural Equation Modeling (SEM). SEM is a multivariate statistical framework used to test whether hypothesized direct and indirect causal relationships among variables are supported by the observed data. We implemented SEMs using the piecewiseSEM R package (Lefcheck 2016). This approach was chosen because it accommodates complex models, allows different types of models to be incorporated within a single SEM framework (e.g. generalized linear and mixed-effects models), and can identify potential missing paths. Model fit was evaluated using Fisher's C and Chi-squared statistics, with p greater than 0.05 indicating good fit (i.e. the hypothesized model is not significantly different from the observed data). Missing paths were incorporated where a causal relationship was considered ecologically plausible; otherwise, variables were allowed to covary freely within the SEM as correlated errors.

We constructed top-down models (Fig. 1A) where the direction of causal pathways was from large and small predators to herbivores, and bottom-up models (Fig. 1B) where the direction of pathways was from generalist and specialist herbivores to predators. Because plant community variables (species richness and forb cover) represent resources for herbivores rather than predators, these were modeled as flowing into herbivores in both approaches; our models therefore test top-down and bottom-up regulation strictly within the arthropod community, with plants treated as a basal resource input rather than a trophic level under reciprocal control. To avoid fully saturating the SEMs, other local and landscape variables fed into predators only in the top-down approach and herbivores only in the bottom-up approach.

In both habitats, our local variables included site age, site area, a measure of habitat structure (mean vegetation height for grasslands and structural complexity for woodlands), and a measure of herbivore food source (forb species richness in grasslands and tree genera richness in woodlands). For grasslands, we also had management intensity and starting seed mix (see above). For woodlands, we included former land use (industrial and agriculture) in an interaction with country (Scotland and England), as preliminary analysis showed this interaction to be a significant driver of structural complexity, and thus potentially an indirect driver of trophic communities.

Model residual fits for all sub-models within each SEM were assessed using the "DHARMa" package (Hartig & Hartig 2017),

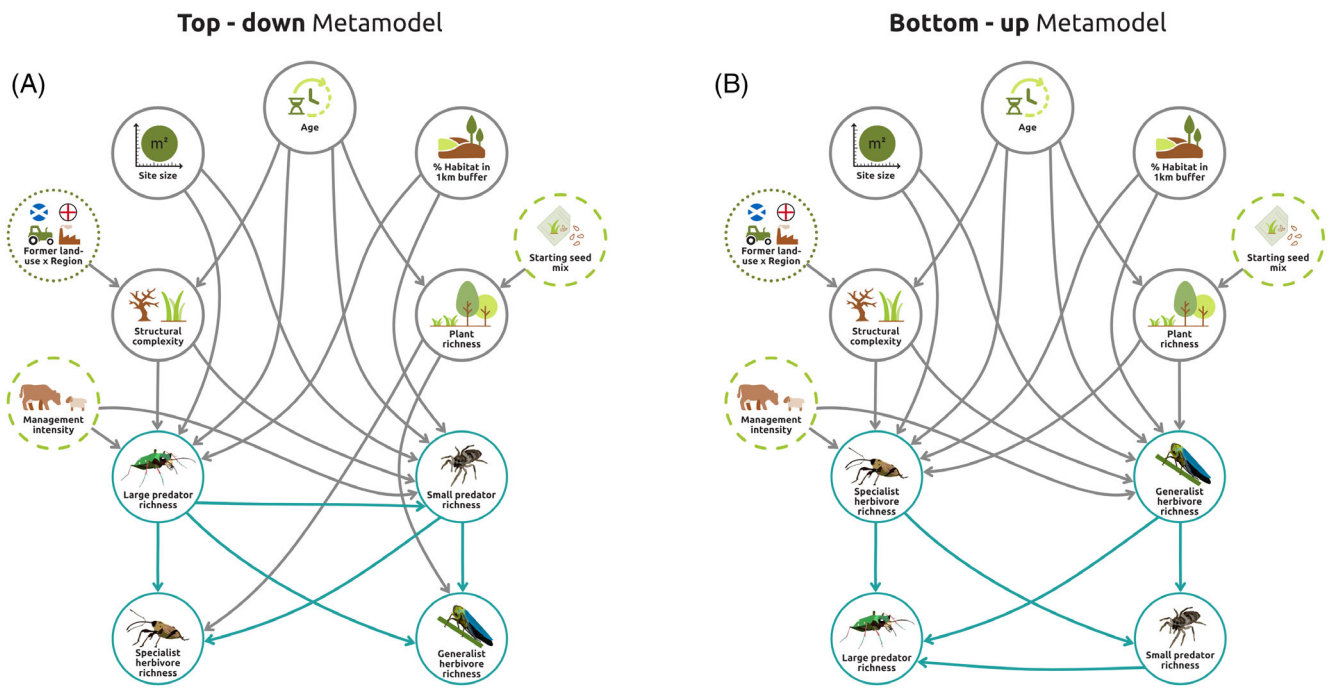

Figure 1. Structural equation metamodels showing hypothesized relationships for (A) top-down and (B) bottom-up processes across grassland and woodland restoration sites. Variables with gray circles are present in both habitat metamodels, variables with light green dashed circles are specific to grassland models, and variables with dark green dotted circles are specific to woodland models. Gray lines indicate hypothesized relationships from local and landscape variables to trophic communities, while blue lines indicate hypothesized relationships between trophic communities. See methods for details on each variable. [Correction added on 18 August 2026, after first online publication: The figure was updated to improve clarity.]

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which tests for model misfit, overdispersion and spatial autocorrelation (see Tables S1–S11; Fig. S1 for details). For trophic guild sub-models, we used generalised linear models with Poisson distributions for count data, or negative binomial when over-dispersion was detected. In cases where diagnostics indicated a better fit, we used linear models (e.g. for large and small predators). Local response variables (forb species richness, vegetation height, and woodland structure) were also analyzed with linear models (see Table S3 for full details of the distribution used for each sub-model). Several missing paths from local and landscape variables to our non-focal communities (i.e. for top-down models, the non-focal communities were the specialist and generalist herbivores) were highlighted and subsequently added as causal relationships (see Tables S4–S11 for summary of these causal missing paths and additional correlated errors included in all SEMs). In grasslands, a missing path between generalist and specialist herbivores was highlighted in all four SEMs, which was included as a causal relationship, in which generalists influence specialists through facilitation (Huisman & Olff 1998).

Results

Across both habitats, we recorded a total of 18,734 individual arthropods (10,637 in grasslands and 8097 in woodlands; Table S1) representing 858 species (439 in grasslands and 489 in woodlands; Tables S1 & S2).

Relationships Between Trophic Guilds

Top-down SEMs best explained guild richness in both habitats, while guild abundance patterns differed between habitats, with top-down processes dominating in grasslands but bottom-up processes in woodlands (Tables S3–S11; Figs. 2 & 3). We consistently found more small predator and generalist herbivore species in sites with more large predator species (Figs. 2A & 3B). However, abundance relationships varied. Grasslands showed top-down control with large predators positively associated with small predators and generalist herbivores (Fig. 2C), whereas the woodland bottom-up model showed small predators as predictors of large predator abundance (Fig. 3D). Notably, all guild interactions were positive across both habitats, including the consistent highlighted (i.e. not in the metamodel) grassland relationship whereby generalist herbivores were linked to specialist herbivores (Fig. 2). Woodland guilds displayed more significant and stronger trophic linkages for richness than abundance metrics (Fig. 3).

Drivers of Trophic Guilds

Site age showed contrasting relationships between habitats. In grasslands, age was positively associated with generalist herbivore abundance, with indirect links to specialist herbivores through this generalist pathway (Fig. 2C). Woodlands revealed more complex dynamics, with age positively related to small predator abundance but negatively related to generalist herbivore richness (Fig. 3A & 3D). Age also had indirect positive associations with woodland generalist herbivores mediated by structural complexity, yet the net result remained negative overall (Fig. 3A).

Habitat size had little relationship with guild metrics in woodlands, with only a positive association with large predator abundance (Fig. 3D). In grasslands, field area was negatively associated with large predator abundance and richness directly, and specialist herbivore richness indirectly through forb species richness (Fig. 2A & 2C). Surprisingly, the amount of surrounding habitat showed minimal relationships with trophic guilds. Only broadleaved woodland in the surrounding landscape was positively associated with both specialist and generalist herbivore abundance (Fig. 3D).

Habitat structure was the only variable with significant pathways to trophic guilds across all models. Structural complexity was strongly positively associated with generalist herbivore abundance and richness in woodlands (Fig. 3A & 3D). In grasslands, vegetation height was positively related to the abundance of specialist herbivores, small predators, and large predators, while also showing positive relationships with large predator richness (Fig. 2A & 2C). Vegetation height also showed indirect positive pathways to grassland guilds through trophic interactions. Across both richness and abundance models, large predators were positively associated with small predators and generalist herbivores, which were in turn linked to specialist herbivores (Fig. 2A & 2C).

Woodland structural complexity was related to both land use history and tree diversity. Structural complexity was lower in Scottish industrial sites and higher with greater tree genus richness, with both generalist herbivore richness and abundance positively associated with structural complexity (Fig. 3A & 3D). In grasslands, management intensity was marginally negatively related to large predator abundance while showing a slight positive association with generalist herbivore abundance (Fig. 2C). Species-rich seed mixes (>15 species) were positively associated with specialist herbivore abundance directly and richness indirectly, through their relationship with forb diversity (Fig. 3A & 3C).

Discussion

Using a space-for-time approach, we investigated how top-down and bottom-up processes act to structure arthropod communities during grassland and woodland restoration. Critically, we considered how local and landscape factors can influence how complex trophic structures establish within arthropod communities during restoration. Overall, we show that top-down predation processes have positive effects on species richness in both habitats, as well as for abundance responses in grasslands. Populations of large predators played an important role in defining the structure of small predator and herbivore communities.

Top-Down Forces Drive Community Assembly in Restoration

Our finding that top-down predation is a dominant factor structuring arthropod communities during grassland and woodland restoration aligns with a growing body of evidence that predators play a critical, though sometimes variable, role in

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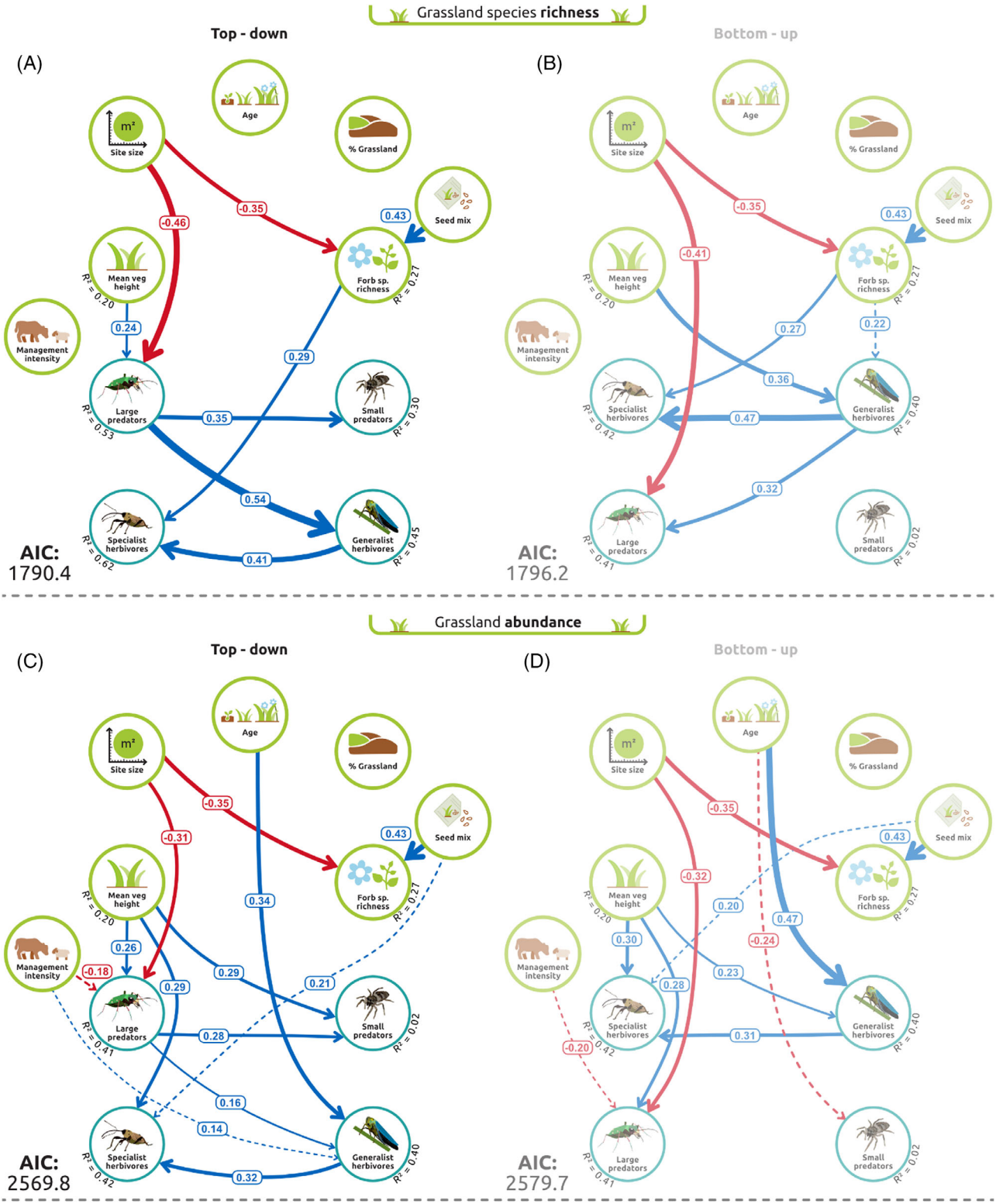

Figure 2. Grassland structural equation models showing top-down and bottom-up processes for species richness (top row; A, B) and abundance (bottom row; C, D). Models with full opacity (A and C) represent the best supported models for each metric. Positive relationships are shown with blue lines and negative relationships with red. Significant relationships ($p < 0.05$) are solid lines and marginally significant ($p < 0.1$) are dashed lines. Numbers are the standardized 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. See Tables S4–S7 for full model outputs.

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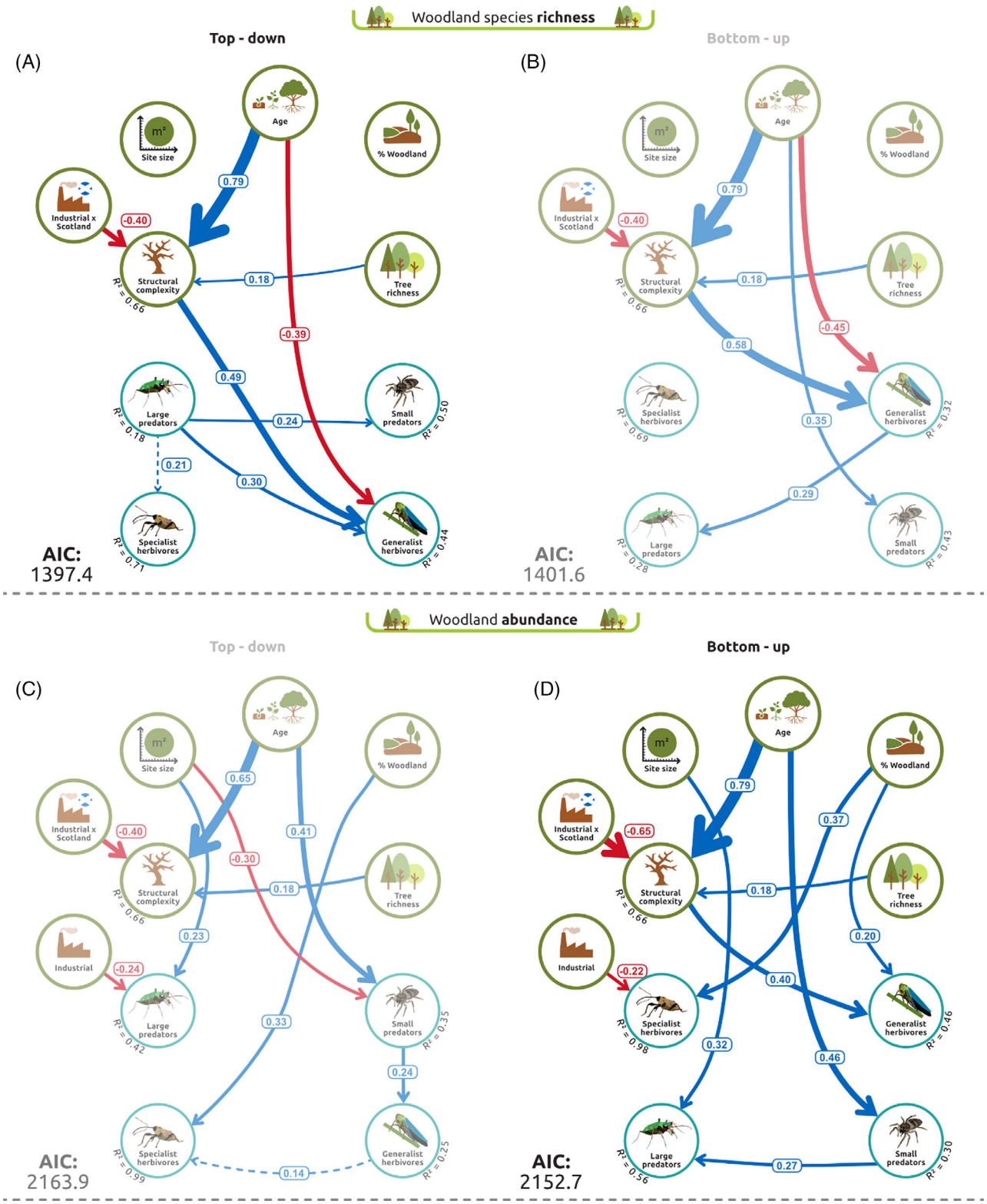

Figure 3. Woodland structural equation models showing top-down and bottom-up processes for species richness (top row; A, B) and abundance (bottom row; C, D). Models with full opacity (A and D) represent the best supported models for each metric. Positive relationships are shown with blue lines and negative relationships with red. Significant relationships ($p < 0.05$) are solid lines and marginally significant ($p < 0.1$) are dashed lines. Numbers are the standardized 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. See Tables S8–S11 for full model outputs.

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recovering ecosystems (Heineke et al. 2023; Xu et al. 2023). Importantly, our findings extend a body of evidence that has largely been based on aquatic systems, demonstrating that similar predation-driven dynamics are also present in terrestrial ecosystems (Sih et al. 1985; Shurin et al. 2002). The role of predation in systems undergoing restoration may reflect the ecological context of such reestablishing habitats, where predator effects could be amplified by simplified food webs or reduced ecosystem functioning (Xu et al. 2023). This is because low species richness reduces the complexity of interactions such as intraguild predation and direct competition, which normally dampen the impact of predators on lower trophic levels (Finke & Denno 2004; O'Gorman 2021). This can result in intensified top-down control by predators, leading to more pronounced trophic cascades (Otto et al. 2008). Consistent with this view, a recent meta-analysis by Heineke et al. (2023) also showed that predator addition can enhance species abundance recovery through trophic cascades in restoration contexts.

The different patterns observed between richness and abundance within this study suggest nuanced assembly mechanics. Top-down processes consistently shaped species richness in both habitats, suggesting that predator-mediated coexistence is operating across both systems. This mechanism has been documented across multiple habitats, including grasslands, woodlands, and aquatic systems (Caswell 1978; Dyer & Letourneau 2003; Amundrud et al. 2015), but often requires that dominant competitive prey are more susceptible to predation than subordinates (Caswell 1978; Sih et al. 1985). Where this is the case, predators indirectly increase prey diversity by suppressing the dominant species, allowing subordinate species to coexist in greater numbers (Sih et al. 1985). Caswell's (1978) coexistence model offers a valuable perspective for interpreting these patterns in restoration contexts. This model predicts that in open systems with migration between habitat patches, predation can maintain species coexistence by periodically reducing competitors, creating opportunities for other species to colonize and establish (Caswell 1978; Duncan et al. 2019).

This dynamic coexistence process is particularly relevant for many restoration sites, including those considered in this study, which exist as habitat patches within a heterogeneous matrix (Hobbs et al. 2014). Habitats in this context are vulnerable to spillover effects and biotic homogenization—where generalist species from surrounding degraded habitats colonize and dominate, resulting in ecologically similar communities (Olden 2006). Large predators, often being more generalist and able to consume a wider variety of prey, are more likely to suppress abundant species and maintain diversity (Van Schalkwyk et al. 2020; Miller-ter Kuile et al. 2022). Moreover, predators can produce cascading benefits for primary producers by reducing herbivore pressure, as demonstrated in recovering coastal wetlands (Wu & He 2024). In this scenario, predators may create conditions where species persist together across the landscape through dynamic processes, rather than through fixed population levels (Caswell 1978; Duncan et al. 2019). This mechanism might help explain why predator impacts on richness remain consistent across habitat types despite differences in their effects on abundance.

Habitat-Specific Patterns in Herbivore Abundance

While predators increased herbivore richness in both habitats, their influence on herbivore abundance varied. Grassland herbivore abundance showed stronger top-down control, whereas woodland herbivore abundance followed primarily bottom-up patterns. This difference may reflect the greater complexity of woodlands, which create diverse micro-habitats facilitating niche partitioning among herbivores (Langellotto & Denno 2004). Similarly, Ulyshen (2011) found that woodland stratification supports distinct arthropod assemblages utilizing different pools of resources. This spatial heterogeneity allows resource specialization even among generalists (Ulyshen 2011), which could allow herbivore abundance to respond more strongly to bottom-up resource availability than predation pressure. An alternative explanation may relate to the resource concentration hypothesis (Root 1973; O'Rourke & Petersen 2017). In woodlands, with fewer tree species than plant species in grasslands, herbivore-induced plant volatiles may yield clearer signals, limiting olfactory disruptions during host plant location and reducing energy costs and dispersal mortality. This concentration of tree resources could strengthen bottom-up effects and operate independently from the detected positive indirect effects of tree genus richness on herbivore abundance and richness via structural complexity. Interestingly, although woodland predators appear to exert reduced pressure on herbivore abundance, their effect on species richness persisted, suggesting predation continues to mediate competitive interactions independent of population size.

Structural Complexity Shapes Assembly Processes

Although many studies have linked structural complexity to predator presence and abundance (Langellotto & Denno 2004; Woodcock et al. 2007), few have examined this relationship in restoration contexts or highlighted the knock-on mediating effects of predators we observed. In grasslands, we showed that sward structural complexity enhanced large-predator diversity, which subsequently cascaded through the community, positively affecting other trophic groups. Structurally complex swards provide increased niche-space for different predator guilds (Woodcock et al. 2007). For example, increased vegetation height accommodates varied spider web architectures, from ground-level sheet webs to aerial orbs, promoting coexistence (Robinson 1981; Harwood et al. 2003).

Although no local or landscape variables in our models predicted sward height, sward height itself was the most consistent predictor of the grassland guilds, positively related to the abundance of specialist herbivores, small and large predators, and to large predator richness. Management intensity, a composite index combining the number of management operations (cutting, cattle, and sheep grazing) with seasonal change in sward height, was marginally negatively correlated with large predator abundance. Sites under more intensive management therefore tended to support slightly fewer large predators, although this relationship was weak. Because the index reflects the overall intensity of management and its cumulative effect on sward structure, rather than a measured frequency of any single

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operation, our data indicate the direction of effect but cannot define an optimal frequency or stocking rate at which the community experiences declines. Our results instead point to sward height itself as the important mechanism. Taller swards support more diverse invertebrate communities (Pöyry et al. 2006) and larger, more diverse predator populations that mediate coexistence (Heineke et al. 2023). Establishing this structure early in restoration, while food webs are simplified and top-down effects are strong, is likely to be particularly valuable. In practice this favors management that lets height and structural heterogeneity develop by reducing the frequency and intensity of cutting or grazing (Woodcock et al. 2009).

In woodlands, structural complexity directly supported herbivores without any effects on predators. Instead, small and large predator abundance was higher in older and larger sites, respectively. In woodlands, management of structural complexity is a different challenge to what is seen in grasslands: structural complexity can take considerable time to develop naturally, requiring 80–160 years to achieve similar structural attributes to ancient sites (Fuentes-Montemayor et al. 2022). Given that facets of structural complexity (such as tree stem variation, canopy cover, and density) support myriad taxonomic groups (e.g. beetles [Rogerson et al. 2025], plants [Waddell et al. 2024], birds [St. Rose & Naithani 2025], and mammals [Sukma et al. 2019]), actively enhancing structural complexity in restoration sites could accelerate establishment across multiple trophic levels. Our models revealed that tree species richness increases structural complexity, offering a simple and effective restoration pathway for temperate broadleaf sites by establishing diverse tree assemblages early. Practitioners could also consider leveraging natural colonization, which has been shown to increase horizontal complexity (Hughes et al. 2026). In existing woodlands, selective thinning can generate the heterogeneity required to support diversity much earlier than natural self-thinning processes alone (Gauthier et al. 2015).

Site Size and Landscape Connectivity

There were fewer species and a lower abundance of large predators in larger grasslands. It is possible that this is a product of spillover effects in smaller sites, where predators from surrounding land use move in from adjacent habitats (Tscharntke et al. 2012), though the exact mechanisms driving this relationship remain unclear and warrant further investigation.

In contrast, larger woodlands supported more large predators, consistent with predictions that predators show stronger area-dependence than lower trophic levels (Holt et al. 1999). Larger restoration sites sustain diverse prey communities providing greater quantity and reliability of prey biomass for predators (Holt & Hoopes 2005). Landscape was also an important determinant of woodland herbivore communities, with specialist and generalists benefiting from increased surrounding landscape woodland cover. This cover likely facilitates movement between patches maintaining source populations, especially those with poor dispersal capabilities (Eycott et al. 2012; Macedo-Reis et al. 2019). However, the positive effect of woodland cover on herbivores has more generally been shown to be context-dependent in other studies (Maguire et al. 2016; Valdés-Correcher et al. 2019). Its importance here may be a product of the U.K.'s intensive agricultural landscape, where woodland cover is relatively low compared to other countries (Forestry Commission 2021a).

More broadly, our study demonstrates that top-down and bottom-up processes operate simultaneously in restoration sites, though predator effects during habitat restoration appear stronger than historically assumed for terrestrial systems (Ritchie et al. 2012). This aligns with recent restoration frameworks that suggest "habitat must be appropriately considered in the context of how it mediates predation" (Lennox et al. 2025), with structural complexity emerging as the key habitat feature influencing trophic interactions across grasslands and woodlands. While the importance of vegetation structure for invertebrates is well established, our findings suggest that its role in facilitating predator-mediated coexistence may be underappreciated in restoration contexts.

The strong top-down control we observed raises questions about whether simplified food webs in the relatively early stages of restoration amplify predator effects, and whether these dynamics persist as communities develop. Current restoration practice largely focuses on facilitating species recovery through resource provisioning and habitat connectivity—providing a place to live, food to eat, and a way to get there—with less attention to how trophic interactions structure assembling communities (Gann et al. 2019). If predator effects are amplified during early assembly stages when food webs are simplified, managing for predator establishment could be particularly effective when top-down control is most influential.

Testing whether the predator effects we documented represent a transitional or a stable state through experiments manipulating both structural complexity and predator presence would help determine whether these dynamics can be leveraged for restoration. For future restoration practice, we suggest simple and effective solutions to increase structural complexity in restoration, by planting mixed tree species and selectively thinning in woodlands and reducing the intensity of mowing or grazing in grasslands to allow a more heterogeneous sward.

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woodlands. The data that support the findings of this study are openly available at the NERC EDS Environmental Information Data Centre. Grassland data are available to download at https://doi.org/10.5285/552977d4-b9aa-4932-a055-5ea3bdf16d56 and woodland data at https://doi.org/10.5285/8c997943-1f90-4897-87b3-491eaef534ec.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Distribution of study sites across the United Kingdom.
Table S1. Summary of data used in the structural equation models.
Table S2. Full species list of all arthropods recorded in this study, identified to species-level.
Table S3. Statistical distributions used for response variables in structural equation models.
Table S4. Model output from SEM showing top-down processes for species richness within restoring calcareous grasslands.
Table S5. Model output from SEM showing bottom-up processes for species richness within restoring calcareous grasslands.
Table S6. Model output from SEM showing top-down processes for species abundance within restoring calcareous grasslands.
Table S7. Model output from SEM showing bottom-up processes for species abundance within restoring calcareous grasslands.
Table S8. Model output from SEM showing top-down processes for species richness within restoring broadleaf woodlands.
Table S9. Model output from SEM showing bottom-up processes for species richness within restoring broadleaf woodlands.
Table S10. Model output from SEM showing top-down processes for species abundance within restoring broadleaf woodlands.
Table S11. Model output from SEM showing bottom-up processes for species abundance within restoring broadleaf woodlands.

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