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Landscape configuration and community structure jointly determine the persistence of mutualists under habitat loss

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Habitat loss poses a major threat to biodiversity. Its effects on ecological communities depend on the complex interplay between the landscape configuration—the pattern of connections between habitat patches, the pattern of interactions between species, and habitat loss patterns. Despite their individual importance, their joint effect on species persistence remains poorly understood. We explore how these three factors influence the persistence of empirical mutualistic communities. By employing spatially explicit metacommunity models, we find that landscapes with a heterogeneous distribution of connections between habitat patches exhibit high persistence under spatially uncorrelated habitat loss but are highly vulnerable to spatially correlated loss, where adjacent habitat patches are destroyed sequentially. Homogeneous landscapes with regularly arranged patches have lower persistence than heterogeneous landscapes but are more robust to correlated habitat loss. The nested structure of metacommunities enhances species persistence, with varying magnitude depending on landscape configuration and the patterns of habitat loss. These findings can help guide conservation strategies by identifying landscape and community features that promote species persistence.

1. Introduction

Habitat loss is one of the leading drivers of biodiversity decline, with far-reaching effects on ecological communities and their functioning [1,2]. The loss of species can propagate through ecological communities, resulting in further extinctions of species and interactions [3]. In mutualistic communities, this equates to the loss of key ecosystem services such as pollination and seed dispersal [4]. Importantly, habitat loss also reshapes spatial connectivity, fragmenting landscapes and reducing opportunities for recolonization [5–7], which can push systems towards tipping points [8,9]. Understanding how species persistence is shaped by habitat loss, landscape configuration and the structure of ecological communities is crucial for anticipating collapse and guiding conservation responses.

The landscape configuration influences metacommunity dynamics, dispersal processes and overall system stability [10–13]. Graph-theoretic approaches provide a useful framework for characterizing landscapes as networks, where habitat patches are represented as nodes connected by dispersal pathways. The structure of these spatial networks determines how readily species move across the landscape and respond to disturbance. For example, homogeneous networks where patches are arranged in a regular grid (hereafter ‘grid’) ensure uniform connectivity among patches but may limit large-scale dispersal and reduce metapopulation capacity [14]. Networks with patches connected randomly (hereafter ‘random’) offer moderate connectivity and are relatively robust to stochastic perturbations [15]. While heterogeneous scale-free networks, which contain few highly connected hub patches and many poorly connected peripheral patches, are robust to random node loss, they remain highly vulnerable to removal of the hubs [16]. Thus, the spatial pattern of habitat destruction further shapes extinction trajectories: spatially correlated loss can sever entire regions and connectivity clusters, whereas spatially uncorrelated loss disrupts patches more diffusely [17]. While previous studies have explored spatial dynamics or habitat loss effects independently, the interaction between landscape configuration, habitat loss patterns and ecological processes remains poorly understood.

Mutualistic communities, such as those composed of plants and their pollinators or seed-dispersers, are structured non-randomly in a way that promotes species coexistence and buffers against collapse [18–20]. Here too, network theory provides a useful tool for analysing the patterns of interactions between species within communities. For example, nestedness—a common pattern where specialist species interact with subsets of generalist partners—enhances community persistence by enabling redundant interaction pathways and indirect facilitation [21,22]. Generalist species often act as anchors for community resilience, whereas specialists tend to be more prone to extinction [23]. However, empirical and theoretical studies on the persistence of mutualistic communities rarely consider landscape-scale processes [24]. In fragmented landscapes, mutualistic community dynamics unfold across spatially structured habitats. Yet, the combined role of landscape configuration and mutualistic community structure in driving extinction remains largely unexplored.

Although important progress has been made in understanding the persistence of metacommunities in fragmented systems [25–27], previous models often treat habitat loss, landscape configuration and community structures in isolation. For instance, many studies focus on a single species or use synthetic interaction networks without taking into account realistic mutualistic community structures [25,28–30]. Others adopt spatially homogeneous models that ignore how dispersal constraints modulate landscape-scale dynamics [31,32]. A more integrative framework is needed to understand the interplay between spatial and community dynamics under different habitat loss regimes.

Here, we investigate how species persistence is shaped by the interaction between landscape configuration, mutualistic community structure and habitat loss patterns. We achieve this by developing a spatially explicit metacommunity model. We embed empirical mutualistic communities with varying structure within three types of spatial networks: grid, random and scale-free, and simulate dynamics under spatially correlated and uncorrelated habitat loss. Building on theory from spatial ecology and ecological networks, we expect landscape connectivity and heterogeneity to play a central role in modulating persistence, with contrasting responses emerging under uncorrelated versus spatially correlated habitat loss [25,26]. At the community level, structural properties of mutualistic networks are expected to buffer species loss, although their effects may depend on the underlying spatial configuration [23]. By linking ecological network theory with spatial dynamics, our work offers mechanistic insights into biodiversity collapse under habitat loss and informs conservation strategies for fragmented landscapes.

2. Methods

We modelled landscapes as spatially explicit unipartite networks, where habitat patches were represented as nodes and dispersal routes as links. Each landscape contained 2500 patches and a total of 5000 dispersal links, allowing spatial networks to differ in connectivity through their degree distributions rather than mean connectivity. Spatial connectivity varied along a gradient of heterogeneity: from homogeneous grid networks where each patch had exactly four connections, to random networks with links assigned randomly resulting in moderate differences in connectivity, and heterogeneous scale-free networks characterized by a power-law distribution of links where a few patches have many connections but most patches are poorly connected (figure 1).

We used 20 empirical mutualistic networks (10 plant–pollinator and 10 seed-dispersal) from the Web of Life database (www.web-of-life.es) [33] as metanetworks, which represent all species and their interactions across the entire landscape [33]. Within each patch, populations of plants and animals formed local networks that were subsets of the metanetwork. We selected empirical networks spanning a range of structural properties (electronic supplementary material, table T1), particularly focusing on variation in network nestedness.

Nestedness was calculated once at the level of the global metanetwork, which remained fixed across simulations; we did not recalculate nestedness for local subnetworks. We measured nestedness of the empirical networks (i.e. our metanetworks) following the approach proposed by [34], which is based on the nestedness metric based on overlap and decreasing fill (NODF) metric [35]. This method quantifies nestedness by assessing the extent to which species with fewer interactions are linked to subsets of the partners of more connected species. It captures the average overlap between species interactions without penalizing networks where species have similar numbers of connections (as in NODF). To control for the effects of network size and connectance, we standardized the observed nestedness against expectations from a null model. Specifically, we generated 100 randomized networks per empirical network by preserving the marginal totals (row and column sums) and recalculated nestedness for each. We then computed the mean (μ) and s.d. (σ) of nestedness from the randomized networks. Finally, we obtained the standardized nestedness z-score as:

$$z = \frac{x - \mu}{\sigma},$$

where x is the observed nestedness of the empirical network. This approach allowed us to compare nestedness across metanetworks of different sizes and link densities. Note that other approaches for quantifying normalized nestedness exist, such as the configuration-model-based method proposed by [36].

We modelled metacommunity dynamics using a patch-based framework in which each patch represents a potential habitat that can be either occupied or empty for a given species [37]. Initially, all patches contained the entire metanetwork (i.e. one of

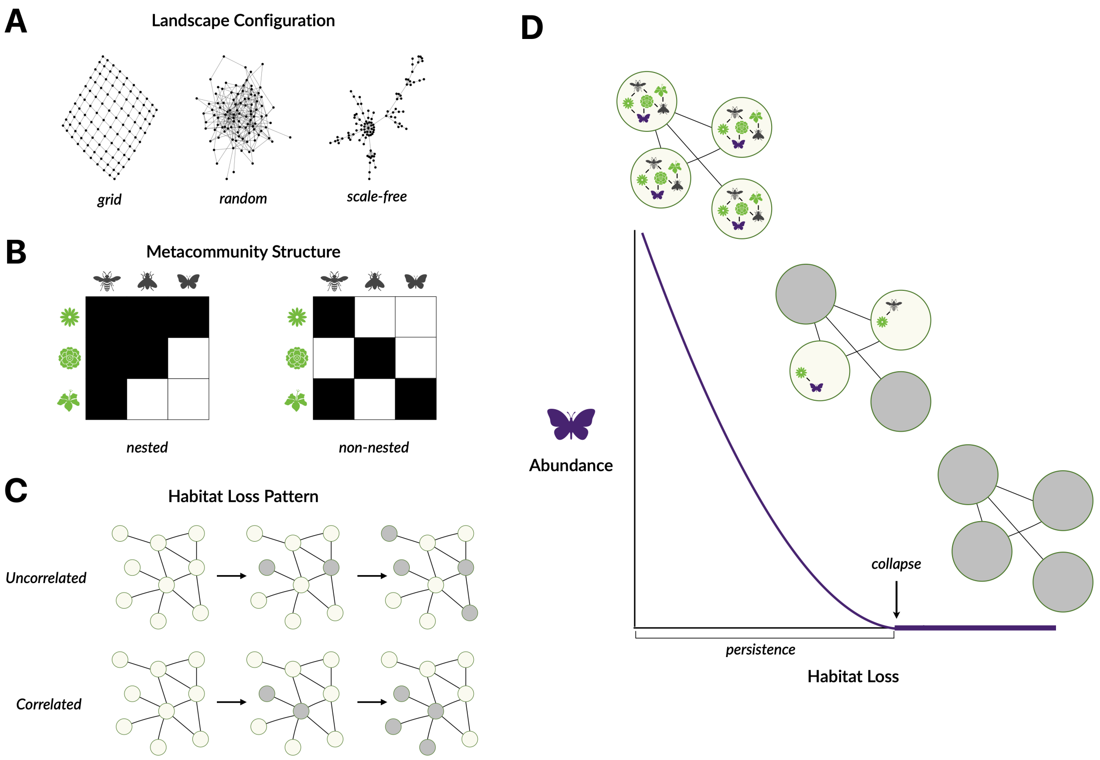

Figure 1. Schematic of our simulation treatments (A–C) and model output (D). We investigate the interplay between landscape configuration, mutualistic community structure and habitat loss scenarios in shaping species persistence. (A) To study the effect of landscape structure, we consider networks of habitat patches with increasing heterogeneity in the distribution of connections per patch—from 'grid' to 'random' to 'scale-free'. (B) We investigate the effect of mutualistic metacommunity structure by adopting empirical networks with varying nestedness—a pattern whereby a core group of generalist species interact with each other and extreme specialists interact with generalist species. (C) We simulate two scenarios of habitat loss. In the 'uncorrelated' scenario, we destroy habitat patches in a random sequence, whereas in the 'correlated' scenario, patches are lost in clusters. (D) As habitat is destroyed, species transition from persistence state to extinction state.

the 20 empirical networks). At each time step and in each patch, we simulated stochastic species colonizations and extinctions which altered the local (i.e. patch) species composition. The resulting local networks were subsets of the metanetwork containing only the species and interactions present in a given patch. Note that we did not allow interactions to rewire. The system evolved through stochastic colonization–extinction dynamics until reaching a steady state where the fraction of patches occupied by each species no longer changed between time steps.

Extinction probabilities were assumed to be uniform across species and patches. For the resource species (i.e. plants) and the mutualistic consumers (i.e. pollinators or seed dispersers), extinction probabilities were defined as [38]:

$$P_{\text{ext},i} = e_{r,i} \quad (\text{for resource } i), \quad P_{\text{ext},j} = e_{c,j} \quad (\text{for consumer } j),$$

where $e_{r,i}$ and $e_{c,j}$ are the intrinsic extinction rates of resource i and consumer j, respectively.

Colonization occurred between directly connected patches and depended on the presence of interaction partners. In mutualistic communities, a resource is more likely to establish when consumers are present in adjacent patches, while a consumer is more likely to colonize a patch if its resources are present there. Therefore, the colonization probability of the resources, $P_{\text{col},i}$, increased with the number of their consumers present in adjacent patches and the number of such patches. The colonization probability of the consumers, $P_{\text{col},j}$, increased with the number of adjacent patches where they were present and the number of their resources in the target patch. These colonization probabilities were calculated as [26,38]:

$$P_{\text{col},i} = 1 - \prod_{n=1}^{N} \prod_{j=1}^{J} (1 - c_{r,i}/j) \quad (\text{for resource } i),$$

$$P_{\text{col},j} = 1 - \prod_{n=1}^{N} \prod_{i=1}^{I} (1 - c_{c,j}/i) \quad (\text{for consumer } j),$$

where $c_{r,i}$ and $c_{c,j}$ are the intrinsic colonization rates of resource i and consumer j, respectively, N is the number of neighbouring patches that can serve as colonization sources, and J or I is the number of interaction partners present in a patch. Here, n indexes neighbouring patches, while i (for resource) or j (for consumer) indexes the sequence of partners contributing to colonization. The double product therefore explicitly represents the cumulative probability across all neighbouring patches and all interaction partners. Dividing the intrinsic colonization probability by the partner index ensures that each successive partner contributes progressively less, reflecting overlapping facilitation and preventing unrealistically high colonization probabilities for species with many partners. This formulation captures the expected increase in colonization probability with both the number of occupied patches and the number of interaction partners, while remaining ecologically realistic.

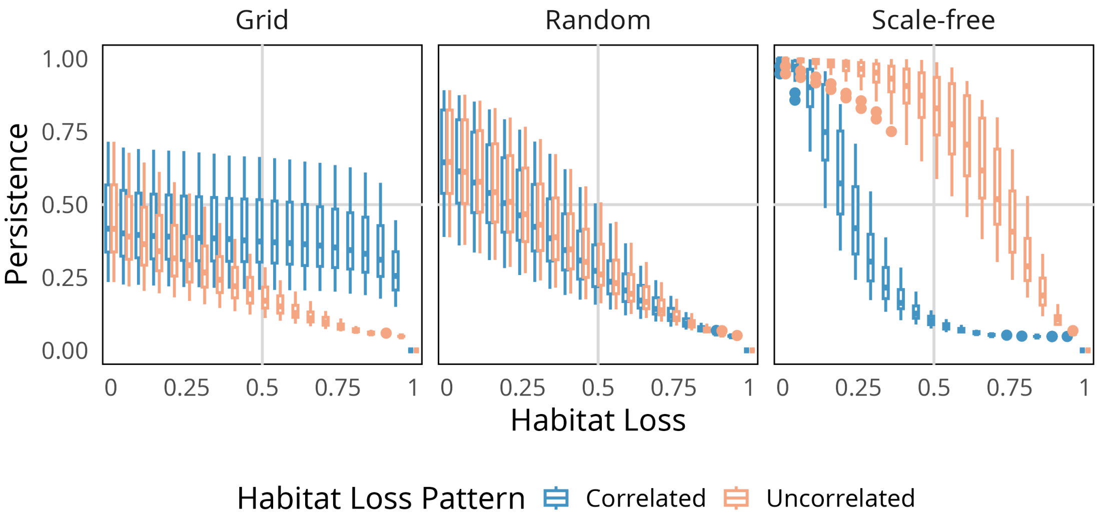

Figure 2. Species persistence probability under habitat loss. Persistence probability represents the proportion of extinction-to-colonization parameter combinations where species abundance remains above zero. Boxplots show the average persistence probability across all species for each of the 20 empirical mutualistic networks. Correlated (blue) and uncorrelated (orange) habitat loss scenarios are compared. The three panels represent different landscape structures, highlighting how spatial configuration influences species persistence under varying habitat loss patterns.

To investigate habitat loss effects, we incrementally removed habitat patches in 5% steps, starting from pristine landscapes (0% habitat loss) and continuing until all patches were destroyed (100% habitat loss). We modelled two habitat loss scenarios: (i) ‘correlated’, where destruction began at 25 (1%) randomly selected patches, and subsequently propagated through connected patches. This scenario represents an encroaching front of habitat destruction, as observed in processes such as wildfire spread or deforestation concentrated around settlements and transportation corridors [39,40]. (ii) ‘Uncorrelated’, where patches were destroyed randomly without regard for spatial connectivity (figure 1). This scenario represents disturbances such as smallholder agricultural clearing, selective logging, or small-scale mining, where habitat loss occurs as spatially dispersed, localized events [41,42]. While real-world disturbances rarely conform exactly to either extreme, both spatial patterns are well documented empirically and provide useful contrasts for examining how the spatial structure of habitat loss interacts with landscape connectivity and metacommunity dynamics to influence species persistence.

At each destruction step (from 0 to 100% habitat loss), we simulated the colonization–extinction dynamics over 1000 time steps. This ensured that the steady state was reached. We verified that the steady-state species abundances are independent of the initial species distribution across patches (see electronic supplementary material, figures S8 and S9). Then, for each fraction of habitat loss, we calculated the steady-state species abundances as the fraction of patches occupied by each species and averaged it over the final 100 time steps (i.e. discarding the first 900 time steps to remove any transient effects).

We repeated these simulations varying the extinction-to-colonization ratios for resources ($e_{r,i}/c_{r,i}$) and consumers ($e_{c,j}/c_{c,j}$) from 0 to 6 in steps of 0.3, keeping colonization rates fixed at $c_{r,i} = c_{c,j} = 0.1$[25] (see electronic supplementary material, figures S1 and S3-S4). This resulted in 441 unique parameter combinations. A species was considered persistent for a given parameter combination if its abundance was greater than zero. The persistence probability of a species was defined as the fraction of all 441 parameter combinations for which it was persistent. We reported the mean persistence probability across all species as a single metric of overall persistence for the metanetwork at each fraction of habitat loss.

To confirm the robustness of our findings to stochastic processes, we ran 10 independent replicates for each scenario. Electronic supplementary material, figure S5 shows the resulting mean abundances, which differ minimally between replicates. All simulations were performed in Julia v. 1.4.2 [43], and data visualization was performed in R v. 3.6.2 [44].

3. Results

The rate of decline of species persistence probability with habitat loss is highly dependent on the interplay between spatial landscape structure and habitat loss pattern (figure 2). Grid landscapes, which have homogeneous connectivity, show lower persistence in pristine landscapes than the more heterogeneous random and scale-free networks. Yet, they exhibit the greatest robustness to habitat loss. In fact, under correlated habitat loss, they enable the highest species persistence out of the three landscapes. In contrast, scale-free landscapes, characterized by highly connected hub patches, show the highest persistence probability at low habitat loss fractions. These networks are particularly robust to uncorrelated habitat loss, maintaining persistence even under high levels of destruction. However, under correlated habitat loss, their persistence declines very sharply, likely owing to the targeted loss of key hub patches and the resulting cascade of extinctions. Random landscape configuration displays intermediate behaviour, with persistence probabilities declining steadily with habitat loss. They respond relatively similarly to both habitat loss patterns, suggesting lower sensitivity to how habitat is removed. In summary, landscapes with homogeneous connection between patches are robust to spatially correlated habitat loss, whereas heterogeneous ones exhibit high robustness to spatially uncorrelated loss of patches.

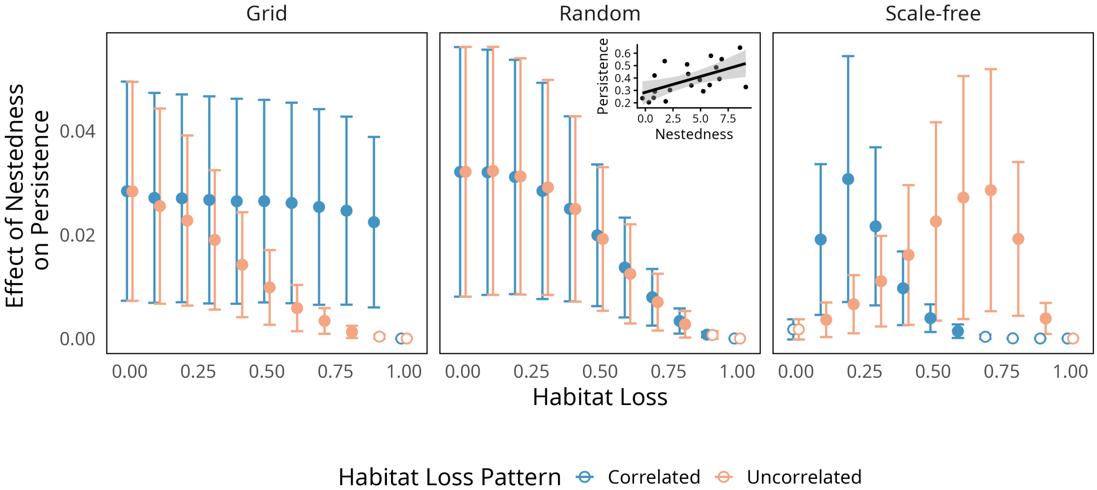

Figure 3. Effect of mutualistic community nestedness on average species persistence probability. Each point represents the estimated slope from a linear model capturing the relationship between nestedness and persistence probability at different habitat loss fractions. Filled symbols indicate statistically significant effects ($p < 0.05$), while empty symbols indicate non-significant effects. The lines indicate 95% confidence intervals, reflecting the uncertainty around the slope estimates. Correlated and uncorrelated habitat loss scenarios are shown in blue and orange, respectively. The three panels correspond to different spatial network structures, highlighting how landscape configuration influences this relationship. The inset provides an example of the nestedness–persistence relationship for a specific habitat loss fraction (see electronic supplementary material, figure S2 for additional scenarios across habitat loss fractions).

We also find variability among mutualistic communities in their response to habitat loss in different landscapes (see the lengths of boxplots in figure 2). High variability indicates that persistence depends on the structure of the community. At low habitat loss fractions, grid and random landscapes display greater variability in persistence than scale-free landscapes. As habitat loss progresses, grid and random networks show a reduction in variability among communities, especially under uncorrelated habitat loss. In contrast, scale-free landscapes exhibit an increase up to intermediate levels of habitat loss, followed by a reduction. Overall, these results highlight that the importance of community structure in driving persistence depends on the interaction between landscape configuration, habitat loss pattern and the level of habitat destruction.

More specifically, we find that nestedness of mutualistic networks has a positive effect on persistence probability across all landscapes and habitat loss patterns (figure 3 and electronic supplementary material, figure S2). However, the strength of this effect varies with both the landscape configuration and the pattern of habitat loss. In grid and random landscapes, the positive influence of nestedness weakens as habitat loss increases, with a more rapid decline under uncorrelated than correlated loss. Scale-free landscapes, in contrast, reveal a unique pattern: the effect of nestedness is relatively weak at both low and high levels of habitat loss but peaks at intermediate levels. Notably, the effect of nestedness remains stronger under uncorrelated loss in most fractions of habitat destruction. These results emphasize that the impact of the nested structure of communities on persistence is not static, but rather dynamically shaped by the landscape, the degree and the spatial pattern of habitat loss.

4. Discussion

Our study investigates how habitat loss affects the persistence of species in mutualistic communities by examining the interplay between three key aspects: landscape configuration, community structure and habitat loss pattern. To quantify these effects, we performed simulations across a broad range of species extinction-to-colonization ratios and defined persistence probability as the fraction of simulations that yield non-zero regional species abundance. While previous studies have explored the three factors separately, our work highlights their combined effects, demonstrating that their interplay is critical for understanding species persistence.

Our findings show that the spatial configuration of habitat fragments shapes metacommunity persistence under habitat loss, with outcomes varying based on community structures and the pattern of habitat loss (figure 2). The trajectory of abundance loss, shaped by extinction-to-colonization dynamics, varies across different landscape configurations and is further modulated by the pattern of habitat loss—whether uncorrelated or correlated (electronic supplementary material, figure S1). Scale-free landscapes, characterized by a few highly connected hubs, show the highest persistence and extinction thresholds (electronic supplementary material, figure S3) under spatially uncorrelated habitat loss throughout the destruction process. These hubs serve as critical reservoirs that buffer species from extinction, maintaining metacommunity cohesion even when many peripheral patches are lost. However, this structural advantage becomes a liability under spatially correlated habitat loss, particularly at low extinction-to-colonization (e/c) ratios (electronic supplementary material, figure S4). The clustered removal of patches disproportionately impacts hub nodes, leading to cascading extinctions and rapid community collapse. Our sensitivity analysis further shows that these differences between correlated and uncorrelated loss in scale-free landscapes emerge only once networks are sufficiently large to exhibit degree heterogeneity and hubs, with persistence patterns remaining robust across landscape sizes (electronic supplementary material, figure S6). In contrast, grid networks, with uniformly connected patches, are more robust under correlated than uncorrelated habitat loss. Random networks show intermediate responses under both loss patterns. Thus, robustness is not dependent solely on landscape configuration, but also on how habitat is lost. These results broadly echo previous findings on the persistence of a single species [25] and its responses to habitat loss [30,45].

We show that the structure of mutualistic communities also plays a pivotal role in species persistence under habitat loss. Specifically, we find that nestedness enhances persistence across all landscapes, thus offsetting some of the negative effects of habitat destruction (figure 3). This finding adds to the body of literature that demonstrates the importance of nestedness in promoting species coexistence, facilitating indirect interactions and buffering communities against perturbations such as species loss or environmental fluctuations [18–21,46,47]. While network connectance generally has a positive effect on persistence, its impact is not consistently significant across habitat loss levels. Nestedness, on the other hand, shows stronger and more robust effects, highlighting its dominant role in shaping persistence outcomes (electronic supplementary material, figure S7). However, we find that the positive effect of nestedness weakens with increasing habitat destruction. In homogeneous landscapes, this decline is gradual, whereas in scale-free networks, the effect of nestedness peaks at intermediate habitat loss fractions before sharply decreasing. This suggests that, while nestedness can confer robustness in the early and intermediate stages of habitat loss, it may not be sufficient to prevent extinction cascades under more severe fragmentation. With severe habitat loss, the surviving local networks collectively fail to reproduce the structural properties of the original metanetwork, reducing the buffering benefits of nestedness and weakening its effect on species persistence. By explicitly incorporating both community structure and spatial landscape configuration, our study bridges a critical gap in understanding how mutualistic network architecture interacts with habitat loss to shape persistence outcomes.

From a conservation perspective, our findings suggest that protecting highly connected hub patches in heterogeneous landscapes or enhancing connectivity in more uniform landscapes can help maintain species persistence. Yet, the effectiveness of these strategies depends strongly on the type of habitat loss and community structure. Enhancing community nestedness, for example by protecting species that disproportionately contribute to the nested pattern of mutualistic interactions [22], may delay collapse. Yet, this strategy alone is insufficient under severe habitat degradation. Conservation planning should therefore integrate knowledge of both landscape and community structure, tailoring strategies to the specific nature of habitat loss. Such integrative approaches can enhance metacommunity stability, support early interventions before tipping points are reached, and provide a more reliable basis for preserving biodiversity in fragmented landscapes [25,48].

While our study offers valuable insights into how landscape configuration and mutualistic network structure influence species persistence under habitat loss, there are important aspects that merit further investigation. Here, we focus on landscape heterogeneity defined in terms of patch connectivity, yet other dimensions of heterogeneity exist. First, heterogeneity in the spatial distribution of habitat patches and their connections may also be encapsulated by varying network modularity or incorporating dispersal barriers, both of which affect species movement across landscapes [49,50]. Second, we assumed uniform habitat quality across all patches and did not account for species-specific habitat preferences. In real systems, variation in habitat quality—such as the presence of resource-rich or poor patches—can strongly affect species persistence [10,51,52]. Incorporating spatial heterogeneity in habitat quality could refine our predictions, particularly for communities with habitat-specialist species. Third, our model treated all patches as equal in area, although empirical and theoretical work shows that patch size plays a critical role in shaping metapopulation dynamics and extinction thresholds [53,54]. Exploring scenarios where patch sizes vary could offer more nuanced insights into landscape design for conservation. Fourth, we focused solely on mutualistic interactions, yet real ecosystems include a mix of interaction types, including antagonistic, which may respond differently to habitat loss [4,55,56]. Extending this framework to include mixed interaction types could help identify the role of mutualism within more complex, interaction-rich communities. Lastly, while our study does not allow rewiring of interactions within local networks, empirical evidence suggests that species' interactions and roles can vary depending on patch-specific conditions [57,58]. Addressing these aspects in future work will enhance the generality of our framework and inform more effective conservation strategies in fragmented landscapes.

Empirical studies have demonstrated that habitat loss is a major driver of biodiversity decline, with cascading effects on ecosystem functions and species interactions. For example, long-term studies on pollination networks have shown that habitat fragmentation disrupts plant–pollinator mutualisms, reducing pollination success and leading to declines in plant reproductive output [59]. Similarly, habitat loss in the Amazon has led to structural shifts in seed dispersal networks, altering connectivity patterns and species persistence [60]. These findings underscore the critical need to study how mutualistic networks respond to habitat loss within spatially structured landscapes. We show that the effects of habitat destruction on mutualistic communities vary across different landscape configurations and habitat loss patterns. However, the nested structure of mutualistic communities enhances species persistence, buffering some of the negative effects of habitat loss—and this buffering capacity itself changes depending on the landscape configuration. By integrating network theory with spatial metacommunity dynamics, our findings provide a framework to study biodiversity loss and ecosystem collapse under habitat destruction. This approach emphasizes the importance of considering both species interactions and spatial landscape structure when designing targeted conservation strategies in rapidly changing environments.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All code and data to reproduce the reported results are available on Zenodo [61]. Supplementary material is available online [62].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. S.B.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; K.A.G.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—review and editing; F.P.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—review and editing; J.B.: conceptualization, funding acquisition, methodology, project administration, supervision, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no competing interests.

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