Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay

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Abstract

Positive effects of habitat patch size on biodiversity are often extrapolated to infer negative effects of habitat fragmentation on biodiversity at landscape scales. However, such cross-scale extrapolations typically fail. A recent, landmark, patch-scale analysis (Chase *et al*. 2020, Nature 584, 238–243) demonstrates positive patch size effects on biodiversity, i.e., "ecosystem decay” in small patches. Other authors have already extrapolated this result to infer negative fragmentation effects, i.e., higher biodiversity in a few large than many small patches of the same cumulative habitat area. We test whether this extrapolation is valid. We find that landscape-scale patterns are opposite to their analogous patch-scale patterns: for sets of patches with equal total habitat area, species richness and evenness decrease with increasing mean size of the patches comprising that area, even when considering only species of conservation concern. Preserving small habitat patches will therefore be key to sustain biodiversity amidst ongoing environmental crises.

Introduction

Ecological dynamics are often complex, making properties of ecosystems notoriously difficult to predict across scales (Wiens 1989; Levin 1992; Chase *et al.* 2018). Ecologists, therefore, have traditionally suggested limiting inferences to the spatial and temporal domains in which a phenomenon is observed (Wiens 1989; Levin 1992). Nevertheless, because the scales at which we study ecological patterns and processes are typically small in comparison to the scales at which ecosystems exist and are managed (Miller *et al.* 2004; Estes *et al.* 2018), the temptation of extrapolating phenomena observed at small scales to broader scales can be alluring. While cross-scale extrapolation is possible in certain conditions, extensive empirical and theoretical work demonstrates it often fails (O’Neill 1977; Miller *et al.* 2004; McGill 2019; Newman *et al.* 2019). Thus, any extrapolation of a pattern across scales should be considered as a prediction to be tested against empirical evidence (Miller *et al.* 2004; Fahrig *et al.* 2019).

In a recent study published in Nature, Chase *et al.* (2020) show that small patches tend to have lower biodiversity than expected solely based on their size. They call this ‘ecosystem decay’ (Lovejoy 1984), and they suggest that accounting for ecosystem decay will improve predictions of biodiversity change under future land use scenarios. Chase *et al*. acknowledge that their findings are restricted to comparisons between individual habitat patches (Fig. 1-b), and thus they do not resolve whether patch size influences biodiversity at a landscape scale, i.e., across multiple patches (Fig. 1-c). Specifically, they state that “*biodiversity might be unaffected or even increase at the landscape scale after fragmentation*”. Therefore, the results of Chase *et al*. do not provide information about how biodiversity responds to different potential scenarios of equal habitat loss resulting in different sizes of the remaining patches (i.e., different levels of fragmentation *per se*, Fahrig 2003). Equivalently, their results do not speak to whether biodiversity is better preserved by protecting many small patches or few large patches of the same total area, the traditional SLOSS question (“*is biodiversity higher in Several Small patches Or a Single Large patch?*”) (Simberloff & Abele 1982; Quinn & Harrison 1988; Fahrig 2020).

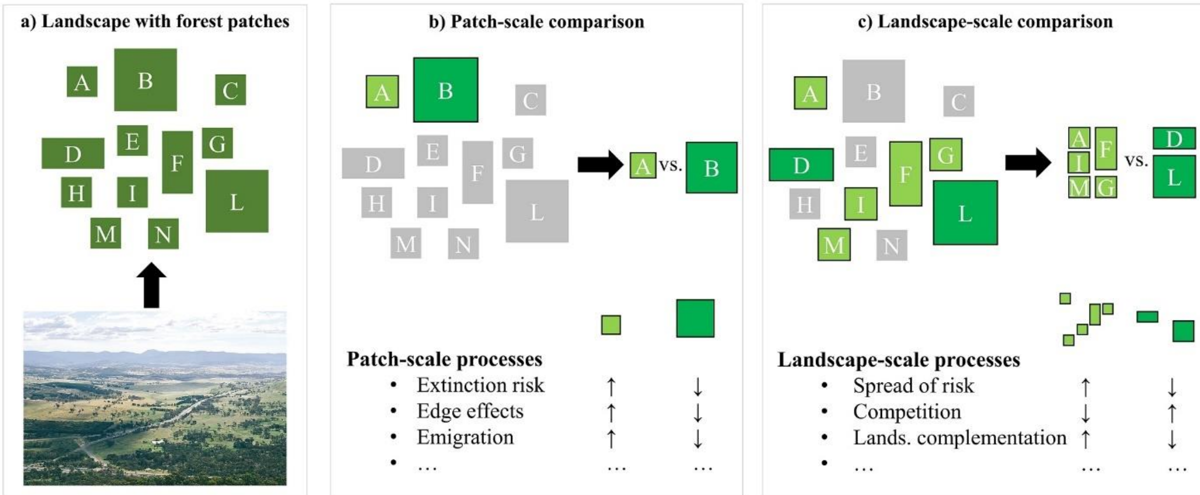

Fig. 1: Human activities have caused widespread loss of natural habitat worldwide, typically resulting in landscapes composed of many small and a few large remnant patches in human-dominated regions (a). The ecological literature abounds with examples of patch-scale comparisons of biodiversity patterns, where a small patch is compared to a large patch (b). A second type of study, less common, evaluates landscape-scale biodiversity patterns by comparing sets of patches varying in patch sizes but totaling the same habitat area (c). Extrapolation of results from patch-scale studies to a landscape scale can be incorrect because the processes that determine biodiversity across sets of patches include both patch-scale and landscape-scale processes (examples in (b) and (c); see [Fletcher et al. (2018), Fahrig et al. (2019)]. Up-arrows indicate "higher" while down-arrows indicate "lower"; "Lands. Complementation" refers to landscape complementation (Dunning et al. 1992), and "…" indicate the several other processes that might affect biodiversity at the patch- and landscape-scale.

Chase *et al.* (2020) cautioned against extrapolation of ecosystem decay because such extrapolations remain widespread in the ecological literature, including in studies of effects of habitat loss and fragmentation. While most authors treat habitat loss and fragmentation as indistinguishable, controlling for the effects of habitat amount is necessary to assess habitat fragmentation *per se* (Fahrig 2003, 2017; Hadley & Betts 2016; Yarnall *et al*. 2022). In several of the 62 papers citing Chase *et al*. (2020) between July 29th 2020 and April 24th 2022, authors appear to extrapolate patch-scale ecosystem decay to infer landscape-scale biodiversity declines from habitat fragmentation (Appendix 1.1). This extrapolation from effects of the sizes of individual patches to habitat fragmentation effects seems intuitive. Several processes observed in small patches, including negative edge effects and increased demographic stochasticity, have been used for decades as evidence that large habitat remnants have a higher value for biodiversity than several small ones of the same total area (Fletcher *et al.* 2018). However, extrapolating patch-scale processes (e.g., edge effects in a patch) to predict a phenomenon at larger scales (e.g., biodiversity across multiple patches) assumes that the effects of processes occurring at the landscape scale are negligible in comparison to the effects of processes occurring at the patch scale (Fahrig *et al*. 2019). Much research in landscape ecology, macroecology, and more broadly the study of complex systems suggests this assumption is often invalid (O'Neill 1977; Wiens 1989; Levin 1992; McGill 2019; Newman *et al.* 2019; Riva & Nielsen 2020).

Evidence to date suggests that extrapolation of patch-scale phenomena to predict landscape-scale phenomena is not valid for SLOSS. In fact, most empirical studies find more species across several small than few large patches (Fahrig 2020), even when only species of conservation concern are considered (Riva & Fahrig 2022). This implies that small patches have disproportionately high biodiversity value, on a per-area basis, as has been found in several empirical studies (Bennett & Arcese 2013; Tulloch *et al.* 2016; Deane & He 2018; Wintle *et al.* 2019; Deane *et al.* 2020; Yan *et al.* 2021). Note that the common pattern of higher species richness across sets of many small patches than few large patches neither invalidates nor contradicts ecosystem decay as documented in Chase *et al*. (2020). Instead, it suggests that other processes acting at the landscape scale increase biodiversity in systems containing a large number of small patches, and that these landscape-scale processes often outweigh effects of the sizes of individual patches (Fig. 1). Processes such as species interactions (Huffaker 1958), environmental heterogeneity resulting in resource complementation/supplementation (Dunning *et al.* 1992), ecological drift (Vellend 2020), or spreading of risk (den Boer 1968), which affect extinction/colonization dynamics and moderate beta diversity patterns across a landscape (Fahrig *et al.* 2019, 2022), could lead to higher biodiversity across several small than few large patches despite ecosystem decay at the patch scale.

With widespread habitat loss putting biodiversity under siege (Caro *et al.* 2022), understanding how ecosystem decay influences biodiversity at a landscape scale is crucial. Recent work reignited interest around SLOSS and the importance of small habitat patches for conservation (Deane & He 2018; Wintle *et al.* 2019; Fahrig 2020; Riva & Fahrig 2022). At the same time, habitat in small patches is more likely to be lost than habitat in large patches (Riva *et al.* 2022). This suggests that conservation policy and action should urgently reconsider protection of small patches of habitat as a means for halting biodiversity loss, a recommendation in apparent contrast with evidence of ecosystem decay. We therefore re-analyze the same compiled database used in Chase *et al*. (2020) to determine whether ecosystem decay "scales up" to the landscape scale.

Our analyses are analogous to those conducted by Chase *et al*. (2020), but instead of comparing individual patches to each other, we compare sets of many small patches to sets of few large patches of the same total area. We ask whether *for an equal cumulative habitat area* (Fig. 1-c), (i) biodiversity decreases in landscapes composed of smaller patches, as would be predicted if cross-scale extrapolation of ecosystem decay is valid (Fig. 2-a), and (ii) whether species turnover weakens the landscape-scale relationship as observed at the patch scale by Chase *et al*. (2020) due to beta diversity patterns (Quinn & Harrison 1988; Deane *et al.* 2020) (Fig 2-b). We also test the prediction that biodiversity in sets of small patches is inflated by the presence of generalist species of lower conservation value (Fahrig *et al.* 2019; Chase *et al.* 2020) by repeating our analyses but including only declining species according to the IUCN Red List (IUCN 2022). We conclude by parameterizing a species-area relationship that accounts for the relationship we found between species richness and mean patch size across sets of patches.

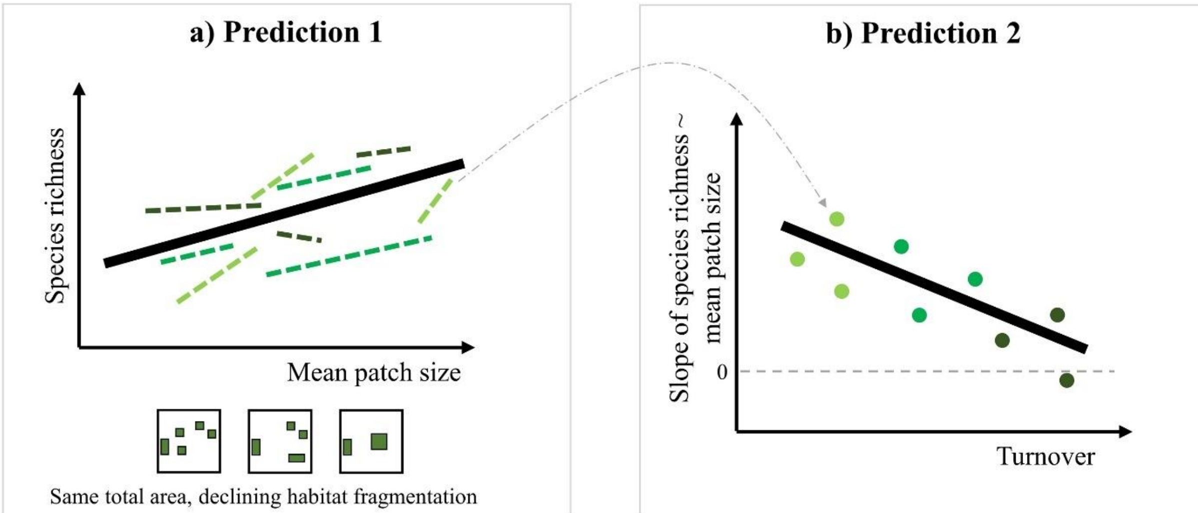

Fig. 2: Predictions based on extrapolation of patch-scale ecosystem decay from Chase et al. (2020) to landscape scales. Prediction (1). When comparing multiple sets of patches totaling the same habitat area, species richness should increase with mean patch size, i.e., as fragmentation decreases (a). This prediction follows from extrapolation of Fig. 2-c in Chase et al. (2020) showing increasing species richness with increasing patch size. The colored, narrow lines illustrate variation in the relationship across different datasets [as in Fig 2 in Chase et al. (2020)] and the thick black line symbolizes an overall trend. Prediction (2). Species turnover across sets of patches should reduce the slope of the positive relationship between species richness and mean patch size. This prediction follows from extrapolation of Fig. 4-a in Chase et al (2020), showing shallower slopes in the relationship between species richness and patch size when species turnover is higher. Colors of lines in (a) match colors of slopes in (b).

Material and methods

Data extraction and preparation

An overview of the database and details of data preparation are provided in Appendix S1.2. Our goal was to compare species richness and evenness across sets of patches with equal cumulative area, but different sizes and numbers of patches. The steps required to this end were: (i) apply criteria for inclusion of datasets and patches from Chase *et al*. (2020), and extract the associated data; (ii) resample individuals and species in each patch and in each dataset, to control for sampling bias and for any relationship between patch size and density of individuals; and (iii) combine the resulting species lists across randomized sets of patches having equal cumulative habitat area but different mean patch size (i.e., different degrees of habitat fragmentation). In all, we analyzed 71 datasets (metacommunities hosting 4351 taxa in 1149 patches) and 425 scenarios (i.e., combinations of dataset × habitat amount that included at least two sets of patches; Table S2) involving 9954 sets of patches.

Predictions and analyses

To determine whether patch-scale ecosystem decay "scales up" to the landscape scale, we followed the same themes and models proposed in Chase *et al*. (2020), but instead of comparing biodiversity in small vs. large patches, we compared biodiversity in sets of patches totaling the same habitat area but differing in their mean patch size. When comparing different sets of patches in a scenario, we used mean patch size as a measure of habitat fragmentation, with smaller mean patch sizes representing a larger number of smaller patches, i.e., higher habitat fragmentation (Fig. 2-a, see x axis). This approach is unusual for the study of habitat fragmentation, where more typical metrics include number of patches or edge density, but it allows clear and direct comparison with the result of Chase *et al*. (2020), including visual comparisons between the figures in the two papers.

We structured the analysis in three sections: (i) testing extrapolation of the patch-scale patterns in Chase *et al*. (2020) to the landscape scale, (ii) testing a mechanism potentially affecting these patterns, i.e., the presumed greater occurrence of generalist species in small patches, and (iii) applying our results to biodiversity conservation in an analysis of combined effects of habitat amount and fragmentation, following on the analysis presented in Extended Data Fig. 8 in Chase *et al*. (2020).

Extrapolation of patch-scale patterns

We tested two predictions derived from cross-scale extrapolation of the results in Chase *et al*. (2020) to landscapes (Fig. 2).

Prediction (1): When comparing multiple sets of patches totalling the same habitat area, species richness and species evenness will increase as the mean size of the patches in a set increases, i.e., as landscape-scale fragmentation *per se* decreases (Fig. 2-a). This prediction is an extrapolation from the patch-scale effects of patch size in Fig. 2-c and 2-d in Chase *et al.* (2020), that richness and evenness per sample increase with patch size. To test these predictions, we measured species richness (S) and species evenness, measured as Hurlbert's Probability of Interspecific Encounter (PIE) (Hurlbert 1971), following Chase *et al*. (2020). Then, we modeled the effect of mean patch size of a set of patches on each of S and PIE. Positive relationships between mean patch size in a set of patches and S and PIE would support extrapolation of the patch-scale results in Chase *et al.* (2020) to the landscape scale. Dataset ID and habitat area sampled, the two factors that determine each of the 425 scenarios (Fig. S1-c), were included as nested random effects. Following Chase *et al*. (2020), we also fit two-way interactions between mean patch size and taxonomic identity, study region, time since patch creation, and matrix quality to evaluate whether these covariates mediate the relationships between mean patch size and richness or evenness. We used the covariate data as provided in Chase *et al*. (2020), to ensure comparability between our analysis and theirs. Note that Chase *et al*. (2020) measured evenness as $S\_PIE = 1/(1 – PIE)$, an asymptotic estimator for Hill numbers of diversity order 2, whereas here we used PIE. We did so because we observed some cases of PIE = 1, for which the estimator was undefined. Because PIE and S_PIE are monotonically and positively related, this does not affect our inferences.

Prediction (2): When comparing multiple sets of patches totalling the same habitat area, the positive relationship between species richness or species evenness and mean patch size [Prediction (1)] will be weaker in scenarios with a higher species turnover (Fig. 2-b). This prediction is an extrapolation to the landscape scale of the second analysis presented in Fig. 4a-b in Chase *et al*. (2020), who found that the slope of the patch-scale relationship between species richness and patch size was shallower (less positive) in datasets where species turnover among the patches in that dataset was higher than for other datasets. To test this prediction, we measured in each scenario (i) the slope, across sets of patches, of the species richness vs. mean patch size relationship, and (ii) the turnover among sets of patches in that scenario (see below for details). A negative relationship between turnover and the slope of the richness vs. mean patch size relationship in a scenario would support extrapolation of the patch-scale pattern to the landscape scale.

To estimate turnover among sets of patches, we followed the same general approach used in Chase *et al.* (2020), but applied at the landscape scale. We calculated for every scenario multi-site dissimilarity metrics that account for compositional heterogeneity in species occurrence and abundance (Baselga 2010, 2017). Specifically, we partitioned beta diversity using incidence-based (Jaccard dissimilarity) and abundance-based (Ruzicka dissimilarity) metrics (Baselga 2010, 2017). The different sets of patches in a scenario were treated as Chase *et al*. (2020) treated patches, by combining the species lists found in all patches in a set of patches. Therefore, our measures of turnover represented variation in species composition across the metacommunities sampled in different scenarios, because the slope of the relationship between species richness and habitat fragmentation was calculated at this level.

<u>Testing whether generalist species determine the observed patterns</u>

Chase *et al.* (2020) suggested that diversity in small patches is inflated by generalist species spilling over from the matrix into small patches. They inferred that this spillover resulted in their observed shallower slopes in the species richness vs. patch size relationships when species turnover was higher. If true, then at the landscape scale, spillover of generalist species into small patches should also inflate species richness in sets of many small patches compared to sets of few large patches. To test this hypothesis, we re-evaluated Prediction (1) for species richness excluding generalist species. We assumed that generalist species are typically those that are either not declining or are increasing in abundance according to the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species (IUCN 2022). We make this assumption because 90% of threatened species based on the IUCN Red List are listed as "declining," and high extinction risk is typically related to species rarity and specialization (Colles *et al.* 2009; Chichorro *et al.* 2019). If small patches harbor primarily generalist species and only a subset of specialist species, then we expect that analyzing only declining species will strengthen the predicted positive relationship between biodiversity and mean patch size (Fig 2-a). Including only declining species should result in both a lower intercept and a steeper positive slope in the species richness vs. mean patch size relationship than when including all species. If this prediction is not supported, then the data do not support Chase *et al*.'s hypothesis that their observed shallower slopes in the species richness vs. patch size relationships when species turnover is higher were due spillover of generalist species from the matrix into small patches.

<u>Application to biodiversity conservation.</u>

As an application of their analysis, Chase *et al*. (2020, Extended Data Fig. 8) proposed a re-parametrization of the species-area relationship (SAR) to account for patch-scale ecosystem decay when habitat is lost. We applied our results in a similar way but at the landscape scale, using the observed species richness from Prediction (1) across all scenarios (from 20% to 80% total habitat in 71 datasets; Table S2). We parameterized a species-area relationship (SAR), where area is the total area in the scenario, and then we incorporated our observed habitat fragmentation effects. To combine datasets with very different ranges of patch sizes, we used as a measure of fragmentation the standardized mean patch size in each scenario, where negative values represent higher fragmentation and positive values lower fragmentation for the same habitat area, and zero is the average mean patch size in a scenario. In this analysis, every scenario corresponds to multiple points for the same habitat area on the SAR x-axis.

Results

We found no support for the hypothesis that patch-scale ecosystem decay extrapolates to the landscape scale. Opposite to Prediction (1) (Fig. 2-a), species richness actually *decreased* with increasing mean patch size across sets of patches, i.e., when habitat was less fragmented (β_{rich} = -0.15, CI = -0.28, -0.02; Fig. 3-a). Thus, when considering an equal total habitat area, sets of several small patches harbored more species than sets of a few large ones. This result holds when accounting for two-way interactions between mean patch size and taxonomic identity, study region, time since patch creation, and matrix quality (Appendix 1.3). It also holds when modeling, instead of species richness, species evenness of the species-abundance distribution of different sets of patches (Appendix 1.3). We note, however, that species richness of amphibians and reptiles did not respond to habitat fragmentation (β_{herp} = 0.12, CI = -0.26, 0.50) (Appendix 1.3).

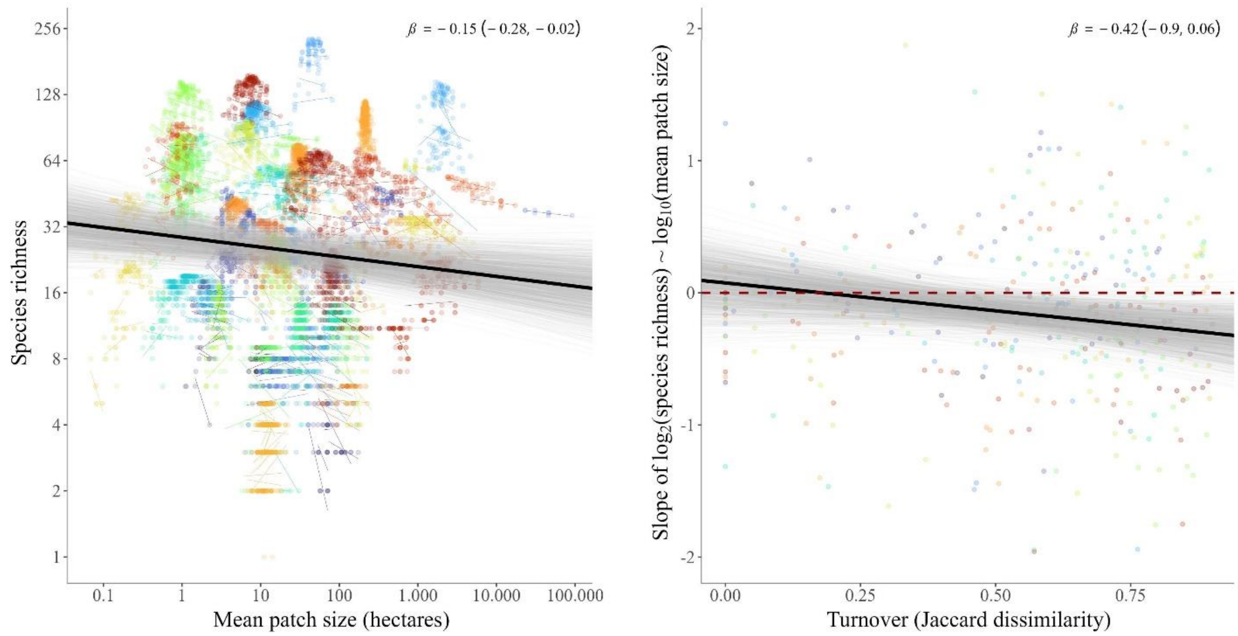

Fig. 3: Test of predictions based on cross-scale extrapolation of ecosystem decay from the patch scale to the landscape scale (Fig. 2). Left inset: results do not support Prediction (1), that ecosystem decay extrapolates to the landscape scale, reducing biodiversity when habitat is fragmented [Fig. 2(a)]. In fact, the pattern is opposite to the prediction, with biodiversity higher in sets of many small patches than in sets of a few large patches. Clouds of colored points represent different metacommunities (n = 71), with up to seven different habitat amounts sampled per metacommunity (from 20% to 80% of the total habitat sampled in a dataset; see Tab. S2). Each colored line represents a trend in species richness with decreasing habitat fragmentation but equal total habitat area, i.e., from several small patches to a few large patches of the same cumulative area, in a metacommunity. Right inset: results support Prediction (2), that species turnover across sets of patches reduces the slope of the relationship between species richness and mean patch size [Fig. 2(b)], i.e. the positive effect of fragmentation on species richness is weaker when turnover is higher. Points in the right inset are the slopes of each colored line in the left inset. The black thick lines are estimated posterior mean relationships, and grey narrow lines represent uncertainty in the models, estimated by sampling from the posterior distributions of the parameters in the two models.

Consistent with Prediction (2) (Fig. 2-b), we found that species turnover increased biodiversity in sets of small patches, as slopes of the species richness vs. mean patch size relationship became more negative as the Jaccard dissimilarity within a scenario increased ($\beta_{turnover}$ = -0.42, CI = -0.90, 0.06; Fig. 3-b). When considering an equal total habitat area, higher species turnover in a metacommunity contributes to the higher species richness across sets of several small than few large patches (Appendix 1.3).

When evaluating only declining species based on the IUCN Red List (IUCN, 2022) (*n* = 299 species from 20 datasets), we found the same relationship between mean patch size and species richness as for the full list of species. Specifically, species richness of declining species decreased with increasing mean patch size in a set of patches, for a given total habitat area. The slope was more steeply negative, but the smaller sample size resulted in higher uncertainty in the estimated slope (β_{IUCN} = -0.55, CI = -1.58, 0.47 vs. β_{full} = -0.15, CI = -0.28, -0.02) (Fig. 4). Sets of several small patches therefore harbor more declining species than sets of few large patches of the same total area. This implies that the increase in total species richness with decreasing mean patch size is not due to spillover of generalist species from the matrix into small patches.

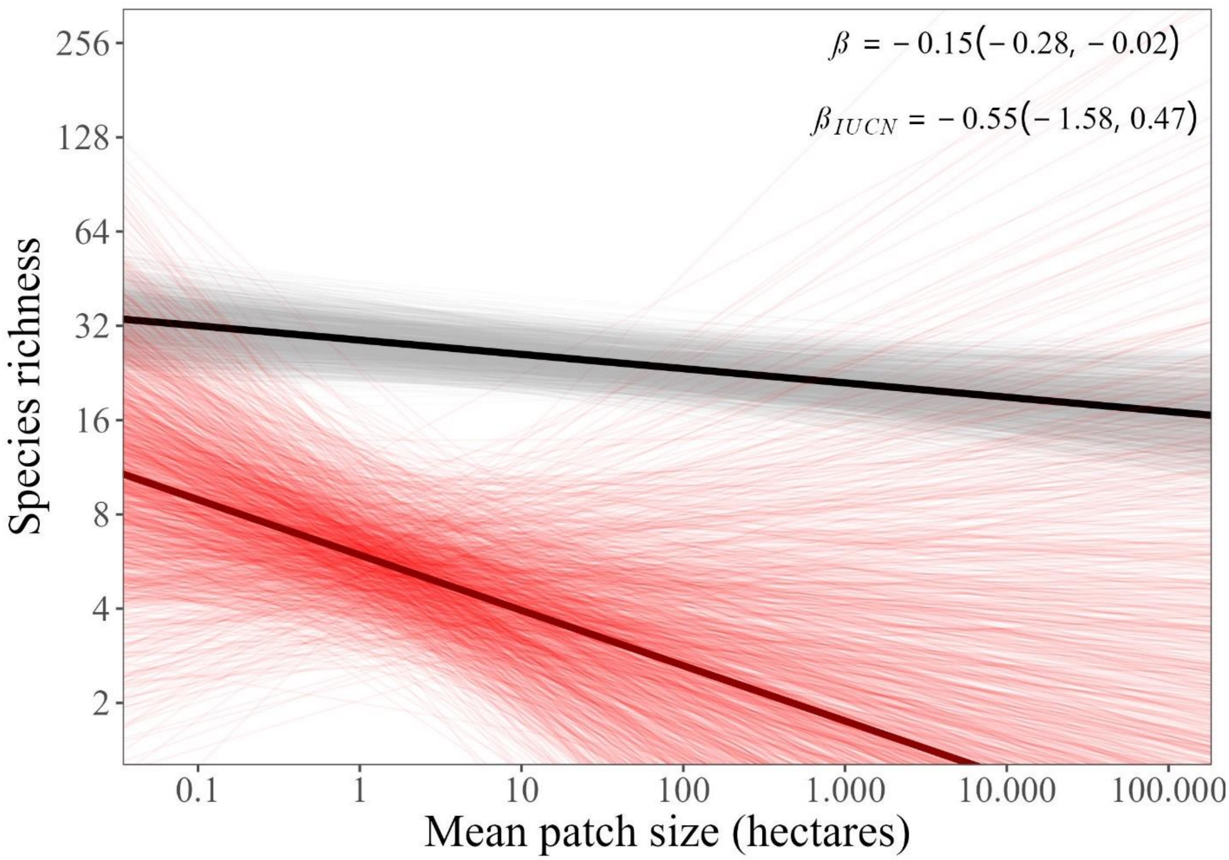

Fig. 4: Relationship between species richness and mean patch size, a measure of declining habitat fragmentation, in multiple scenarios (see Methods), for the entire dataset (upper thick black line; n = 71 datasets; also in Figure 3, left inset) and for the subset of species classified as "Declining" in the IUCN Red List of Threatened Species (lower thick red line; n = 20 datasets). Narrow lines represent uncertainty in the models, estimated by sampling from the posterior distributions of the parameters in the two models.

Last, models of the species-area relationship including our observed fragmentation effect indicate that total habitat area is overwhelmingly more important than habitat fragmentation in influencing biodiversity (Appendix 1.3). For instance, at the average mean patch size in a set of patches, species richness increased from 3 to 250 species from lowest to highest total habitat area (Tab. S2), whereas at the average total habitat area in a set of patches (185 ha), species richness increased from 24 to 27 species from lowest to highest fragmentation.

Discussion

Ecosystem decay does not determine biodiversity patterns at the landscape scale

Our study demonstrates that ecosystem decay does not extrapolate to the landscape scale, and confirms that cross-scale extrapolation risks misinforming environmental management (Miller *et al.* 2004; Fahrig *et al.* 2019). First, our results suggest that over large numbers of small patches, landscape-scale processes often enhance biodiversity and outweigh ecosystem decay occurring in each patch individually (Fig. 3-a). Second, they suggest that turnover across small patches underlies this pattern (Fig. 3-b). Third, they are not consistent with the hypothesis that specialist species require large patches, as declining species were also more common in sets of many small than few large patches. And finally, they confirm that protecting more habitat – regardless of how it is arranged – is critical for biodiversity protection (Fahrig 1997, 2003). Most importantly, these results mean that, contrary to a long list of national and international policies (Wintle *et al.* 2019; Fahrig *et al.* 2022; Riva & Fahrig 2022), there is no apparent ecological reason to prioritize large patches over large numbers of small patches when the objective is maximizing biodiversity protection in human-dominated landscapes.

Interestingly, we detected some additional patterns at the landscape scale that did not emerge when the same data were analyzed at the patch scale (Chase *et al.* 2020). For instance, we found that species richness of amphibians and reptiles responded slightly positively to increasing mean patch size. This could indicate that these species are particularly vulnerable to dispersal mortality; for example, a meta-analysis (Rytwinski & Fahrig 2012) found that amphibians and reptiles are the taxa suffering the strongest population-level impacts of roads and traffic. Consistent with this, we also found that biodiversity in sets of several small patches is especially higher than biodiversity in sets of few large patches when the patches are embedded in a less harsh matrix, with species richness declining from ~ 35 to ~ 22 species as the mean patch size in a set of patches increased, in contrast to shallower declines in intermediate and harsh matrices from 32 and 18 species to 28 and 16 species respectively (Appendix 1.3). Differences between "intermediate" and "harsh" matrix were less clear, perhaps due to the general classification of matrix harshness provided in FragSAD, and to other metacommunity properties, which more broadly might have influenced effects in both our analysis and in Chase *et al*. (2020). On the other hand, similar to the finding of Chase *et al*. (2020) at the patch scale, we did not find that sets of small patches accumulate 'extinction debt' (Figueiredo *et al.* 2019). In fact, biodiversity in sets of several small patches was especially higher than in sets of few large patches for systems of older patches (Appendix 1.3), as also found in Fahrig (2020).

Two processes – extinction risk and ecological drift – illustrate why extrapolation of patch-scale ecosystem decay to infer landscape-scale biodiversity patterns fails. Small patches typically harbor smaller populations, and thus they are exposed to a higher extinction risk due to demographic, genetic, and environmental stochasticity (Shafer 1995; Laurance 2002). Therefore, there is an expectation that increased extinction risk in each of many small patches will result in increased extinction risk across a set of many small patches than across a set of a few large ones (Diamond 1975; Hanski 2015). However, when comparing sets of patches totaling the same area, as patches become smaller they also become more numerous, reducing the probability of extinction over the entire set of patches (e.g., due to spreading of risk; den Boer 1968). This has been predicted in models and demonstrated in experimental microcosms (Fox *et al.* 2017; Hammill & Clements 2020). Similarly, smaller populations are more susceptible to ecological drift, which can increase stochastic extinctions in each of many small patches. Nevertheless, ecological drift can also increase biodiversity in sets of many small patches due to reduced competitive exclusion and a higher chance of stochastic divergence in community composition (Vellend *et al.* 2014; Gilbert & Levine 2017).

The overall low explanatory power attributed to mean patch size in our study [and to patch size effects in Chase *et al*. (2020)] is likely related to the fact that the database contains a very wide range of species, habitats, regions, and landscape attributes. This is evident in the large amount of variation explained by the random effect for Study ID in the models. In an attempt to understand some of this variation we conducted *post hoc* analyses evaluating the roles of taxa mobility, landscape heterogeneity, and study extent (details in Appendix S1.2 and S1.3). While study extent and landscape heterogeneity did not affect the slope of the relationship between species richness and mean patch size, we found that taxa mobility, approximated by the capacity of taxa to fly, is associated with a higher diversity in more fragmented habitats. However, given our coarse estimates of mobility (Appendix S1.2) and the potential for complex interactive effects between the mobility of taxa, landscape heterogeneity, connectivity, and study extent, we caution that this result is preliminary.

Unfortunately, we could not evaluate effects of habitat configuration other than mean patch size (e.g., connectivity), because the data analyzed in Chase *et al.* (2020) do not include the locations of the individual patches in the datasets. Of particular concern would be if, in most datasets, the sets of several small patches tend to be more spread out (patches farther from each other) than sets of few large patches. In that case, several small patches might have more species because they include a greater variety of habitat types or because they sample different biogeographical regions. However, we believe this is unlikely in the Chase *et al*. database, for two reasons. First, as in most ecological studies (Estes *et al.* 2018), for practical reasons the total extents of the study areas are limited and so the same habitat types and species are likely represented across each study area: 82% of datasets were collected within extents smaller than 50 km diameter (Appendix S1.3), suggesting that variation across space in the species pool should be limited in most datasets. Indeed, a model including an interaction term between study extent and mean patch size did not reveal different slopes (Fig. 2-a, 3-a) in datasets assessing smaller or larger extents (Appendix S1.3), whereas if small patches tended to be more broadly spread, one would expect that the slope of the (positive) habitat fragmentation effect would be steeper for studies at larger extents. Second, an analysis of multiple landscapes in 32 spatially-referenced datasets analyzed by (Watling *et al.* 2020) and reported in Appendix 2 of Fahrig *et al*. (2022), found that patches in landscapes containing many small patches are not typically more (or less) spread out than patches in landscapes containing few large patches. It seems likely that the same would be true of the studies in Chase *et al*. (2019), also based on visual inspection of the maps provided in the original manuscripts.

<u>Ecosystem decay does not contradict the conservation value of small patches</u>

Our analysis suggests that, to maximize biodiversity, one should strive to protect as much natural habitat as possible, even if it occurs in small habitat patches. Therefore, large patches should not be preferred *a priori* because, for an equivalent habitat area, groups of many small patches typically harbor more species – including more species of conservation concern – than few large patches of the same total area (Fig. 3-a, 4). However, because the mechanisms underlying the pattern remain unclear, it will also be important to understand if there are situations when small patches have disproportionately low conservation value (Deane *et al.* 2020; Fahrig *et al.* 2022). In the meantime, we conservatively suggest that we should take advantage of all opportunities to protect and restore habitat, regardless of patch sizes.

We note that landscapes studded with many small patches are already sustaining populations of species that were previously assumed to depend strictly on large habitat patches. For instance, large mammals are recovering from historical declines both in Europe and North America across human-dominated landscapes, where most natural habitat occurs in small patches (Chapron *et al.* 2014; Magle *et al.* 2021; Riva *et al.* 2022). Restricting populations of these taxa to large patches would result in extinctions across much of Europe, where individual large patches are too small to host persistent populations (Chapron *et al.* 2014). Therefore, protection and restoration of small habitat patches can facilitate the coexistence of these charismatic taxa with humans.

In addition to ecological considerations, there are also social and pragmatic reasons that make acknowledging small patches crucial in conservation. Protection of small patches can provide communities with opportunities to access nature, which can elicit environmental engagement, reduce unsustainable behaviors, and stimulate environmental advocacy (Novacek 2008). Awareness of the importance of small patches will also legitimize and foster the local conservation actions of institutions, individuals, and communities, including indigenous groups (Riva & Fahrig 2022). Last, the delivery of many ecosystem services can be disproportionately high in small patches (Hunter *et al.* 2017; Valdés *et al.* 2020). Taken together, these arguments suggest great potential benefits in acknowledging the role of small patches in conservation.

<u>Concluding remarks: a paradigm shift in conservation</u>

Patch-scale ecosystem decay as documented in Chase *et al*. (2020) highlights that habitat loss resulting in declining patch size depletes biodiversity in that patch disproportionately more than expected solely on area effects. Using the same dataset as in Chase *et al*. (2020), our results do not support the extrapolation of this patch-scale ecosystem decay to sets of patches in a landscape. Instead, our results suggest that, for the same total area, sets of many small patches generally have higher biodiversity than sets of few large patches (Fig. 3-a). From this we infer that ecosystem decay does not determine biodiversity patterns across sets of patches at the landscape scale, but rather these depend on both patch-scale and landscape-scale processes (Fig. 1), and that the latter outweigh the former.

We hope that our results, along with a growing body of related evidence (Bennett & Arcese 2013; Tulloch *et al.* 2016; Deane & He 2018; Wintle *et al.* 2019; Deane *et al.* 2020; Fahrig 2020; Hammill & Clements 2020; Yan *et al.* 2021; Riva & Fahrig 2022), will catalyze a transition to conservation practices that recognize the high biodiversity value of small patches. While large patches play important roles in conservation (Shafer 1995; Arroyo-Rodríguez *et al.* 2020; Fahrig *et al.* 2022), the assumption that some patches are too small to aid in biodiversity protection has been a deadly sin of modern conservation.

Recent concern over biodiversity loss has led to important objectives for habitat protection, including the goal of doubling protected areas to 30% of the Earth's surface by 2030, and potentially increasing this to 50% by 2050 (Dinerstein *et al.* 2019; Maxwell *et al.* 2020). To effectively conserve biodiversity, we must apply these goals at the ecoregion level, as different ecoregions house different species. Small patches are often all that remains in many human-dominated ecoregions (Taubert *et al.* 2018; Riva & Nielsen 2021), but are also disproportionately likely to suffer from habitat loss (Riva *et al.* 2022). Our results suggest that we can halt global biodiversity losses by protecting these small patches and by restoring sufficient habitat to reach total area goals (Damiens *et al.* 2021; Fischer *et al.* 2021).

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