Received: 20 March 2024 | Accepted: 3 October 2024

DOI: 10.1111/1365-2435.14695

Functional Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Why there are more species in several small patches versus few large patches: A multispecies modelling approach

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Funding information
Fondo para la Investigación Científica y Tecnológica, Grant/Award Number: PICT-2020-SERIEA-02628

Handling Editor: Liza Holeski

Abstract

1. As global biodiversity is rapidly declining due to habitat loss, it is important to determine how to protect it. The policies of many conservation agencies are still prioritizing the preservation of a single large habitat area (SL) versus several small areas of the same size (SS), despite empirical support favouring SS. However, to date, while many studies have explored this issue using model communities, the results are mixed. In competitive community models, fragmentation has a negative effect at low habitat amounts, whereas neutral community models suggest positive effects.
2. This work aims to explore spatial multispecies models to verify the SS > SL pattern and determine its causes. We used three types of models: a classical neutral, neutral with habitat selection and a competitive hierarchical model. All models have three parameters, namely extinction, reproduction and dispersal distance. In the classical neutral model, species are equivalent and have the same parameters; when there is a reproduction event, they send the propagule to a surrounding patch blindly, and if the patch is already occupied, the propagule dies. In the neutral with habitat selection model, the propagules select an empty patch, so their survival is ensured. In the hierarchical model, species have competitive dominance and more dominant ones can replace the less dominant with a replacement rate parameter. We use 100 species and start simulating the colonization of an empty area; then, we destroy a fixed amount of habitat using different regular patch sizes.
3. The results for all models are almost always that SS retains more species than SL. The extinction of species in patches depends on the quotient between reproduction and extinction rates in relation to patch size. The only case when SL > SS is when dispersal is insufficient to connect patches, and patch size is smaller than the minimum to prevent extinction. If patch size is above the critical size to maintain local populations, the SS > SL pattern is due to the sampling effect of aggregated species distribution combined with the reduction of dispersal ability of species.

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4. High-dispersal rates produce the homogenization of species distribution and a reduction of species richness and this is why habitat fragmentation by habitat loss retains more species when patches are smaller. The model predicts that if a set of species have more dispersal capabilities, the SS effect would be lower than for species with less dispersal.

KEYWORDS
biodiversity, habitat fragmentation, multispecies models, neutral theory, spatially explicit models

1 | INTRODUCTION

Global biodiversity is rapidly declining due to, among other factors, habitat loss (Chase et al., 2020; Newbold et al., 2015; Young et al., 2016). As habitat fragmentation occurs at the same time as habitat loss, the effects of both processes are difficult to disentangle (Haddad et al., 2015). Landscape connectivity and organism mobility are critical features for population persistence (Taylor et al., 1993). Starting from a landmark paper (Diamond, 1975), conservation biologists engaged in the challenging task of recommending protection measures given the environmental crisis coupled with a lack of knowledge of most of the world's biodiversity and limited funding for conservation. In that context, early recommendations claiming to follow ecological theory derived simple thumb rules to better design protected areas. However, as noted rapidly, species/area relationships do not have a clear association with fragmentation per se but mainly with overall habitat loss (Simberloff & Abele, 1982). Aiming to design better management practices, this led to a nearly 50-year single large versus several small (SLOSS) debate. While some authors argue that habitat loss is the most overwhelming effect on species loss, for others, the complex factors arising from fragmentation further enhance species extinctions (Fahrig, 2017; Fletcher et al., 2018).

The SLOSS debate has been an important academic and intellectual discussion in conservation biology. However, in practical implementation, numerous conservation agencies persist in prioritizing the safeguarding of extensive, contiguous habitat areas, often neglecting the protection of smaller patches of natural habitat (Armsworth et al., 2018). As an example, the current emphasis on 'rewilding' in Europe is geared towards the conservation and restoration of contiguous natural habitats, with a specified 'core area' of at least 10,000 ha (Europarc Federation, 2013). Similarly, conservation efforts for large water bodies take precedence, leaving small ponds or pondscapes largely excluded from priority considerations (Hill et al., 2018).

While the overall habitat loss is widely accepted as a process leading to long-term biodiversity loss (Hodgson et al., 2011; Keil et al., 2015), the proposition that single large reserves retain more species than several small reserves of the same area (SL > SS) remains at a similar hierarchical state, even after several criticisms (reviewed in Fahrig, 2017). Empirical observational and experimental data show the predominance of the opposite pattern (SS > SL) ever since the 80s and this fact has been reinforced to this day (Fahrig, 2020; Hammill & Clements, 2020; Simberloff & Abele, 1982). The actual processes driving it remain elusive and it is probably multicausal. In that scenario, model simulations could produce useful hypotheses to better understand the processes leading to non-intuitive patterns of biodiversity loss.

The SLOSS debate has been approached from several theoretical frameworks, but many cases have been based on single-species models (Fahrig et al., 2021). Despite the long-standing discussion, there remains a notable scarcity of multispecies models explicitly designed to validate fragmentation theories. However, recent studies using spatially explicit simulations of competitive communities have revealed that, while high fragmentation leads to more local extinctions due to reduced habitat size, at low levels of fragmentation, competitive exclusion is more prevalent, resulting in decreased diversity (Rybicki et al., 2020). Conversely, studies based on neutral models have shown that fragmentation can have a positive effect on species richness, particularly when the habitat amount is low (Smith et al., 2024). Additionally, spatially implicit models with competition–colonization trade-offs result in nonlinear oscillatory responses to both habitat loss and fragmentation (Zhang et al., 2023).

The recently proposed SLOSS cube hypothesis by Fahrig et al. (2021) serves as a comprehensive framework summarizing existing SLOSS predictions and empirical findings. This hypothesis posits that the condition where single large (SL) patches contribute more to biodiversity conservation than several small (SS) patches is contingent upon the simultaneous occurrence of specific conditions: a low between-patch movement rate, minimal impact of spreading of risk on population dynamics and low-species spatial clumping (Fahrig et al., 2021).

This research aims to investigate multispecies spatially explicit models, incorporating a fixed level of habitat destruction, neutral and competitive community dynamics, diverse dispersal-related traits and various geometries of habitat loss. The principal objective is to verify the conditions under which the SS > SL pattern holds and discern the underlying causes. Through this examination, we seek to contribute insights that can help determine if the conditions outlined in the SLOSS cube hypothesis are supported by our modelling approach.

Specifically, our approach involves simulating species retention under diverse fragmentation scenarios, all characterized by a fixed amount of habitat loss. We vary parameters such as patch sizes, community type (competitive or neutral), species dispersal capabilities and the community's persistence status—whether it is near extinction and degraded or in a healthy state. This comprehensive exploration enables us to account for the interacting effects of habitat loss and a range of model parameters on species retention.

2 | METHODS

2.1 | A spatial stochastic model

We developed a spatially explicit multispecies model to explore the relationship between habitat loss and species retention at the regional metapopulation level. In this model, space is discretized into a grid and only one individual of one species can occupy a particular position. Each position represents an area fixed by the investigator to mimic the real system. Time is continuous, so the update of the model is asynchronous. Sites are selected at random, and to perform one complete time interval, J sites have to be updated, where J is the size of the grid.

We use absorbing boundary conditions, which means that if an individual tries to disperse outside the grid it dies. The size of the community is given by $J = dimX \times dimY$, where $dimX$ and $dimY$ are the dimensions of the grid. Thus, J is the maximum number of individuals in the simulated area. As in a classical neutral model, there is a metacommunity, that is, a regional species pool from where species migrate (Hubbell, 2001). All individuals have the same parameters and each species is assigned an indicator number.

The model consists of three variations: a classical neutral model, a neutral model with habitat selection and a competitive hierarchical model.

The classical neutral variation is where propagules (e.g. seeds) disperse passively and cannot actively choose their establishment site. During reproduction events, individuals disperse their propagules blindly to surrounding patches. If a patch is already occupied, the propagule fails to establish, resulting in its death. This variation captures the random dispersal and colonization processes typical of many plant species.

The neutral variation with habitat selection is where individuals can actively select suitable habitat patches. In this variation, propagules can choose unoccupied patches, ensuring their survival and successful establishment. This modification reflects the influence of habitat availability and selection on species colonization and persistence. By incorporating habitat selection, this variation better captures the ecological processes and behaviours of species that are capable of actively seeking out suitable habitats for reproduction and survival, like most animals.

The competitive hierarchical variation extends the neutral variation with an additional layer of complexity by incorporating competitive interactions among species. Each species has an indicator number that determines its competitive dominance level, and more dominant species can replace less dominant ones at a specified replacement rate. This variation captures the influence of species interactions and competitive exclusion on species composition and abundance. It is particularly relevant for understanding communities where competitive interactions play a significant role in shaping species distributions and community structure (e.g. hummingbirds).

The following processes are included in the model: habitat loss, migration, reproduction, local dispersal, competition and death. After setting initial conditions, the following events can happen:

1. Habitat loss: The sites are marked as non-habitable, making them unsuitable for occupancy, up to a fixed percentage of degraded habitat. Different degradation scenarios are modelled:
   Regular degradation: Habitat is removed in a way that results in habitable patches forming a regular pattern of squares, with side lengths determined by a habitat-size parameter. While the percentage of degraded habitat remains constant, varying the habitat-size parameter leads to either a few large patches (SL) or many smaller ones (SS). The algorithm adjusts either the number or the size of patches to maintain the constant percentage of degradation, especially when only one patch fits within the grid. We quantify this pattern using the mean habitat patch size.
   Random block degradation: Habitat square patches of a fixed size (habitat size parameter) are located at random throughout the landscape. The sizes are identical to those used for regular degradation simulations, but it results in habitat patches that have a minimum size corresponding to the habitat size, but a maximum size that is bigger because habitat patches can overlap between them producing a larger patch. Then, we characterize this with the mean habitat patch size.
2. With $migration - rate$ an individual of a species i can migrate from the metacommunity. A random site on the border of the grid is selected and if it is empty and habitable, the site is occupied[d].
3. All individuals reproduce with $growth - rate$. When an individual reproduces the propagule disperses to the neighbourhood with a dispersal kernel. Here, we use an inverse power kernel (Marco et al., 2011):

   $d(x) = \left(\frac{x}{x_{\min}}\right)^{-\alpha}$ with mean $= \frac{\alpha - 1}{\alpha - 2} x_{\min}$ where $\alpha > 1$ and $x \geq x_{\min}$.
   where $d(x)$ is the probability that an individual disperses a distance x from the parent. In all cases, we used $x_{\min} = 1$. We use as a parameter the mean $dispersal - distance$.
   What happens to the propagule when arrives at the selected site is determined by the variation of the model simulated:
   a. Classical neutral: If the target patch is already occupied by a species, the propagule perishes.
   b. Neutral with habitat selection: Propagules selectively target unoccupied patches for reproduction within the distance given by the dispersal kernel, ensuring their survival.

c. Competitive hierarchical: Species are ranked by a competitive dominance hierarchy based on their internal identification (id) number. If a dispersing propagule arrives at an occupied site, it will only be established if its id number is higher than the resident species. Otherwise, the propagule perishes without establishing. This simulates a system where dominant competitor species displace rarer or weaker species through interspecific competition during colonization of new sites. The hierarchy prioritizes species with lower id numbers as stronger competitors.

4. Individuals die with a $death - rate$ independent of other events. For all simulations, we used a metacommunity of 100 species. The simulations begin with the colonization of an empty habitat area. After 600 time steps, a fixed amount of habitat (40%, 60% or 80%) is subsequently subjected to destruction, employing either regular or random block degradation to mimic habitat fragmentation due to habitat loss. The results were collected after 1500 time steps.

The parameters encompass a range of $growth - rates$ while holding the $death - rate$ fixed at 1. In this model, the relationship between these parameters, $\lambda = growth - rate / death - rate$, is the main determinant of the fate of an individual of a species. In similar non-spatial models, this relationship must exceed 1 for a species to persist. Thus, we used a minimum λ of 1.7 and fixed the migration rate at 0.0001. We simulated each model variant using the parameters shown in Table 1, with both regular and random block habitat patterns. For each combination of parameters, we ran 30 simulations up to 1500 time steps and recorded the number of species, the Shannon Diversity index (Magurran, 2013) and the total number of individuals. For some representative combinations of parameters, we take snapshots of the model output showing the typical dynamics on time of the three recorded quantities and the rank abundance species distribution (May, 1975; Newman, 2005).

The classical neutral model and the habitat selection model could represent endpoints on a continuum of models where the matrix is either completely adverse or not adverse but still unsuitable for reproduction. In the habitat selection model, individuals can search across both the matrix and suitable habitat until they find an empty place. In contrast, for the classical neutral model, individuals have limited or no capacity to search, and the matrix is necessarily detrimental because it increases the probability of death by landing on an unsuitable site.

The model was developed in Netlogo 6.3.0 and the model source code is available at Github https://github.com/lsaravia/DynamicForestExtinction, the Overview, Design concepts, Details (ODD), protocol for describing individual-based models is included within the model source code (Grimm et al., 2010). We performed the simulations and analysis using R version 4.3.1 (R Core Team, 2023); the R source code to perform simulations and analysis is available at https://github.com/EcoComplex/multiSLOSS.

TABLE 1 Parameter values utilized in simulations, with factorial combinations of these parameters employed to run simulations.

λ	Dispersal distance	Habitat patch size
1.7	1.1	3
2.0	1.2	9
3.0	1.5	29
4.0	2	61
	3	

Note: The symbol λ represents the ratio of growth rate to death rate. “Dispersal distance” denotes the mean of the power law dispersal kernel, while “Habitat patch size” indicates the side length of habitat patches modelled as squares. Both the dispersal distance and habitat patch size are measured in grid cells.

3 | RESULTS

The spatial pattern of habitat loss is illustrated in Figure 1. Simulations with regular degradation (Figure 1c,e,g) produce habitat patches of uniform size, evenly spaced across the landscape. In contrast, simulations using randomly arranged block patterns result in patches of variable sizes, where the habitat size parameter defines the minimum size, and superposition of patches creates a larger maximum size (Figure 1d,f,h). Consequently, the mean patch size is higher for random block degradation than for regular degradation. In some cases, to achieve the targeted percentage of habitat loss, the effective patch size in regular degradation exceeds the defined habitat size parameter (Figure 2). Simulations with the neutral model illustrate species' spatial distributions before fragmentation (Figure 1a,b) and after fragmentation (Figure 1c–f), with habitat destruction depicted in purple. Immediately after fragmentation, species distributions closely resemble pre-fragmentation patterns, but diverge over time.

In our neutral model simulations with a migration rate of 0.0001 and regular habitat degradation patterns, species richness varied with habitat patch sizes, influenced by dispersal distance and the λ parameter (Figure 2). Species richness increased with λ, with the highest richness at smaller patch sizes for higher λ values. Conversely, a λ less than 3 showed reduced richness at the smallest patch sizes for lower dispersal distances. In these cases, only migrants survive in the smallest patches, and no local populations are established (Figure 1e and Figures S19 and S20).

The interplay of dispersal distances, mean patch sizes, λ and percent of habitat destruction impacts community survival and species richness. For $\lambda < 4$, this suggests a threshold patch size influenced by these three parameters; for $\lambda = 4$, patch size decreases species richness. The differences between increasing λ almost disappear when dispersal distance is higher. Extended dispersal distances could enhance species survival in scenarios with low λ and smaller patches but reduce richness beyond a certain threshold. Similar patterns are evident for Shannon diversity (Figures S1 and S2).

For random block habitat degradation, the overall pattern is analogous to the regular case (Figure 3), with a peak in richness occurring for the second patch sizes, for λ less than 3. However, for values of λ greater than 2, maximum richness shifts to the smallest

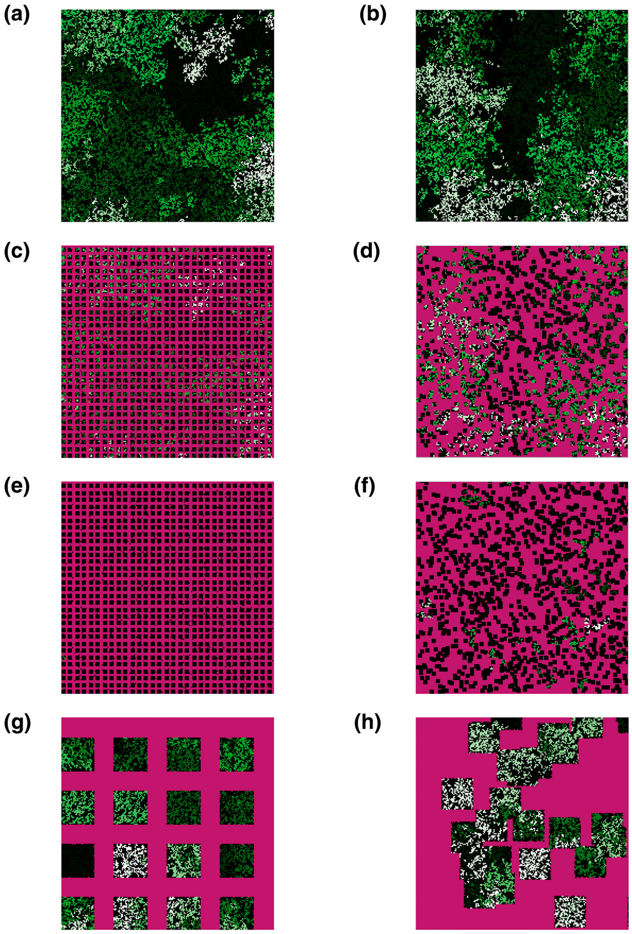

FIGURE 1 Examples of species spatial patterns before and after fragmentation for the neutral model under different habitat loss patterns. Different shades from dark green to white represent distinct species, while destroyed habitat is shown in purple. Simulations were run with a fixed growth rate ($\lambda = 2$), a migration rate of 0.0001 and a dispersal distance of 1.5. (a and b) Spatial patterns before fragmentation. (c and d) Patterns immediately after 60% habitat destruction, with patch sizes of 3 and regular degradation (c) or random block degradation (d). (e and f) Spatial patterns after 1500 time steps, showing population extinction with regular degradation (e). (g and h) The spatial pattern after 1500 time steps with a habitat patch size of 29.

habitat patch size. Patches in the random block simulations are generally larger than in regular degradation, leading to lower species richness and diversity, except at the minimum patch size (Figure 3). Simulations comparing random block and regular habitat patterns (Figure 1) show that, for the smallest patch size, only migrant species persist in regular patterns under neutral and hierarchical models (Figures S19, S20, S27 and S28), but not in the neutral model with habitat selection.

When comparing the three model versions at $\lambda = 2$, the neutral model exhibits higher species richness at larger patch sizes, followed by the neutral with habitat selection model and the hierarchical model (Figures 4 and 5). A similar pattern is seen for Shannon diversity (Figures S11 and S12). At smaller patch sizes, the neutral with habitat selection model supports populations in all cases, whereas in the other models with low dispersal and λ below 3, only migrants are present, unable to establish local populations and leading to extinction (Figure 1, Figures S3 and S5). Consequently, intermediate patch sizes with maximum species richness are not observed in the habitat selection model. Additionally, the hierarchical model shows a strong dominance of more competitive species, resulting in very low Shannon diversity at higher dispersal rates (Figures S4 and S6).

More examples of species and habitat spatial patterns are illustrated in Figures S15–S38. In the hierarchical model, differences between simulations with varying dispersal distances are evident. Individual patches are often dominated by a single species, and with short dispersal distances, regions where different species dominate can be established (Figures S23–S30). The impact of minimum patch size on species survival is also clear (Figure 5e, Figures S19, S20, S27 and S28).

The primary difference between varying percentages of habitat destruction is that lower percentages result in a higher number of species in the smallest patch sizes, particularly at higher dispersal distances. In the regular habitat destruction pattern, the increased number of patches shortens the distance between them, facilitating the persistence of local populations. In the random block pattern, patches are generally larger due to overlap, which increases the minimum patch size, allowing local populations to persist as well (Figures 2–5).

4 | DISCUSSION

Our research contributes to the ongoing SLOSS debate in conservation biology, offering new insights based on our model findings. Consistent with previous studies, the results from our simulations primarily support the SS > SL pattern for species retention, as observed across various model scenarios (Fahrig, 2020). This trend underlines the greater efficacy of multiple smaller habitats in preserving species diversity compared to a single large habitat under equal conditions of habitat loss. A critical factor in this dynamic is the balance between reproduction and extinction rates (λ parameter) and dispersal relative to the size of the habitat patches, influencing their role as sources of propagules. Notably, the SL > SS scenario emerges only when dispersal limitations prevent patch connectivity, and λ is relatively small so patch sizes above a certain threshold are needed to prevent local extinctions, aligning with Rybicki et al.'s (2020) findings. In these cases, an unimodal relationship between species diversity and patch size is observed, with maximum species diversity occurring at larger patch sizes for shorter dispersal distances. Notably, habitat destruction levels do not substantially alter this pattern.

In neutral models, where species are considered equivalent, one species, by chance, tends to dominate a patch (Hubbell, 2001). Consequently, in fragmented landscapes, once a species increases its density, the likelihood of another species replacing is low. With more patches, the probability of having a greater number of species is heightened. This effect is further amplified when individuals can

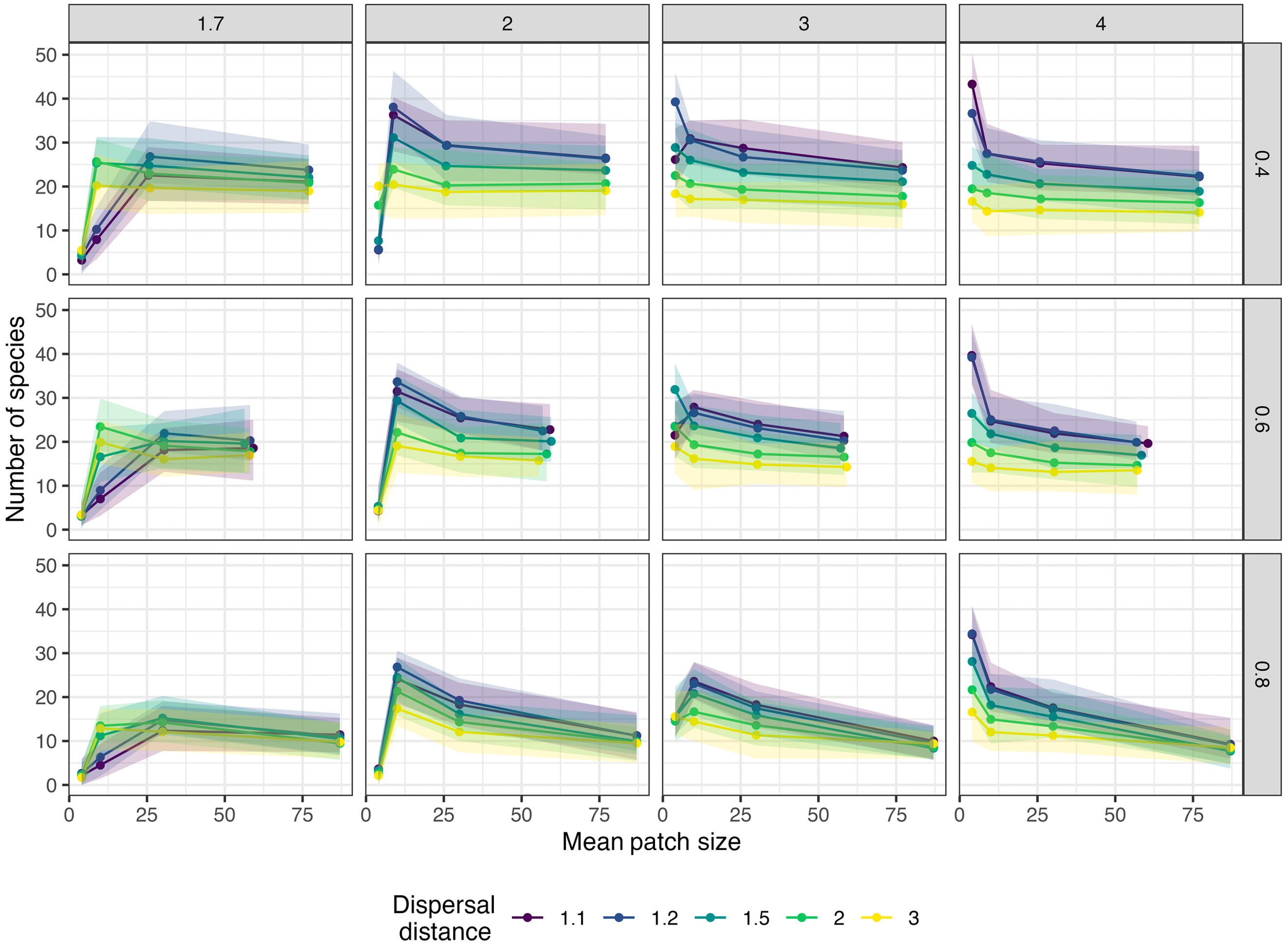

FIGURE 2 Relationship between the number of species and mean habitat patch size across varying dispersal distances. The horizontal panels show the relationship between growth rate and death rate, parameter λ, while the vertical panels represent different percentages of habitat destruction. Simulations were performed using a neutral model with a constant migration rate (0.0001). After 600 time steps, the specified percentage of the habitat was destroyed, making it unavailable for species colonization. The habitat destruction follows a regular pattern, with all patches being of equal size and uniformly spaced from one another.

actively select their habitat, leading to increased survival of propagules. Consequently, fragmentation exhibits a positive influence on the number of species in such scenarios.

For competitive communities, there is a higher probability that different species dominate different smaller patches, compared with a bigger patch. Thus, again fragmentation has a positive effect on the number of species, this effect is called stochastic divergence (Riva & Fahrig, 2023). In smaller patches, there is an increase in extinction risk because they support smaller populations (Laurance et al., 2002; Shafer, 1995), however as patches become smaller, they also become more numerous, reducing the probability of extinction over the entire set of patches due to spreading the risk effect (Crowley, 1977). The combination of these two effects, the stochastic divergence and the risk effect, explains the highest number of species with patch size over the threshold of species survival.

This positive effect is counteracted by dispersal, high dispersal rates tend to a homogenization of species distributions, so fragmented landscapes tend to be more like not fragmented ones reducing overall species richness. This pattern was particularly pronounced for species combining high dispersal capabilities with competitive strengths, indicating a complex interplay between dispersal, competitive interactions and species diversity (Fahrig, 2020).

Edge effects are present in the neutral and hierarchical models, but not in the neutral with habitat selection model. In the first two models, the edge effect is because individuals in the patch's border have fewer neighbours and the probability of extinction is higher. In the neutral with habitat selection model, the edge effect is not present because the individuals search for empty patches, so the individuals on the border of the patch have the same probability of extinction as the individuals in the interior of the patch. Thus, when patches are smaller, the edge proportion is higher and the edge effect is more important, but this plays a more important role in the minimal patch size for the survival of species than for the species richness.

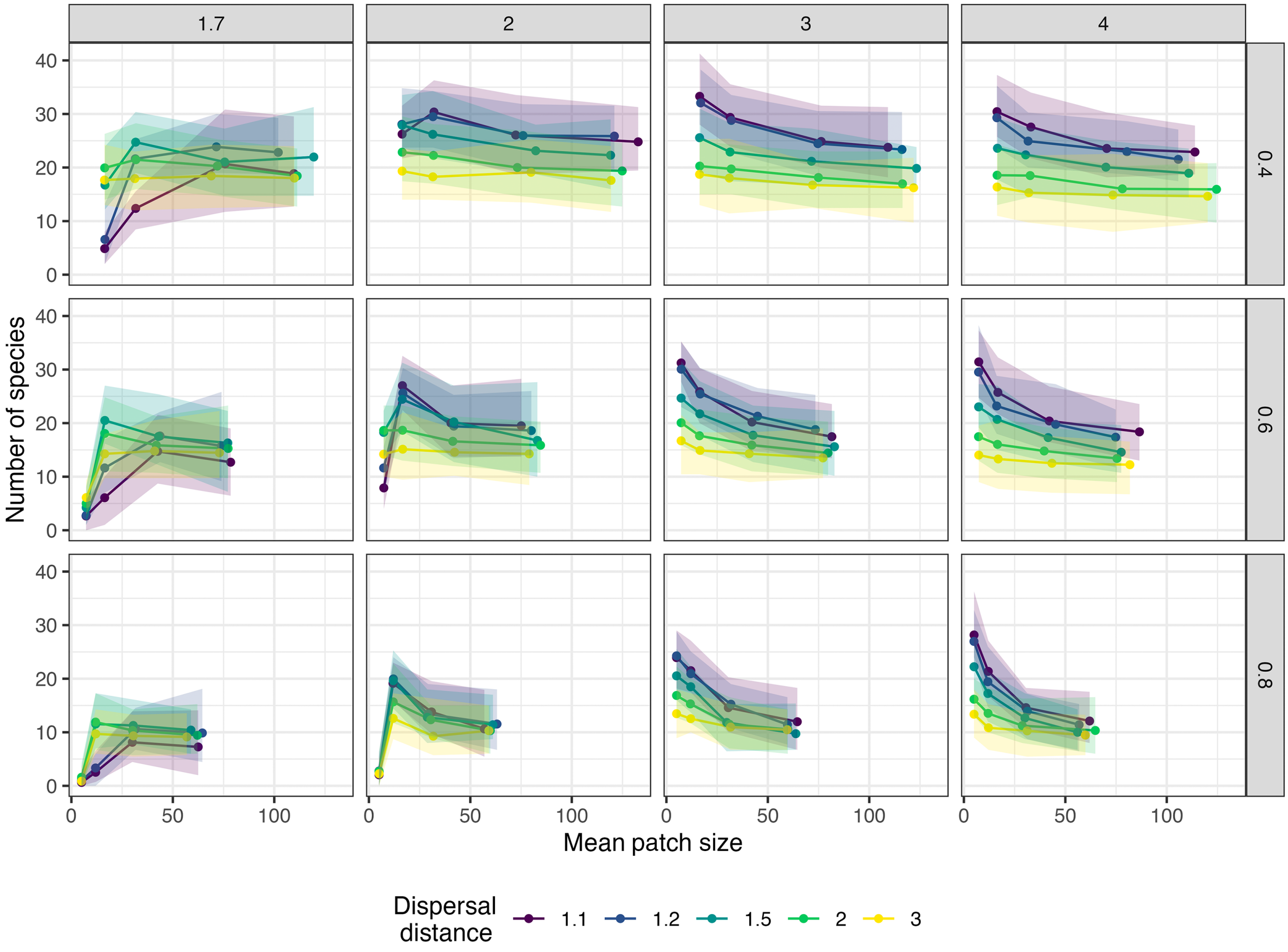

FIGURE 3 Relationship between the number of species and mean habitat patch size across varying dispersal distances for the neutral model. The horizontal panels show the relationship between growth rate and death rate, parameter λ, while the vertical panels represent different percentages of habitat destruction. Simulations were performed with a constant migration rate (0.0001). After 600 time steps, the specified percentage of the habitat was destroyed, making it unavailable for species colonization. Habitat blocks of the same size (habitat patch size) were randomly distributed over the simulation grid. As a result, some patches overlapped, leading to a distribution of patch sizes.

The spatial arrangement of habitat patches, contrary to some expectations, did not produce different species richness patterns when habitat patch size is accounted. The exceptions are stressed communities—represented in our models with lowest λ—with low dispersal may have a continuous increment of richness with wider increment of patch sizes, observed only in random block degradation patterns. The aggregation of patches in the random block pattern (implies aggregation of the degraded habitat) could be positive if individual habitat patches are very small because it allows some patches to surpass the minimum size required for survival. For bigger patch sizes, it could be detrimental because the aggregation produces even bigger patch sizes that decrease species richness. A similar effect was observed on experimental landscapes (Fletcher et al., 2023); aggregated patterns of habitat loss are detrimental to patch occupancy and eventually could produce the same effects observed in our models about richness.

Naturally, there are limitations to our modelling work. First, it is important to note that more research is needed to apply our model to determine the effect of fragmentation in real-world communities. We assume that all species have the same parameters, thus hypothetically determining these parameters for all the species, and using the mean to determine the responses to fragmentation would render an approximate value for the effects and thresholds. Also, an improved version of the model with different values of the parameters for each species could be developed and compared with the neutral model. The effects of fragmentation could be influenced by many other ecological/behavioural characteristics of the species not considered in the model, including environmental heterogeneity, matrix permeability and individual's cost of dispersal, among others. Furthermore, the size of the focal landscape compared to dispersal distances, which determines the scale of the dynamics, could influence quantitative results (Rybicki et al., 2020). Additionally, the application of mean parameter values in relatively simple multispecies models has been successfully employed and tested for predicting species biomass, as demonstrated by Fort (2018).

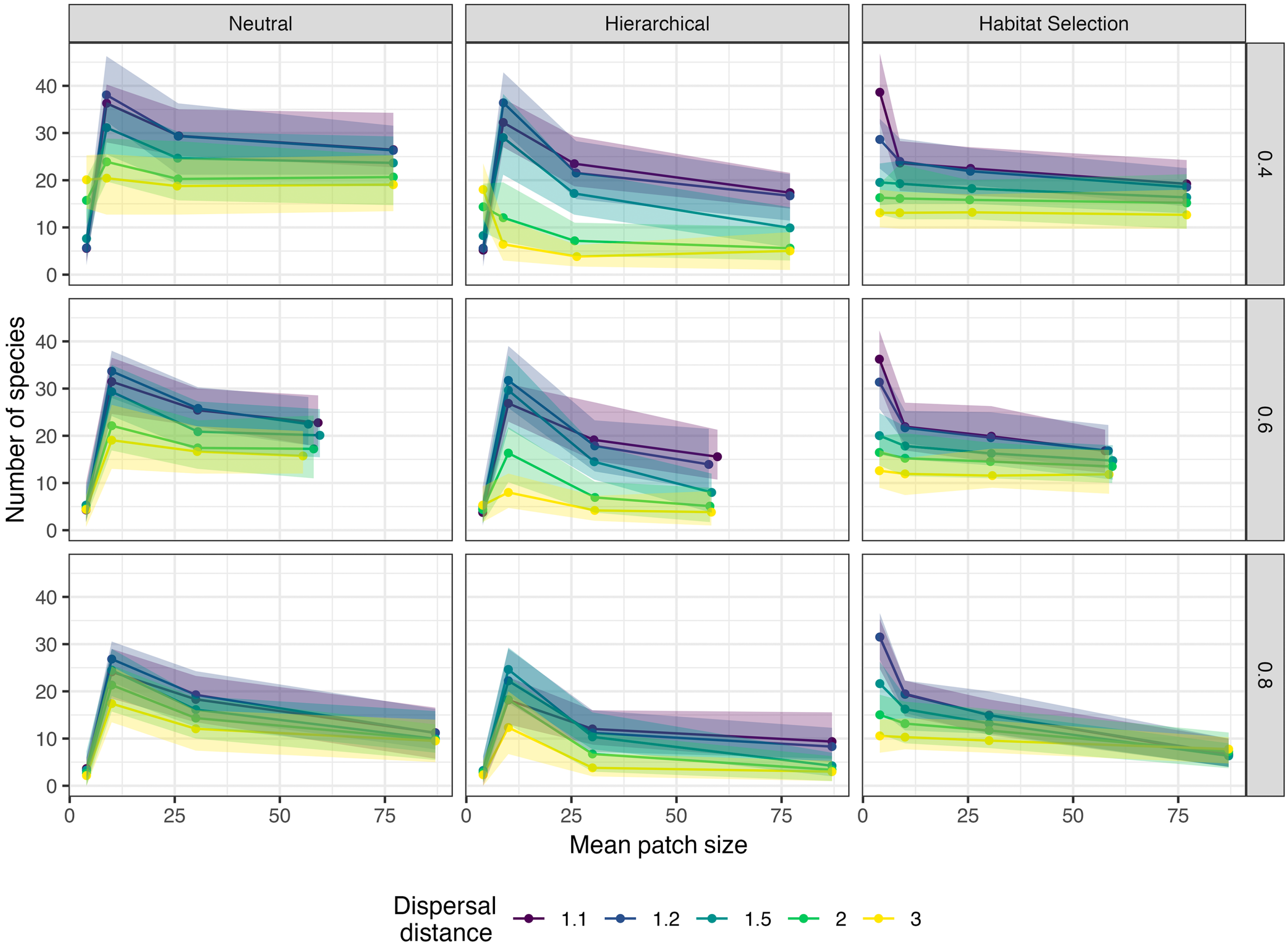

FIGURE 4 Relationship between the number of species and habitat patch size across panels representing different model versions and varying dispersal distances under regular habitat destruction. The vertical panels correspond to different percentages of habitat destruction. In the neutral model, species are equivalent and share the same parameters; in the hierarchical model, species exhibit competitive dominance, with more dominant species replacing less dominant ones; and in the neutral with habitat selection model, species are neutral but propagules search for empty patches, ensuring survival. Simulations were performed using a fixed growth rate ($\lambda = 2$), with migration and replacement rates of 0.0001 and 0.3, respectively. After 600 time steps, the specified percentage of the habitat was destroyed, making it unavailable for species. The habitat destruction follows a regular pattern, with all patches being of equal size and uniformly spaced from one another.

In previous simulation studies, the importance of fragmentation was demonstrated to be pronounced when the habitat amount is low, approximately around 10% (Hanski, 2015; Rybicki & Hanski, 2013). However, experimental studies have observed that, with habitat levels around 10%–20%, the impact of fragmentation can be positive or shows an intermediate maximum (Loke et al., 2019; With, 2016). When habitat amounts are lower (e.g. 7%), the arrangement of patches appears to have no significant effect. Interestingly, our study replicated similar patterns even within a range of 60%–20% habitat amount. Moreover, other studies employing comparable habitat amounts (32%) also reported higher species richness with increased fragmentation (Rybicki et al., 2020).

One novel aspect of our model is that it considers communities that are assembled from a metacommunity in which individuals migrate to an empty habitat. After the number of species is stabilized, the habitat is fragmented. This scenario is deemed more realistic than having all species initially present with random patterns in an already fragmented habitat (Rybicki et al., 2020). This could be more important the more heterogeneous was species spatial distribution pattern before fragmentation, as the cube hypothesis states.

In terms of the cube hypothesis, low between-patch movement, minimal impact of spreading of risk on population dynamics and low species spatial clumping are needed for SL > SS. In our model, dispersal distance increases between patch movements, but for higher dispersal distances, the sizes of the patches are less important and the relationship tends to be SS = SL. Spreading of risk is influenced by λ, which represents the relationship between the growth and death rates. For smaller λ, spreading of risk becomes more significant because the probability of local extinction is higher. A very low dispersal distance combined with low λ favours SL > SS up to a threshold in patch size, beyond which SL = SS. The spatial clumping of species is influenced by the dispersal distance; a higher dispersal

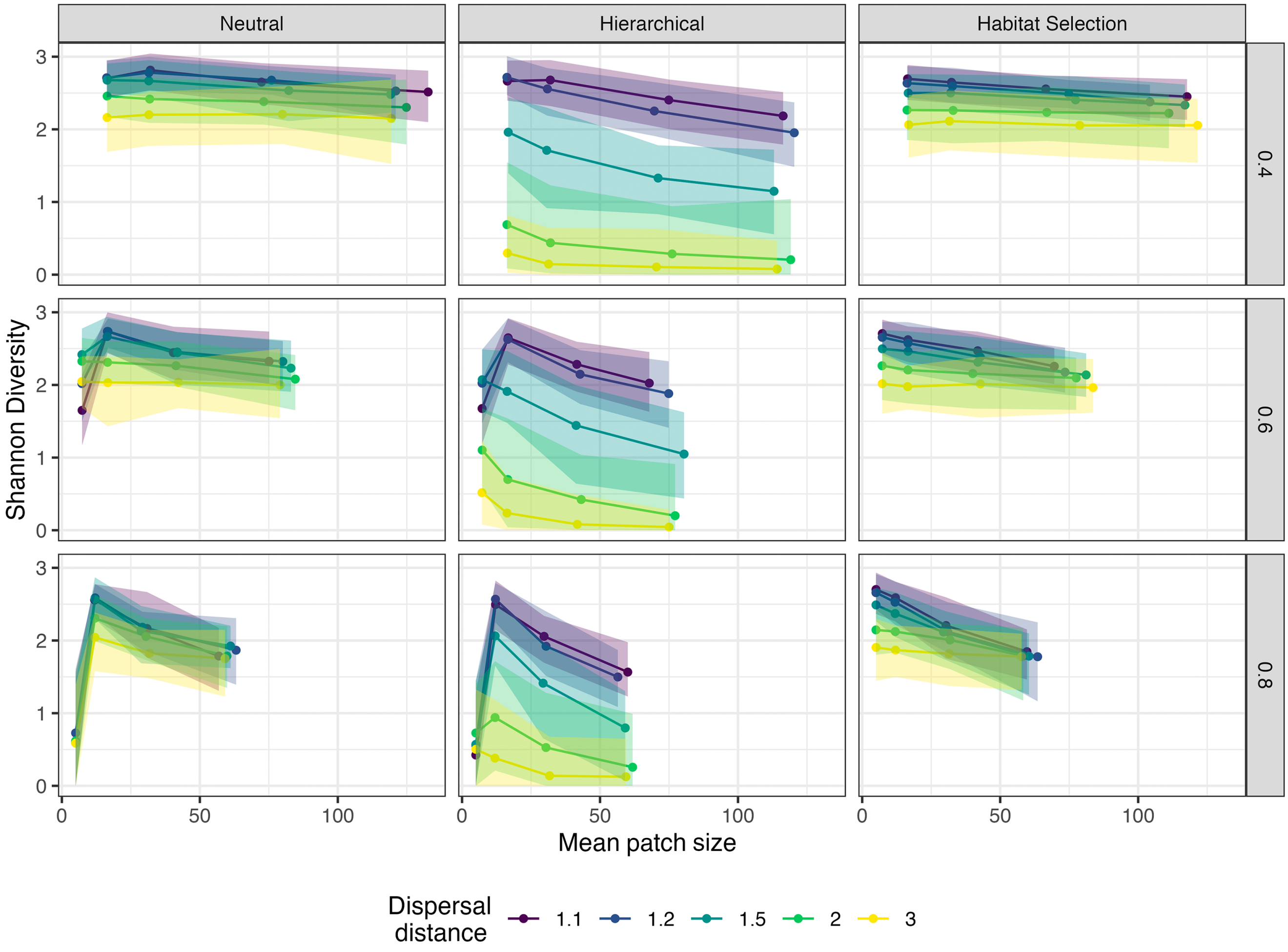

FIGURE 5 Relationship between the number of species and habitat patch size across panels representing different model versions and varying dispersal distances under random block habitat destruction. The vertical panels correspond to different percentages of habitat destruction. In the neutral model, species are equivalent and share the same parameters; in the hierarchical model, species exhibit competitive dominance, with more dominant species replacing less dominant ones; and in the neutral with habitat selection model, species are neutral but propagules search for empty patches, ensuring survival. Simulations were performed using a fixed growth rate ($\lambda=2$), with migration and replacement rates of 0.0001 and 0.3, respectively. After 600 time steps, the specified percentage of the habitat was destroyed, making it unavailable for species. Habitat blocks of the same size (habitat patch size) were randomly distributed over the simulation grid. As a result, some patches overlapped, leading to a distribution of patch sizes.

distance produces less clumpiness. However, this is confounded with patch movement, making it challenging to disentangle the effect. Therefore, the results of our model are generally compatible with the cube hypothesis.

Our findings support Fahrig et al.'s (2021) conclusion that conditions favouring SL > SS are limited and infrequently observed in nature. Under conditions of adequate patch size and dispersal capabilities, the SS scenario typically retains more species. This underscores the ecological significance of smaller habitat patches in maintaining biodiversity and landscape connectivity (Manning et al., 2006; Shafer, 1995; Yan et al., 2021). Our results thus challenge the conventional preference for larger reserves in conservation planning and support the paradigm shift in conservation towards considering sets of many small patches generally having higher biodiversity than sets of few large patches (Riva & Fahrig, 2023). The model's primary outcomes could be validated using empirical data by assessing the prediction that species with greater dispersal capabilities would exhibit a lower SS effect compared to species with limited dispersal.

In conclusion, we believe our study adds valuable perspectives to the SLOSS debate, illustrating the complexities of habitat fragmentation and species conservation. While our model has inherent limitations, it provides a useful framework for understanding key ecological processes. Future research should aim to extend these findings to more diverse ecological settings and incorporate how heterogeneity between species influence biodiversity in fragmented landscapes.

AUTHOR CONTRIBUTIONS

Leonardo A. Saravia, Ulises Balsa and Fernando Momo conceived the project. Leonardo A. Saravia designed, developed and performed the simulations. He analysed the data in close consultation with all co-authors. Leonardo A. Saravia and Ulises Balsa wrote the first draft of the manuscript. All authors contributed to the manuscript's revision and finalization.

ACKNOWLEDGEMENTS

We acknowledge the financial support provided by the 'Fondo para la Investigación Científica y Tecnológica FONCYT' (grant no. PICT-2020-SERIEA-02628). Additionally, we extend our gratitude to the National University of General Sarmiento (UNGS), especially to Dr. Santiago Doyle, for granting access to the computational resources utilized in this study.

CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The NetLogo model is available for download on GitHub: https://github.com/lsaravia/DynamicForestExtinction and Zenodo https://doi.org/10.5281/zenodo.8157152. Data and R scripts can also be accessed on GitHub: https://github.com/EcoComplex/multiSLOSS and Zenodo (Saravia et al. 2024).

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SUPPORTING INFORMATION

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

Supporting Information S1.

How to cite this article: Saravia, L. A., Balza, U., & Momo, F. (2024). Why there are more species in several small patches versus few large patches: A multispecies modelling approach. *Functional Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2435.14695