

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

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1 Abstract

2 Habitat loss poses a major threat to biodiversity. Its effects on ecological communities depend
3 on the complex interplay between the landscape configuration — the patterns of connections
4 between habitat patches, community structure — the patterns of interactions between species,
5 and habitat loss patterns. Despite their individual importance, their joint effect on species persis-
6 tence remains poorly understood. We explore how these three factors influence the persistence of
7 empirical mutualistic communities. By employing spatially explicit metacommunity models, we
8 find that landscapes with a heterogeneous distribution of connections between habitat patches
9 exhibit high persistence under spatially-uncorrelated habitat loss but are highly vulnerable to
10 spatially-correlated loss, where adjacent habitat patches are destroyed sequentially. Homoge-
11 neous landscapes with regularly arranged patches have lower persistence than heterogeneous
12 landscapes but are more resilient to correlated habitat loss. The metacommunity nested structure
13 of species interactions enhances persistence, with varying magnitude depending on landscape
14 configuration and the patterns of habitat loss. These results can guide conservation strategies by
15 identifying landscape and community features that promote species persistence.

16

Introduction

17 Habitat loss is one of the leading drivers of biodiversity decline, with far-reaching effects on eco-
18 logical communities and their functioning (Chase et al., 2020; Tylianakis et al., 2008). The loss of
19 species can propagate through ecological communities, resulting in further extinctions of species
20 and interactions (Memmott et al., 2004). In mutualistic communities, this equates to the loss of
21 key ecosystem services such as pollination and seed dispersal (Bascompte and Jordano, 2007).
22 Importantly, habitat loss also reshapes spatial connectivity, fragmenting landscapes and reduc-
23 ing opportunities for recolonization (Kindlmann and Burel, 2008; Turner and Ruscher, 1988),
24 which can push systems toward tipping points (Rockström et al., 2009; Scheffer et al., 2001).
25 Understanding how species persistence is shaped by habitat loss, the landscape, and ecological
26 community structure is crucial for anticipating collapse and guiding conservation responses.

27 The landscape configuration influences metacommunity dynamics, dispersal processes, and
28 overall system stability (Arancibia, 2024; Hanski, 1999; Urban and Keitt, 2001). Graph-theoretic
29 approaches provide a useful framework for characterizing landscapes as networks, where habi-
30 tat patches are represented as nodes connected by dispersal pathways. The structure of these
31 spatial networks determines how readily species move across the landscape and respond to dis-
32 turbance. For example, homogeneous networks where patches are arranged in a regular grid
33 (hereafter “grid”) promote local stability through uniform connectivity but may limit large-scale
34 dispersal (Hanski and Ovaskainen, 2000). Networks with patches connected randomly (here-
35 after “random”) offer moderate connectivity and are relatively robust to stochastic perturbations
36 (Erdos et al., 1960). While the heterogeneous scale-free networks, which contain few highly con-
37 nected hub patches and many poorly connected peripheral patches, are robust to random node
38 loss but remain highly vulnerable to removal of the hubs (Barabási and Albert, 1999). Thus, the
39 spatial pattern of habitat destruction further shapes extinction trajectories: spatially correlated
40 loss can sever entire regions and connectivity clusters, whereas spatially uncorrelated loss dis-
41 rupts patches more diffusely (Keitt et al., 1997). While previous studies have explored spatial

42 dynamics or habitat loss effects independently, the interaction between landscape configuration,
43 habitat loss patterns, and ecological processes remains poorly understood.

44 Mutualistic communities, such as those composed of plants and their pollinators or seed-
45 dispersers, are structured non-randomly in a way that promotes species coexistence and buffers
46 against collapse (Bascompte et al., 2003; Bastolla et al., 2009; Lever et al., 2014). Here too, network
47 theory provides a useful tool for analyzing the patterns of interactions between species within
48 communities. For example, nestedness — a common pattern where specialist species interact
49 with subsets of generalist partners — enhances community persistence by enabling redundant
50 interaction pathways and indirect facilitation (Saavedra et al., 2011; Thébaud and Fontaine, 2010).
51 Generalist species often act as anchors for community resilience, whereas specialists tend to be
52 more prone to extinction (Hagen et al., 2012). However, empirical and theoretical studies on the
53 persistence of mutualistic communities rarely consider landscape-scale processes (Guimarães Jr,
54 2020). In fragmented landscapes, mutualistic community dynamics unfold across spatially struc-
55 tured habitats. Yet, the combined role of landscape configuration and mutualistic community
56 structures in driving extinction remains largely unexplored.

57 Although important progress has been made in understanding the persistence of metacom-
58 munities in fragmented systems (Fortuna et al., 2013; Gilarranz and Bascompte, 2012; Liao et al.,
59 2016), previous models often treat habitat loss, landscape configuration, and community struc-
60 tures in isolation. For instance, many studies focus on a single species or use synthetic interaction
61 networks without taking into account realistic mutualistic community structures (Gilarranz and
62 Bascompte, 2012; Guo et al., 2022; Liao et al., 2020; Zhang et al., 2021). Others adopt spatially
63 homogeneous models that ignore how dispersal constraints modulate landscape-scale dynamics
64 (Liao et al., 2022; Shen et al., 2019). A more integrative framework is needed to understand the
65 interplay between spatial and community dynamics under different habitat loss regimes.

66 Here, we investigate how species persistence is shaped by the interaction between landscape
67 configuration, mutualistic community structure, and habitat loss patterns. We achieve this by
68 developing a spatially explicit metacommunity model. We embed empirical mutualistic commu-

69 nities with varying structure within three types of spatial networks: grid, random, and scale-free,
70 and simulate dynamics under spatially-correlated and uncorrelated habitat loss. By linking eco-
71 logical network theory with spatial dynamics, our work offers mechanistic insights into biodiver-
72 sity collapse under habitat loss and informs conservation strategies for fragmented landscapes.

73 **Methods**

74 We modeled landscapes as spatially explicit unipartite networks, where habitat patches were
75 represented as nodes and dispersal routes as links. Each landscape contained 2,500 patches and
76 5,000 links, ensuring an average of four connections per patch. Connectivity varied along a
77 gradient of heterogeneity: from grid networks, where each patch had exactly four connections,
78 to random networks with links assigned randomly, and scale-free networks characterized by a
79 power-law distribution of links while maintaining an average degree of four (Figure 1).

80 We used 20 empirical mutualistic networks (10 plant-pollinator and 10 seed-dispersal) from
81 the Web of Life database (www.web-of-life.es) (Fortuna et al., 2014) as metanetworks, which
82 integrated all species and their interactions across the entire landscape (Fortuna et al., 2014).
83 Within each patch, populations of plants and animals formed local networks which were subsets
84 of the metanetwork. We selected empirical networks spanning a range of structural properties
85 (Table T1 in Supplementary), particularly focusing on variation in network nestedness.

86 We measured network nestedness following the approach proposed by (Fortuna et al., 2019),
87 which is based on the NODF (Nestedness metric based on Overlap and Decreasing Fill) metric
88 (Almeida-Neto et al., 2008). This method quantifies nestedness by assessing the extent to which
89 species with fewer interactions are linked to subsets of the partners of more connected species.
90 It captures the average overlap between species interactions without penalizing networks where
91 species have similar numbers of connections (as in NODF). To control for the effects of network
92 size and connectance, we standardized the observed nestedness against expectations from a null
93 model. Specifically, we generated 100 randomized networks per empirical network by preserv-

94 ing the marginal totals (row and column sums) and recalculated nestedness for each. We then
95 computed the mean (μ) and standard deviation (σ) of nestedness from the randomized networks.
96 Finally, we obtained the standardized nestedness z-score as:

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

97 where x is the observed nestedness of the empirical network. This approach allowed us to
98 compare nestedness across networks of different sizes and link densities.

99 At each time step, species faced a probability of extinction within the patches they occupied.
100 Extinction probabilities were assumed to be uniform across species and patches. For the resource
101 species (i.e., plants) and the mutualistic consumers (i.e., pollinators or seed dispersers), extinction
102 probabilities were defined as (Gawecka and Bascompte, 2023):

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

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

104 Colonization occurred between directly connected patches. For both resources and con-
105 sumers, the probability of colonization increased with the number of neighboring patches and
106 the presence of interaction partners (Gawecka and Bascompte, 2023):

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

$$P_{\text{col},j} = 1 - \prod_{n=1}^N \prod_{k=1}^J (1 - c_{c,j}/k) \quad (\text{for consumers}),$$

107
108 Where $c_{r,i}$ and $c_{c,j}$ are the intrinsic colonization rates of resource i and consumer j , respectively,
109 J is the number of interaction partners of species i , and N is the number of neighboring patches
110 that are suitable sources for colonization.

111 The system was simulated over 1,000 time steps to capture metacommunity dynamics, dis-
112 carding the first 900 time steps to remove transient effects. Steady-state abundances were calcu-
113 lated as the mean number of patches occupied by each species over the final 100 time steps.

114 To investigate habitat loss effects, we incrementally removed habitat patches in 5% steps, start-
115 ing from pristine landscapes (0% habitat loss) and continuing until all patches were destroyed.
116 We modeled two habitat loss scenarios: (1) “correlated”, where destruction began at 25 (1%)
117 randomly selected patches and extended to their connected neighbors, and (2) “uncorrelated”,
118 where patches were destroyed randomly without regard for connectivity (Figure 1). After each
119 increment, the system was simulated until reaching a new steady state.

120 We varied the extinction-to-colonization ratios for resources ($e_{r,i}/c_{r,i}$) and consumers ($e_{c,j}/c_{c,j}$)
121 from 0 to 3 in steps of 0.3, keeping colonization rates fixed at $c_{r,i} = c_{c,j} = 0.1$ (Gilarranz and
122 Bascompte, 2012) (Supplementary Fig. S1, S4, S5). These ratios capture a wide range of eco-
123 logical dynamics, from populations with low extinction risk and high colonization potential to
124 those with high extinction risk and limited colonization. This resulted in 441 unique parameter
125 combinations , spanning a broad spectrum of demographic dynamics for both resources and
126 consumers. Persistence probability was defined as the proportion of parameter combinations
127 where the mean abundance of all species exceeded zero. This approach allows us to account for
128 a wide range of extinction and colonization rates, thus generalizing our results. We quantified
129 this persistence probability at each fraction of habitat loss.

130 All simulations were performed in Julia version 1.4.2 (Bezanson et al., 2017), and data visual-
131 ization was performed in R version 3.6.2 (R Core Team, 2024).

132 Results

133 The rate of decline of species persistence probability with habitat loss is highly dependent on the
134 interplay between spatial landscape structure and habitat loss pattern (Fig.2). Grid landscapes,
135 which have homogeneous connectivity, show lower persistence in pristine landscapes than the
136 more heterogeneous random and scale-free networks. Yet, they exhibit the greatest robustness to
137 habitat loss. In fact, under correlated habitat loss they enable the highest species persistence out
138 of the three landscapes. In contrast, scale-free landscapes, characterized by highly connected hub

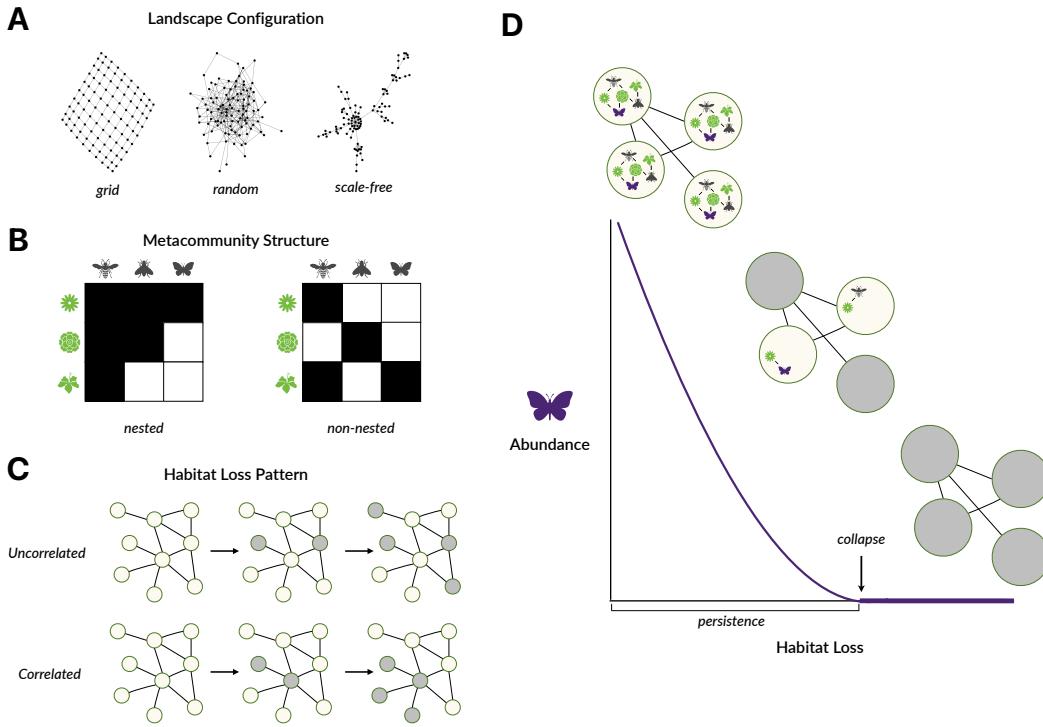


Figure 1: Schematic of our simulation treatments (A-C) and model output (D). We investigate the interplay between landscape configuration, mutualistic community structure, and habitat loss scenarios in shaping species persistence. (A) To study the effect of landscape structure, we consider networks of 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 community 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 a clusters. (D) As habitat is destroyed, species transition from persistence state to extinction state.

139 patches, show the highest persistence probability at low habitat loss fractions. These networks are
 140 particularly resilient to uncorrelated habitat loss, maintaining persistence even under high levels

141 destruction. However, under correlated habitat loss, their persistence declines very sharply, likely
142 due to the targeted loss of key hub patches and the resulting cascade of extinctions. Random
143 landscape configuration display intermediate behavior, with persistence probabilities declining
144 steadily with habitat loss. They respond relatively similarly to both habitat loss patterns, sug-
145 gesting lower sensitivity to how habitat is removed. In summary, landscapes with homogeneous
146 connection between patches are resilient to spatially-correlated habitat loss, whereas heteroge-
147 neous ones exhibit high resilience to spatially-uncorrelated loss of patches.

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

157 More specifically, we find that nestedness of mutualistic networks has a positive effect on
158 persistence probability across all landscapes and habitat loss patterns (Fig. 3, S3). However, the
159 strength of this effect varies with both the landscape configuration and the pattern of habitat
160 loss. In grid and random landscapes, the positive influence of nestedness weakens as habitat
161 loss increases, with a more rapid decline under uncorrelated than correlated loss. Scale-free
162 landscapes, in contrast, reveal a unique pattern: the effect of nestedness is relatively weak at
163 both low and high levels of habitat loss but peaks at intermediate levels. Notably, the effect
164 of nestedness remains stronger under uncorrelated loss in most fractions of habitat destruction.
165 These results emphasize that the impact of the nested structure of communities on persistence is
166 not static, but rather dynamically shaped by the landscape, the degree and the spatial pattern of
167 habitat loss.

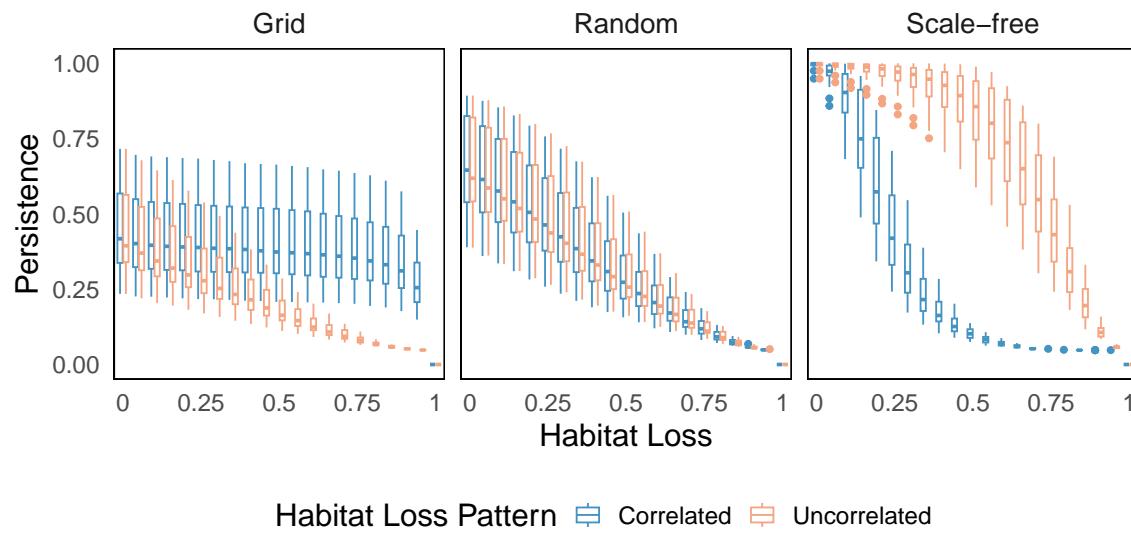


Figure 2: Species persistence probability under habitat loss. Persistence probability represents the proportion of extinction-to-colonization parameter combinations where species abundance remains above zero. Boxplots show the average persistence probability across all species for each of the 20 empirical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

168

Discussion

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

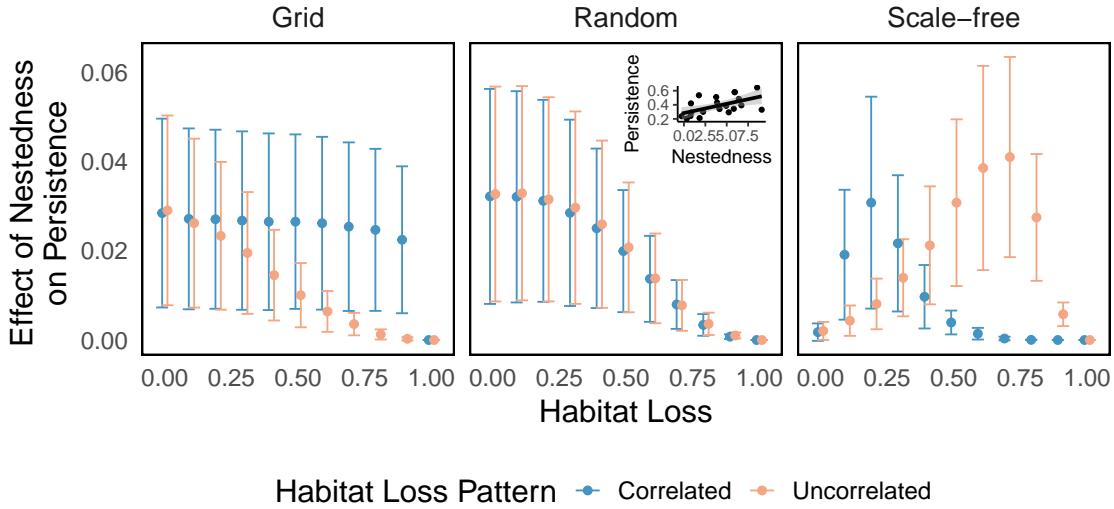


Figure 3: Effect of mutualistic community nestedness on average species persistence probability. Each point represents the estimated slope from a linear model capturing the relationship between nestedness and persistence probability at different habitat loss fractions. The lines indicate 95% confidence intervals, reflecting the uncertainty around the slope estimates. Correlated and uncorrelated habitat loss scenarios are shown in blue and red, 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 Fig. S2 for additional scenarios across habitat loss fractions).

176 Our findings show that the spatial configuration of habitat fragments shapes metacommunity
 177 persistence under habitat loss, with outcomes varying based on community structures and
 178 the pattern of habitat loss (Fig. 2). The trajectory of abundance loss, shaped by extinction-
 179 to-colonization dynamics, varies across different landscape configurations and is further mod-
 180 ulated by the pattern of habitat loss—whether uncorrelated or correlated (Supplementary Fig.
 181 S1). Scale-free landscapes, characterized by a few highly connected hubs, show the highest per-

182 persistence and extinction thresholds (Fig. S3) under spatially-uncorrelated habitat loss throughout
183 the destruction process. These hubs serve as critical reservoirs that buffer species from extinction,
184 maintaining metacommunity cohesion even when many peripheral patches are lost. However,
185 this structural advantage becomes a liability under spatially-correlated habitat loss, particularly
186 at low extinction to colonisation ratios (Fig. S4). The clustered removal of patches disproportio-
187 nately impacts hub nodes, leading to cascading extinctions and rapid community collapse. In
188 contrast, grid networks, with uniformly connected patches, are more resilient under correlated
189 than uncorrelated habitat loss. Random networks show intermediate responses under both loss
190 patterns. Thus, resilience is not solely dependent on landscape configuration, but also on how
191 habitat is lost. These results broadly echo previous findings on the persistence of a single species
192 (Gilarranz and Bascompte, 2012) and its responses to habitat loss (Heer et al., 2021; Liao et al.,
193 2020).

194 We show that the structure of mutualistic communities also plays a pivotal role in species
195 persistence under habitat loss. Specifically, we find that nestedness enhances persistence across
196 all landscapes, thus offsetting some of the negative effects of habitat destruction (Fig. 3). This
197 finding adds to the body of literature which demonstrates the importance of nestedness in pro-
198 moting species coexistence, facilitating indirect interactions, and buffering communities against
199 perturbations such as species loss or environmental fluctuations (Bascompte et al., 2003; Bastolla
200 et al., 2009; Bhandary et al., 2023; Domínguez-Garcia et al., 2024; Lever et al., 2014; Thébault and
201 Fontaine, 2010). However, we find that the positive effect of nestedness weakens with increasing
202 habitat destruction. In homogeneous landscapes, this decline is gradual, whereas in scale-free
203 networks, the effect of nestedness peaks at intermediate habitat loss fractions before sharply
204 decreasing. This suggests that while nestedness can confer resilience in the early and interme-
205 diate stages of habitat loss, it may not be sufficient to prevent extinction cascades under more
206 severe fragmentation. By explicitly incorporating both community structure and spatial land-
207 scape configuration, our study bridges a critical gap in understanding how mutualistic network
208 architecture interacts with habitat loss to shape persistence outcomes.

209 From a conservation perspective, our findings suggest that protecting highly connected hub
210 patches in heterogeneous landscapes or enhancing connectivity in more uniform landscapes can
211 help maintain species persistence. Yet, the effectiveness of these strategies depends strongly on
212 the type of habitat loss and community structure. Enhancing community nestedness, for exam-
213 ple by protecting species which disproportionately contribute to the nested pattern of mutualistic
214 interactions (Saavedra et al., 2011), may delay collapse. Yet, this strategy alone is insufficient un-
215 der severe habitat degradation. Conservation planning should therefore integrate knowledge of
216 both landscape and community structure, tailoring strategies to the specific nature of habitat loss.
217 Such integrative approaches can enhance metacommunity stability, support early interventions
218 before tipping points are reached, and provide a more reliable basis for preserving biodiversity
219 in fragmented landscapes (Blüthgen and Staab, 2024; Gilarranz and Bascompte, 2012).

220 While our study offers valuable insights into how landscape configuration and mutualistic
221 network structure influence species persistence under habitat loss, there are important aspects
222 that merit further investigation. First, we assumed uniform habitat quality across all patches and
223 did not account for species-specific habitat preferences. In real systems, variation in habitat qual-
224 ity—such as the presence of resource-rich or resource-poor patches—can strongly affect species
225 persistence and the spatial stability of interactions (Ferraz et al., 2007; Hanski, 1999; Kremen
226 et al., 2007). Incorporating spatial heterogeneity in habitat quality could refine our predictions,
227 particularly for systems with specialized mutualisms. Second, our model treated all patches
228 as equal in area, although empirical and theoretical work shows that patch size plays a critical
229 role in shaping metapopulation dynamics and extinction thresholds (Fahrig, 2003; Hanski and
230 Ovaskainen, 2003). Exploring scenarios where patch sizes vary—such as comparing a few large
231 patches versus many small ones—could offer more nuanced insights into landscape design for
232 conservation. Third, we focused solely on mutualistic interactions, yet real ecosystems include a
233 mix of interaction types, including antagonistic and competitive, which may respond differently
234 to habitat loss (Allesina and Tang, 2012; Bascompte and Jordano, 2007; Gawecka et al., 2022).
235 Extending this framework to include mixed interaction types could help identify the role of

236 mutualism within more complex, interaction-rich communities. Addressing these aspects in fu-
237 ture work will enhance the generality of our framework and inform more effective conservation
238 strategies in fragmented landscapes.

239 Empirical studies have demonstrated that habitat loss is a major driver of biodiversity decline,
240 with cascading effects on ecosystem functions and species interactions. For example, long-term
241 studies on pollination networks have shown that habitat fragmentation disrupts plant-pollinator
242 mutualisms, reducing pollination success and leading to declines in plant reproductive output
243 (Aguilar et al., 2006). Similarly, habitat loss in the Amazon has led to structural shifts in seed
244 dispersal networks, altering connectivity patterns and species persistence (Galetti et al., 2013).
245 These findings underscore the critical need to study how mutualistic networks respond to habitat
246 loss within spatially structured landscapes. We show that the effects of habitat destruction on
247 mutualistic communities vary across different landscape configurations and habitat loss patterns.
248 However, the nested structure of mutualistic communities enhances species persistence, buffering
249 some of the negative effects of habitat loss—and this buffering capacity itself changes depending
250 on the landscape configuration. By integrating network theory with spatial metacommunity
251 dynamics, our findings offer a framework for studying biodiversity loss and ecosystem collapse
252 under ongoing habitat destruction. Understanding how mutualistic networks respond to habitat
253 loss within different spatial contexts is crucial for developing targeted conservation strategies,
254 particularly in landscapes undergoing rapid environmental change. These insights highlight the
255 need for conservation planning that simultaneously considers the spatial landscape configuration
256 and species interactions.

257 **Data Availability**

258 Codes and data are available in a Github repository (<https://github.com/subhendu-math/Habitat->
259 [loss-project.git](#)).

260

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