



On the emergence of ecosystem decay: A critical assessment of patch area effects across spatial scales

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ABSTRACT

Recent analyses suggest that positive patch area effects on biodiversity occur ubiquitously when comparing equal-effort samples from remnant habitat patches. The mechanisms underlying the emergence of this so-called “ecosystem decay” remain poorly understood despite conservation relevance. We leverage spatially-explicit information on the occurrence of plant species across the Swiss Alps (415 plots, 668 species) to test two mechanisms compatible with the emergence of patch-scale ecosystem decay: (i) plots sampled within small patches might have lower biodiversity than plots sampled within large patches (plot-scale decay hypothesis), and (ii) plots sampled within large patches might share a lower proportion of species (turnover hypothesis). We found that patch-scale ecosystem decay occurs also in our system. While plots sampled in large patches tended to be more dissimilar, supporting the turnover hypothesis, we did not find support for the plot-scale decay hypothesis. Additionally, distance between plots and elevational changes explain turnover between plots better than patch area effects. Taken together, these results indicate that applications of ecosystem decay in biodiversity conservation require a better understanding of the mechanisms that potentially underlie this pattern. Patch area effects might be less important than previously assumed when assessing landscape-scale biodiversity, because such effects can be confused with the effects of distance-decay in community similarity, environmental heterogeneity, and sampling effort. More broadly, our findings align with mounting evidence that protecting as much habitat as possible – regardless of whether such habitat exists continuous or fragmented – might be the most effective means to sustain biodiversity across human-dominated landscapes.

1. Introduction

Protecting biodiversity is a pressing challenge of our times. Some of the most threatened ecosystems on Earth are those that experience the largest anthropogenic footprints, particularly human activities that result in the loss of native habitat across large regions (Dirzo et al., 2014; Caro et al., 2022). Understanding how to sustain and manage biodiversity in these regions has, therefore, emerged as a central theme in ecology and conservation (Kremen and Merenlender, 2018; Arroyo-Rodríguez et al., 2020). In this context, ecosystem decay – positive effects of patch area on biodiversity estimates based on equal or standardized samples – was recently proposed as a general phenomenon occurring in remnant habitat patches (Chase et al., 2020) (Fig. 1-a).

The idea of ecosystem decay resonated with the scientific community (Fig. S1), likely because it relates with a tradition of island biogeography

(Laurance, 2009) and with popular views on habitat fragmentation (Haddad et al., 2015). The rapid diffusion of ecosystem decay in academic circles suggests that managers and policy makers will consider it when acting to protect biodiversity [e.g., to improve forecasts of biodiversity loss with habitat loss; (Chase et al., 2020)]. Still, confusion around ecosystem decay appears widespread. Around 40 % of authors citing Chase et al. (2020) relate it to landscape-scale biodiversity patterns, extrapolating effects observed within individual patches to infer effects across landscapes containing the same cumulative area, but made up of patches of different sizes (Riva and Fahrig, 2023). This extrapolation clashes with empirical evidence accumulated in the SLOSS avenue of research [“is biodiversity higher in a Single Large patch, Or in Several Small patches of the same cumulative area?” (Fahrig et al., 2022)]. Studies that evaluated hundreds of metacommunities have shown that, often, cumulative species richness at the landscape scale is higher when

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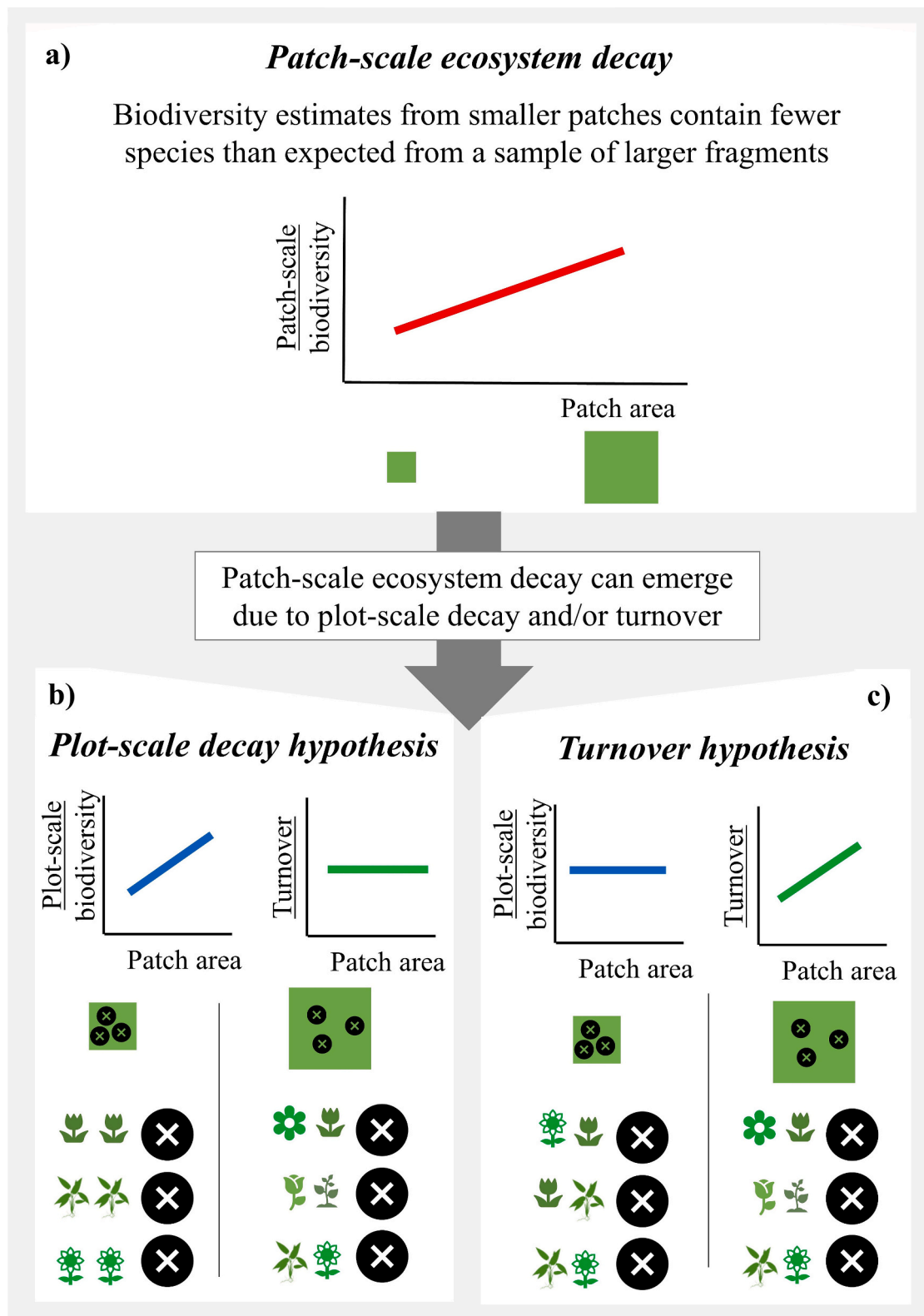


Fig. 1. Hypothesized relationships between the emergence of patch-scale ecosystem decay, i.e., positive patch area effects on biodiversity estimates from standardized patch-scale samples (top half, inset a), and plot-scale biodiversity patterns (bottom half). Black circles with crosses symbolize plots, different plant silhouettes represent different plant species sampled in different plots, and green squares illustrate the habitat patches in which the plots are sampled. In both examples at the bottom of the figure, biodiversity estimates for the small patch are equal to three species vs. six species estimated in the large patch, a pattern consistent with patch-scale ecosystem decay. Nevertheless, the mechanisms resulting in this pattern differ. Patch-scale ecosystem decay could occur because plots within small patches have lower biodiversity than plots within large patches (“Plot-scale decay hypothesis”, inset b), or because turnover across plots might be higher when considering large patches (“Turnover hypothesis”, inset c). Colors of regression lines (i.e., blue, red, green) correspond to results presented in Figs. 3 and 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

considering habitat existing fragmented into many small patches rather than continuous (Quinn and Harrison, 1988; Fahrig, 2020; Deane et al., 2020). Indeed, such a pattern was confirmed when re-analyzing the datasets used to illustrate ecosystem decay (Riva and Fahrig, 2023).

Understanding the mechanisms underlying the emergence of ecosystem decay will therefore be important to dispel confusion and to ensure appropriate applications in conservation. Finding more species in equal samples taken in large patches than in small patches (Chase et al., 2020) (Fig. 1-a), and finding more species when habitat in a landscape persists in large numbers of small patches than in a small number of large patches totaling the same area (Fahrig, 2020), are not mutually exclusive results because different mechanisms affect biodiversity at different spatial scales (Fahrig et al., 2019; Riva and Fahrig, 2023). Many ecological patterns are scale-dependent (Preston, 1960, O'Neill, 1979, Wiens, 1989, Levin, 1992), and while some ecological phenomena can be predicted across spatial scales (Miller et al., 2004; Marquet et al., 2005), scale invariance cannot be assumed due to the complexity of ecological systems (Guisan and Rahbek, 2011, Newman et al., 2019, McGill, 2019, Riva et al., 2023b, Fahrig, 2024). Together with these considerations around spatial scaling, the fact that we do not know why ecosystem decay emerges confuses the management implications of this phenomenon for biodiversity conservation.

One limitation of previous data syntheses that evaluated ecosystem decay is that they are based on spatially-implicit datasets (Chase et al., 2020; Riva and Fahrig, 2023). Therefore, we do not know how spatial processes contribute to the emergence of ecosystem decay. However, distance-decay in similarity is ubiquitous when assessing ecological communities (Graco-Roza et al., 2022), and might contribute to ecosystem decay because large patches occupy a larger extent than small patches. Furthermore, it is also possible that comparing one small patch to one large patch might result in differences in habitat heterogeneity, which are typically an important driver of biodiversity (Stein et al., 2014; Yan et al., 2023). Stochastic and deterministic turnover between ecological communities depend on many processes related to patch area (see, e.g., Preston, 1960, MacArthur and Wilson, 1967, Chave et al., 2002, Fahrig et al., 2022), but turnover within fragments has not been investigated as a mechanism influencing ecosystem decay.

Addressing this knowledge gap is important because whether ecosystem decay emerges due to patch area effects, or due to other processes like distance decay in community similarity and habitat heterogeneity that generate within-patch turnover, has important management consequences. If the attribution of ecosystem decay to patch

area effects – for instance, to demographic processes triggered by smaller population sizes (e.g., Allee effect) or negative edge effects – is artefactual, then prioritizing biodiversity conservation in large patches might not always be optimal. When distance decay in community similarity and environmental heterogeneity generate clustered distributions of species, protecting a greater number of smaller patches might better capture biodiversity than protecting a few large ones of the same cumulative area (May et al., 2019; Fahrig et al., 2022; Riva and Fahrig, 2022). Ultimately, understanding ecosystem decay is important to many ongoing conversations in conservation biology such as land sharing and sparing, habitat fragmentation per se, and more broadly to how habitat remnants should be managed, restored, and protected (Kremen and Merenlender, 2018; Grass et al., 2019; Arroyo-Rodríguez et al., 2020; Fahrig et al., 2022; Fletcher et al., 2023; Riva et al., 2024).

Here, we analyze an extensive dataset including 668 plant species from 415 vegetation plots located in the Swiss Alps (Fig. 2) to test candidate mechanisms determining the emergence of ecosystem decay (Fig. 1). We investigate how biodiversity changes in relation to patch area at both the plot-scale, focusing on biodiversity measured in individual vegetation plots (Fig. 1-b,c), and patch-scale, measured based on equal-effort estimates summarized at the patch level by combining multiple plots (i.e., resampling an equal number of plots in each patch) (Fig. 1-a). We hypothesized that two non-exclusive mechanisms might underlie the emergence of patch-scale ecosystem decay sensu (Chase et al., 2020): (i) plot-scale ecosystem decay, i.e., a propensity of vegetation plots located within small patches to contain a smaller number of species than plots located within larger patches (Fig. 1-b), and (ii) turnover, i.e., a propensity of plots located within a larger habitat patch to be more dissimilar than plots located within a smaller patch of habitat (Fig. 1-c). The effects of patch area on species richness might therefore change in direction across spatial scales (see, e.g., Riva and Fahrig, 2023, Fahrig, 2024).

Patch area effects have been assessed in a variety of ecosystems, finding widespread positive effects of the occupancy and diversity of animal and plant species within patches (see, e.g., Prugh et al., 2008, Keinath et al., 2017, Deane et al., 2024 for data syntheses based on hundreds of studies). These include grassland patches across different biomes, for which positive patch area effects have been widely documented (e.g., Bruun, 2000; Loos et al., 2021; Yan et al., 2023). To our knowledge, nevertheless, variation in patch size effects between the plot- and patch- scales, particularly in the context of understanding ecosystem decay, (Fig. 1) has not been previously studied.

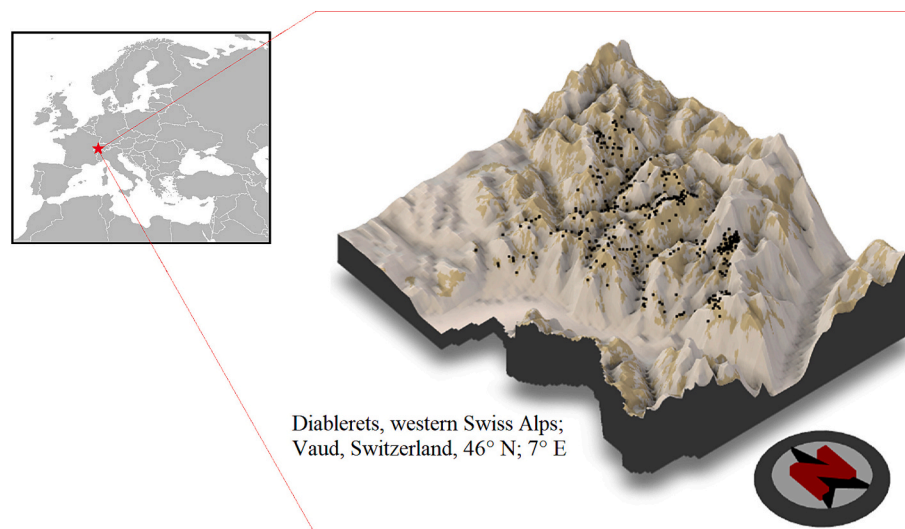


Fig. 2. Map of the study region. Black dots represent 415 vegetation plots sampled within the ~ 700 km² area. Brown shades represent the grassland habitat identified in the region. See Methods for details on the study area and sampling protocol. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Methods

2.1. Overview

We propose a series of analyses designed to assess the mechanisms underlying ecosystem decay (sensu Chase et al., 2020; Fig. 1-a). Such analyses were conducted using software R v. 4.3.0 (R Core Team, 2023) and the packages *raster* (Hijmans and van Etten, 2012) and *landscapemetrics* (Hesselbarth et al., 2019) to perform geospatial operations, *vegan* to calculate biodiversity metrics (Oksanen et al., 2022), *brms* to fit Bayesian mixed effect models (Bürkner, 2017), and *ggplot2* (Wickham, 2011) to visualize results. Data and script used to generate results are openly available (<https://zenodo.org/doi/10.5281/zenodo.11190403>).

2.2. Biodiversity and geospatial data

We leverage a unique dataset counting 415, 4-m² vegetation plots sampled across 56 grassland patches in an agropastoral landscape in the Swiss Alps. This dataset documents the occurrence of 668 plant species. Data are openly available with the original publication and were collected between 2002 and 2009 across an area of approximately 700 km² encompassing all areas of the Alps of the canton of Vaud, Switzerland (Fig. 2) (Dubuis et al., 2011). The original data counts 912 vegetation plots and 795 species sampled based on a random-stratified sampling design in open environments, e.g., grasslands, scree, or rocks. Sampling targeted only vascular plant species in open and non-woody vegetation, with species identifications conducted by botanists. To minimize spatial autocorrelation, each plot was located at least 200 m from other plots. Samples were collected at elevations between 375 and 3200 m. The area harbors primarily calcareous soils and is in a temperate climate. Temperature and precipitation range between 8 °C and 1200 mm at an elevation of 600 m, and between -5 °C and 2600 mm at an elevation of 3000 m (Dubuis et al., 2011). Here, we focus only on vegetation plots located in grassland patches, identified based on geospatial data, because these habitats harbor the highest diversity of plant species in the region (~ 84 % of the species assessed in Dubuis et al., 2011).

The dataset compiled by Dubuis et al. (2011) does not include the size of habitat patches containing each vegetation plot, which was needed to test our hypotheses (Fig. 1). To generate this information, we created a map of grassland habitats across the study areas based on the Corine land cover dataset for the year 2012 (available at <https://land.copernicus.eu/pan-european/corine-land-cover>). We considered as grassland habitat the categories “natural grasslands”, “pastures”, and “moors and heathland”, and classified the rest of the land cover categories as “non-habitat”. We acknowledge that our definition of habitat underlies our conclusions, although this is true for any study that defines habitat patches (Fahrig, 2017). For instance, in the Swiss Alps, pastures might slightly differ from natural grasslands in habitat quality. Nevertheless, we believe that our categorization is meaningful because low-intensity pastures are biodiversity hotspots in Switzerland, and our study area is in a region with a history of very low land use intensity (Weber et al., 2023). Additionally, the classification accuracy of Corine land cover data discriminates poorly among the classes that we here considered “habitat” (Aune-Lundberg and Strand, 2021). Last, sub-setting the data would not allow testing patch-scale ecosystem decay due to the limited number of patches containing multiple plots in our dataset (see below for inclusion criteria in the patch-scale analyses). Therefore, we aggregated natural and semi-natural grassland cover types in our analysis.

Using this binary habitat map, we filtered out every plot that did not occur within grasslands and calculated the size of the grassland patches within which each remaining plot fell. We used a digital elevation model downloaded through the R package *raster* with the function `getData()` to extract the elevation at which every plot was sampled. Elevation was included in our models because it is the most important environmental

gradient occurring in this system (Dubuis et al., 2011; Descombes et al., 2017).

2.3. Analysis

Our analyses are designed to evaluate biodiversity patterns at two scales: (i) plot-scale, i.e., analyses *contrasting patterns among individual plots* (Fig. 1-b,c), and (ii) patch-scale, i.e., analyses *comparing multiple plots sampled within the same patch* among patches (Fig. 1-a). We used as a measure of biodiversity the species richness, total number of species found in a plot or in a patch, and as a measure of turnover the Jaccard dissimilarity, an index representing the proportion of species shared between two assemblages. Jaccard dissimilarity ranges between 0 and 1, where 1 represents samples with completely different species assemblages, and 0 represents equal assemblages (Anderson et al., 2011). While Chase et al. (2020) discussed ecosystem decay assessing trends in population density, species richness, and evenness, here we limit ourselves to species richness due to the type of spatial data we had access to (i.e., species occurrence data). We also did not apply the turnover decomposition method used in Chase et al. (2020) and Riva and Fahrig (2023), because this approach can produce counterintuitive results (Matthews et al., 2019). Patch area was log₁₀ transformed in our analyses for consistency with previous assessments of ecosystem decay (Chase et al., 2020; Riva and Fahrig, 2023).

All models were fitted in a Bayesian framework. We used Generalized Linear Mixed-effect Models (GLMMs), a statistical framework that allows estimating the effect of variables of interest (fixed effects) while controlling for dependency structures in the data (random effects) (Harrison et al., 2018). For instance, our fixed effect was typically the effect of patch size on species richness at both plot and patch scales, estimated accounting for a “patch ID” random effect when comparing plots sampled across different patches, because all plots sampled from the same patch should be expected to be more similar to each other. Contrary to traditional statistical inference, which relies on *p*-values, here we do not focus on statistical significance of parameter effects, but rather report posterior parameter estimates and their 95 % Credible Intervals (CIs) to assess support for our a priori hypotheses (Fig. 1). Such support can be evaluated based on the direction of effects identified by the models, and the strength of the observed relationships was assessed based on the overlap of posterior distributions with the Region Of Practical Equivalence (ROPE), estimated as the proportion of samples within the ROPE (*p* ROPE; Kruschke, 2014). Strong effects have a low proportion of posterior estimates inside the ROPE. Sample sizes, parameter coefficients, and formulae are reported for all the models we discuss in Supplementary Information. Uncertainty around model estimates is shown in our figures by plotting posterior estimates of the relationship around the mean prediction.

We began by asking whether plot-scale biodiversity patterns are positively correlated with the area of the habitat patch containing each plot, testing the “plot-scale decay hypothesis” (Fig. 1-b). We fitted a mixed-effect linear model assuming a Gaussian distribution to predict our response, species richness of plants in the 415 plots, in relation to the additive and interactive effects of the area of the patch in which each plot is located, and of its elevation. We included a “patch ID” random effect to account for the non-independence of plots located within the same patch (Harrison et al., 2018).

Second, we evaluated patch-scale biodiversity patterns, testing (i) the “patch-scale decay hypothesis” (Fig. 1-a), and (ii) the “turnover hypothesis” (Fig. 1-c). For (i), we constructed for every patch with at least seven plots (*n* = 10 patches) a hundred, randomized resamples of five plots. Treating the information contained in these plots as a single, patch-scale biodiversity estimate is equivalent to the information analyzed in Chase et al. (2020), where many datasets synthesized contain a single vector of species-by-site abundance estimates generated from multiple samples across each patch. Sensitivity analysis models where five or ten plots were selected instead of seven plots affected the

number of patches retained ($n = 11$ and 6 patches respectively) and the magnitude – but not the direction – of the effects we observed (Supplementary Information). Using these resampled datasets, we fitted a model assessing how patch area relates to the cumulative number of species found in the five plots within a patch, assuming a Gaussian distribution of the model response. For (ii), we assessed turnover within patches by modeling the Jaccard dissimilarity across two plots randomly selected in every patch containing at least three plots ($n = 21$ patches). This model was fitted assuming a Beta distribution of the response. Both response variables were modeled as a function of patch area and including two independent random effects on “patch ID” and “resample number”, the latter representing one-hundred randomizations.

Finally, we evaluated how dissimilarity between plots across the entire study area (Fig. 2) responded to spatial and environmental gradients. We randomly generated 5,000 unique pairs from the 415 vegetation plots, and calculated their Jaccard dissimilarity, the Euclidean distance between the two plots (based on projected coordinates and elevation), the difference in the elevation at which the plots were located, and the difference in size between the two patches hosting the plots. We modeled assuming a Beta distribution of our response the turnover between plots as a function of the additive and interactive effects of Euclidean distance between plots and their difference in elevation, plus an additive effect of the difference in patch area between the two plots. We scaled (i.e., subtracted the mean and divided by the standard deviation) these three covariates to facilitate model fitting and comparison of estimated coefficients, and included in the model a random effect to account for randomized pairs of plots generated from the same patch. We fitted this model reasoning that, elevation being a major environmental gradient determining species turnover in Alpine grasslands (Dubuis et al., 2011; Descombes et al., 2017), evaluating spatial effects required accounting for both spatial distance and environmental similarity between plots, here approximated by differences in elevation, as well as patch area effects that are accounted for by the term representing differences in size between the patches hosting two plots. Because p ROPE is sensitive to covariate scaling (Kruschke, 2014), we do

not discuss it for this last model. Resampling was conducted without replacement in all analyses.

3. Results

Our analysis is based on 415 vegetation plots located at elevations between 600 and 2300 m MSL (Fig. S2). The 56 grassland patches hosting these plots vary in area from ~ 15 to $\sim 15,000$ ha, with most patches in the 30–300 ha range (Fig. S4). On average, plots hosted 32.4 species, with a standard deviation of 12.4 species.

We found no support for the plot-scale decay hypothesis (Fig. 1-b). The species richness found in a plot decreased slightly with the size of the patch in which the plot was located (Fig. 3, left inset in blue; $\beta_{\text{area}} = -2.33$, CI = $-8.91, 3.86$). Not only this model suggests limited support for an effect of patch size (p ROPE = 0.24), but the direction of effect observed is contrary to the hypothesized one (Fig. 1-b). The effect of patch area on plot-scale species richness was not mediated by elevation ($\beta_{\text{area} \cdot \text{elev}} = 0$, CI = $-0.01, 0.01$, p ROPE = 0.99), and plots located at higher elevations had slightly lower species richness than plots located at lower elevations, with a decrease of ~ 5 species for every 1000 m MSL ($\beta_{\text{elev}} = -0.01$, CI = $-0.02, 0.01$, p ROPE = 0.99) (Fig. S4).

Meanwhile, assessing patch-scale biodiversity estimates found support for the emergence of patch-scale ecosystem decay in our system (Fig. 1-a). Modeling a hundred random resamples of five plots in ten patches found that equal-effort, patch-scale species richness estimates increased with patch area (Fig. 3, right inset in red; $\beta_{\text{area}} = 13.90$, CI = $-1.67, 29.86$). The model identified a clear effect of patch size on patch-scale species richness estimates (p ROPE = 0.04).

Concurrently, analysis of twenty-one patches containing at least three plots suggests that this pattern is the result of turnover among plots increasing with patch area (Fig. 4; $\beta_{\text{area}} = 0.63$, CI = $0.27, 0.87$, p ROPE = 0.01).

Finally, analysis of pairwise dissimilarity between randomly-paired plots across the entire study area found that distance between plots and changes in elevation are more important than differences in patch

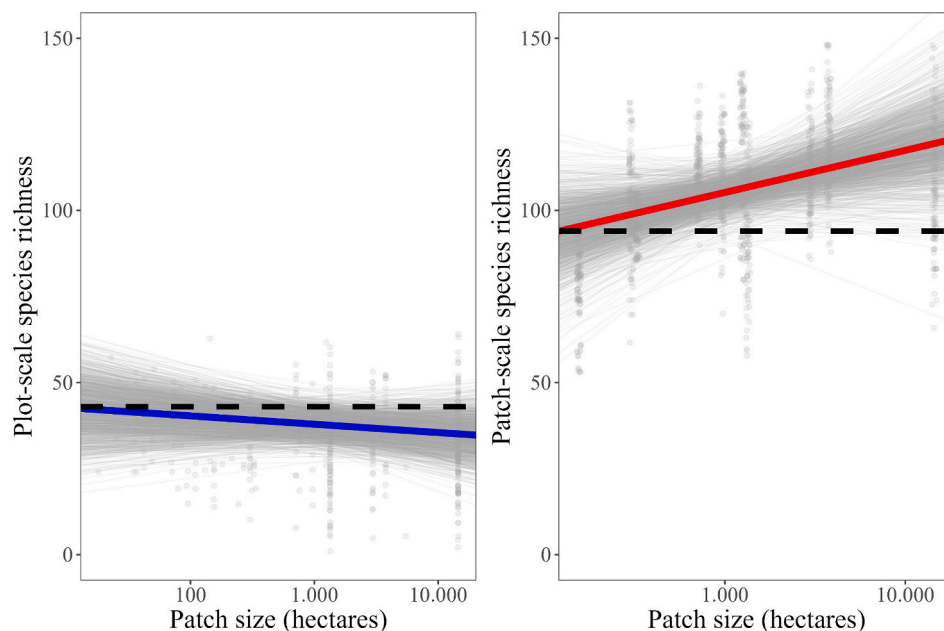


Fig. 3. Relationship between patch area and equal-effort biodiversity estimates at the plot scale (left, in blue) and at the patch scale (right, in red). Plot-scale biodiversity was measured as the number of species found in each of the 415 vegetation plots located within 56 different grassland patches, and patch-scale biodiversity estimates are based on five vegetation plots resampled a hundred times in ten grassland patches (see Methods). The positive relationship between patch-scale species richness estimates and patch area confirmed the emergence of patch-scale ecosystem decay in our system, whereas the weak negative relationship between plot-scale species richness and patch area suggests that patch-scale ecosystem decay did not emerge from plot-scale decay (see Fig. 1-b). These results suggest support for the patch-scale ecosystem decay hypothesis (Fig. 1-a), and no support for the plot-scale ecosystem decay hypothesis (Fig. 1-b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

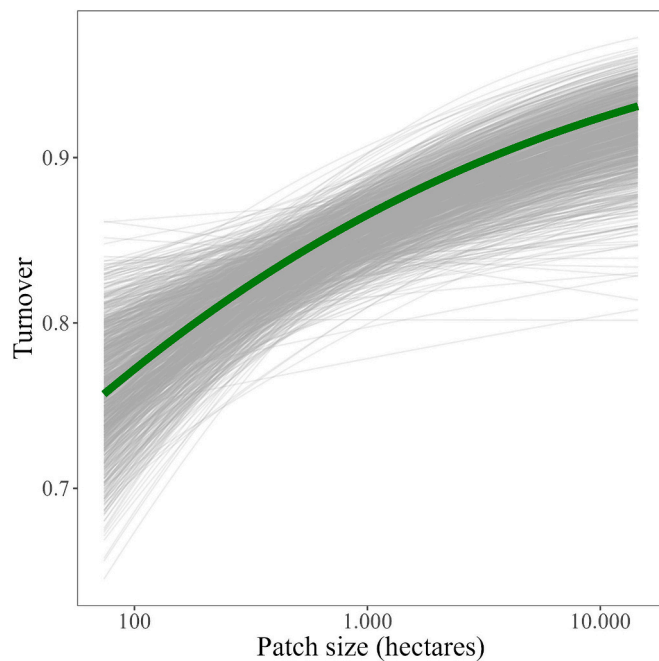


Fig. 4. Predicted turnover (Jaccard dissimilarity) between two vegetation plots resampled a hundred times within twenty-one grassland patches, as a function of the size of such patches (see Methods). As the size of a patch increases, the plots resampled within it tend to be more dissimilar. This result suggests support for the Turnover hypothesis (Fig. 1-c).

area in determining pairwise plot similarity (Fig. 5). Turnover between plots increased as the plots were more distant in space ($\beta_{\text{dist}} = 0.08$, CI = 0.04, 0.11), were located at increasingly different elevations ($\beta_{\text{diff_elev}} = 0.22$, CI = 0.20, 0.24), and did not change when plots were located in patches of increasingly different sizes ($\beta_{\text{diff_area}} = 0.01$, CI = -0.05,

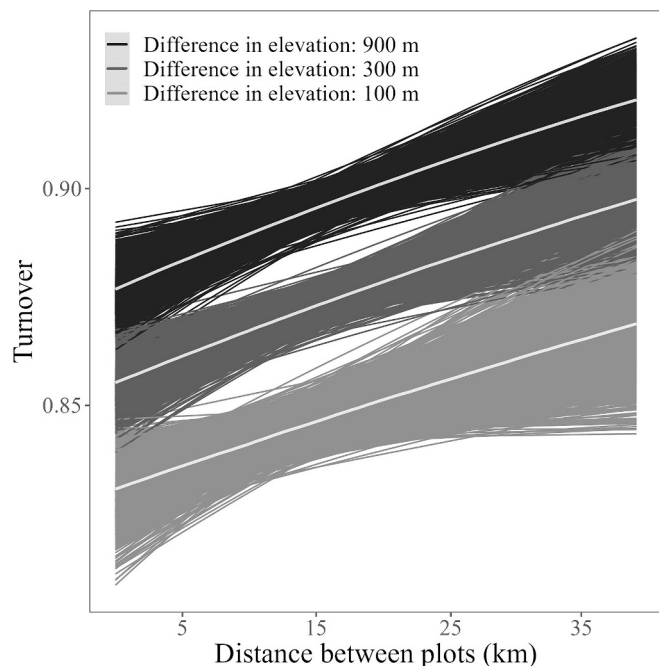


Fig. 5. Predicted pairwise turnover (Jaccard dissimilarity) between 5,000 randomized plot pairs, generated from the 415 plots analyzed in this study. Turnover between plots increases when the two plots are more distant in space and when the difference in elevation between the two plots is higher, but not when plots come from patches of different sizes.

0.07). The effect of distance between plots was weakly mediated by the difference in elevation across the two plots ($\beta_{\text{dist*diff_elev}} = 0.02$, CI = 0, 0.04).

4. Discussion

Our results suggest that ecosystem decay can emerge due to increasing turnover across plots located in larger patches (Figs. 1, 3, 4). In our system, such turnover depends primarily on distance-decay in community similarity and on environmental heterogeneity (Fig. 5). Therefore, while ecosystem decay has been predominantly conceptualized as the result of deterministic patch area effects, expected to negatively affect the demography of populations persisting within small patches (Chase et al., 2020; Riva and Fahrig, 2023), our analysis shows that mechanisms like within-patch heterogeneity (Stein et al., 2014) and distance between plots (Graco-Roza et al., 2022) could be responsible for this phenomenon. We stress that these results are compatible with the species-area relationship (Matthews et al., 2019), because ecosystem decay is evaluated for samples equal in effort (i.e., of the same total area).

Because ecosystem decay can emerge due to spatial processes and within-patch environmental heterogeneity, which are independent from patch-area effects on demography (Figs. 3–5), it is not possible to conclude how often patch area effects alone determine ecosystem decay without accounting for such processes. Meanwhile, what determines ecosystem decay has important implications for biodiversity conservation in fragmented landscapes. If patch area effects dictate ecosystem decay in most ecosystems, then managers interested in protecting biodiversity should prioritize protecting the largest remaining patches in a landscape. Conversely, when spatial processes and/or environmental heterogeneity dictate ecosystem decay (Fig. 1-a), then patch density should be given priority, because retaining more patches across a landscape will typically cover a larger spatial extent, and often more diverse habitats (Fahrig et al., 2022). Note this is true even if each of many smaller patches suffers from inevitable negative effects of reduced area, because turnover across such patches balances these effects when considering cumulative (gamma) diversity across landscapes (Riva and Fahrig, 2023).

Focusing on the plot scale, we found that plant biodiversity within plots decreased slightly with grassland patch area (Fig. 3, left inset). This is contrary to the hypothesis that patch-scale ecosystem decay emerges because plots located in small patches have lower biodiversity (Fig. 1-b). While the support for this negative effect is weak, it is possible that plots located in small grassland patches might be slightly more diverse because they are surrounded by different habitat types, e.g., due to edge effects promoting the occurrence of ecotonal species (Willmer et al., 2022; Ren et al., 2023; Vanneste et al., 2024). It is also possible that the grasslands we evaluated are not “functionally small”, hiding minimum patch area effects. For instance, while our smallest patches were approximately 15 ha in size, a recent paper found a 5-ha area as a tipping point in the relationship between plant biodiversity and patch area in Chinese agro-pastoral landscapes (Yan et al., 2023). We also do not know if the amount of remnant grasslands in the study area was sufficient for the most sensitive plant species in the regional species pool to persist in these patches (Riva et al., 2023a, 2023b). Definitive statements on the mechanisms underlying the patterns we observed would require further analyses based on the identity and traits of the 668 plant species analyzed, which is beyond the objectives of this study.

Analysis of the same data aggregated at the patch-scale found support for ecosystem decay (Fig. 3, right inset). Three parallel lines of evidence suggest that ecosystem decay emerges because of species turnover in our system: (i) increasing Jaccard dissimilarity among plots within larger patches (Fig. 4); (ii) no relationship between plot-scale biodiversity estimates and patch area (Fig. 3, left inset); and (iii) pairwise turnover across all the plots in our dataset responding primarily to differences in elevation and distance between plots (Fig. 5). Because

most datasets analyzed so far when assessing ecosystem decay were summarize at the patch-scale, with no information on the spatial distribution of the plots underlying such data and/or on habitat heterogeneity within patches, we cannot exclude that previous results – both at the patch-scale (Chase et al., 2020) and at the landscape-scale (Riva and Fahrig, 2023) – were also affected by spatial processes and environmental heterogeneity. If anything, this seems likely given the universality of these processes (Stein et al., 2014; Graco-Roza et al., 2022). Therefore, we suggest that further tests of ecosystem decay are needed to ensure that the mechanisms underlying this pattern, and how they change in different systems, are better understood. Our analysis provides a framework to develop such tests.

Our results imply that managers aiming to protect species richness within a landscape must consider, in addition to total habitat area in a landscape, both geographical and ecological coverage of habitat within that landscape (May et al., 2019; Fahrig et al., 2022; Simberloff and Abele, 1976). In systems like the Alpine grasslands studied here, maximizing spatial coverage by managing many patches across space and a gradient of elevations – even if such patches are comparatively small – might be the best strategy to maintain the largest number of species. Our result should be interpreted keeping in mind that we do not have information on grassland patches smaller than 15 ha, and therefore our recommendation should not be extrapolated to patches smaller than this area. Additionally, systematic conservation planning could provide more accurate directions for managing systems in which the distribution of species is well known. And finally, contrary to previous tests of ecosystem decay, we did not assess how the abundance of species changes from plots to patches; it is possible that patterns in abundance might “scale-up” differently or respond differently than patterns in species richness to the environmental gradients assessed in this study. Whether patterns in abundance differ from patterns in species richness when assessing patch area effects at different spatial scales (e.g., plots vs. patches vs. landscapes) remains unknown and appears to be an interesting research direction for future studies.

All in all, for many landscapes worldwide in which biodiversity data remains scarce (Hortal et al., 2015) and habitat loss has already occurred, our results suggest that maximizing the number of patches protected, while pursuing the highest possible cumulative area of native habitat maintained, would sustain the largest number of species. This strategy should be complemented by plans to sustain and maintain habitat for species that respond negatively to habitat fragmentation per se (i.e., effects of habitat configuration independent from the effects of habitat area; Riva et al., 2024) by sustaining a few larger patches (Arroyo-Rodríguez et al., 2020), although such species appear to be relatively uncommon (Fahrig, 2017).

5. Conclusions

Our study should alert managers and policy makers that, based on evidence of ecosystem decay, plan to always prioritize large habitat remnants in area-based conservation efforts. Because it has been assumed that ecosystem decay originates from patch area effects, this phenomenon has been received as evidence that it is more desirable to invest in protecting native habitat existing in large, continuous patches when attempting to maintain biodiversity (Riva and Fahrig, 2023). This follows an intuitive and long-standing view in biodiversity conservation (Diamond, 1975; Laurance, 2009). Nevertheless, such view has been challenged on theoretical and empirical grounds (Simberloff and Abele, 1976; Quinn and Harrison, 1988; Fahrig, 2020). When habitat area is controlled for, biodiversity tends to respond weakly to habitat fragmentation per se – the property of a given habitat area to exist as broken into many small patches instead of as a continuous large patch (Fahrig, 2017; Riva and Fahrig, 2022; Riva et al., 2024) – and recent work suggests that fragmented habitat has value also for species of conservation concern (Fahrig, 2020; Riva and Fahrig, 2023). Further emphasizing protection of large remnants implies the risk of neglecting unique

assemblages persisting in small patches that remain in the landscapes we experience and live in. While small patches can host unique species, they are rapidly disappearing globally (Birch et al., 2022; Riva et al., 2022), degrading biodiversity (Riva and Fahrig, 2022). We therefore propose that maximizing the total area of native habitat available for species in a landscape, regardless of how such habitat exists in relation to patch area, can be an effective way to sustain biodiversity. This approach is also the only solution for biodiversity conservation in many human-dominated landscapes where large habitat tracts have long been lost (Riva et al., 2024).

Significance statement

We show that recent work demonstrating the relevance of ecosystem decay for biodiversity conservation [i.e., Chase et al., 2020 in *Nature*, Riva and Fahrig, 2023 in *Ecology Letters*] might artefactually attribute patch area effects to the effects of distance decay in similarity between communities and of within-patch habitat heterogeneity.

Declaration of generative AI in scientific writing

No AI tool used in this research.

Data archiving statement

The data analyzed and R script used to conduct the analysis are publicly available at <https://zenodo.org/doi/10.5281/zenodo.11190403>.

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Ethics approval statement, patient consent statement, permission to reproduce material from other sources, and clinical trial registration

Not applicable.

CRediT authorship contribution statement

Federico Riva: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Eléa Pierre:** Writing – review & editing, Software, Data curation, Conceptualization. **Antoine Guisan:** Writing – review & editing, Investigation.

Declaration of competing interest

None.

Data availability

Data used in analysis have been made available on a Zenodo, free and open repository (link in the Methods section).

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References

- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B.,

- Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist: roadmap for beta diversity. *Ecol. Lett.* 14 (1), 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchamol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Tschamtké, T., 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecol. Lett.* 23 (9), 1404–1420. <https://doi.org/10.1111/ele.13535> doi:10.1111/j.1600-0587.2000.tb00307.x.
- Aune-Lundberg, L., Strand, G.-H., 2021. The content and accuracy of the CORINE land cover dataset for Norway. *Int. J. Appl. Earth Obs. Geoinf.* 96, 102266 <https://doi.org/10.1016/j.jag.2020.102266>.
- Birch, W.S., Drescher, M., Pittman, J., Rooney, R.C., 2022. Trends and predictors of wetland conversion in urbanizing environments. *J. Environ. Manag.* 310, 114723 <https://doi.org/10.1016/j.jenvman.2022.114723>.
- Bruun, H.H., 2000. Patterns of species richness in dry grassland patches in an agricultural landscape. *Ecography* 23 (6), 641–650.
- Bürkner, P.-C., 2017. Brms: an R package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80 (1), 1–28. <https://doi.org/10.18637/jss.v080.i01>.
- Caro, T., Rowe, Z., Berger, J., Wholey, P., Dobson, A., 2022. An inconvenient misconception: climate change is not the principal driver of biodiversity loss. *Conserv. Lett.* 15 (3), e12868 <https://doi.org/10.1111/conl.12868>.
- Chase, J.M., Blowes, S.A., Knight, T.M., Gerstner, K., May, F., 2020. Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature* 584 (7820), 238–243. <https://doi.org/10.1038/s41586-020-2531-2>.
- Chave, J., Muller-Landau, H.C., Levin, S.A., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *Am. Nat.* 159 (1), 1–23. <https://doi.org/10.1086/324112>.
- Deane, D.C., Nozohourmehrad, P., Boyce, S.S.D., He, F., 2020. Quantifying factors for understanding why several small patches host more species than a single large patch. *Biol. Conserv.* 249, 108711 <https://doi.org/10.1016/j.biocon.2020.108711>.
- Deane, D.C., Hui, C., McGeoch, M., 2024. Mean landscape-scale incidence of species in discrete habitats is patch size dependent. *Glob. Ecol. Biogeogr., Early View* 1–14. <https://doi.org/10.1111/geb.13805>.
- Descombes, P., Vittoz, P., Guisan, A., Pellissier, L., 2017. Uneven rate of plant turnover along elevation in grasslands. *Alp. Bot.* 127 (1), 53–63. <https://doi.org/10.1007/s00035-016-0173-7>.
- Diamond, J.M., 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biol. Conserv.* 7 (2), 129–146. [https://doi.org/10.1016/0006-3207\(75\)90052-X](https://doi.org/10.1016/0006-3207(75)90052-X).
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345 (6195), 401–406. <https://doi.org/10.1126/science.1251817>.
- Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., Guisan, A., 2011. Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. *Divers. Distrib.* 17 (6), 1122–1131. <https://doi.org/10.1111/j.1472-4642.2011.00792.x>.
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. *Annu. Rev. Ecol. Evol. Syst.* 48 (1), 1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>.
- Fahrig, L., 2020. Why do several small patches hold more species than few large patches? *Glob. Ecol. Biogeogr.* 29 (4), 615–628. <https://doi.org/10.1111/geb.13059>.
- Fahrig, L., 2024. Patch-scale edge effects do not indicate landscape-scale fragmentation effects. *Conserv. Lett.* 17 (1), e12992 <https://doi.org/10.1111/conl.12992>.
- Fahrig, L., Arroyo-Rodríguez, V., Bennett, J.R., Boucher-Lalonde, V., Cazetta, E., Currie, D.J., Eigenbrod, F., Ford, A.T., Harrison, S.P., Jaeger, J.A.G., Koper, N., Martin, A.E., Martin, J.-L., Metzger, J.P., Morrison, P., Rhodes, J.R., Saunders, D.A., Simberloff, D., Smith, A.C., Watling, J.I., 2019. Is habitat fragmentation bad for biodiversity? *Biol. Conserv.* 230, 179–186. <https://doi.org/10.1016/j.biocon.2018.12.026>.
- Fahrig, L., Watling, J.I., Arnillas, C.A., Arroyo-Rodríguez, V., Jörgen-Hickfang, T., Müller, J., Pereira, H.M., Riva, F., Rösch, V., Seibold, S., Tschamtké, T., May, F., 2022. Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biol. Rev.* 97 (1), 99–114. <https://doi.org/10.1111/brv.12792>.
- Fletcher, R.J., Betts, M.G., Damschen, E.I., Hefley, T.J., Hightower, J., Smith, T.A.H., Fortin, M., Haddad, N.M., 2023. Addressing the problem of scale that emerges with habitat fragmentation. *Glob. Ecol. Biogeogr.* 32 (6), 828–841. <https://doi.org/10.1111/geb.13658>.
- Graco-Roza, C., Aarmio, S., Abrego, N., Acosta, A.T.R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Bastrup-Spohr, L., Barrera-Alba, J.J., Belmaker, J., Biurrun, I., Bonari, G., Bruehlheide, H., Burrascano, S., Carboni, M., Cardoso, P., Carvalho, J.C., Soinin, J., 2022. Distance decay 2.0 – a global synthesis of taxonomic and functional turnover in ecological communities. *Glob. Ecol. Biogeogr.* 31 (7), 1399–1421. <https://doi.org/10.1111/geb.13513>.
- Grass, L., Loos, J., Baensch, S., Batáry, P., Librán-Embidi, F., Ficiyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., Tschamtké, T., 2019. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People Nat.* 1 (2), 262–272. <https://doi.org/10.1002/pan3.21>.
- Guisan, A., Rahbek, C., 2011. SESAM - a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages: predicting spatio-temporal patterns of species assemblages. *J. Biogeogr.* 38 (8), 1433–1444. <https://doi.org/10.1111/j.1365-2699.2011.02550.x>.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on earth's ecosystems. *Sci. Adv.* 1 (2), e1500052 <https://doi.org/10.1126/sciadv.1500052>.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E. D., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ* 6, e4794. <https://doi.org/10.7717/peerj.4794>.
- Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K., Nowosad, J., 2019. Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42 (10), 1648–1657. <https://doi.org/10.1111/ecog.04617>.
- Hijmans, R., van Etten, J., 2012. Geographic analysis and modeling with raster data. *R Package Version* 2, 1–25.
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 46, 523–549. <https://doi.org/10.1146/annurev-ecolsys-112414-054400>.
- Keinath, D.A., Doak, D.F., Hodges, K.E., Prugh, L.R., Fagan, W., Sekercioglu, C.H., Buchart, S.H.M., Kauffman, M., 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. *Glob. Ecol. Biogeogr.* 26 (1), 115–127. <https://doi.org/10.1111/geb.12509>.
- Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. *Science* 362 (6412), eaau6020. <https://doi.org/10.1126/science.aau6020>.
- Kruschke, J.K., 2014. *Doing Bayesian Data Analysis: A Tutorial With R, JAGS, and Stan (Edition 2)*. Academic Press.
- Laurance, W.F., 2009. Beyond island biogeography theory. In: Losos, J.B., Ricklefs, R.E., MacArthur, R.H. (Eds.), *The Theory of Island Biogeography Revisited*. Princeton University Press, pp. 214–236.
- Levin, S.A., 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73 (6), 1943–1967. <https://doi.org/10.2307/1941447>.
- Loos, L., Krauss, J., Lyons, A., Föst, S., Ohlendörfer, C., Racky, S., Röder, M., Hudel, L., Herfert, V., Tschamtké, T., 2021. Local and landscape responses of biodiversity in calcareous grasslands. *Biodivers. Conserv.* 30, 2415–2432. <https://doi.org/10.1007/s10531-021-02201-y>.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press.
- Marquet, P.A., Quinones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M., Rivadeneira, M., 2005. Scaling and power-laws in ecological systems. *J. Exp. Biol.* 208 (9), 1749–1769. <https://doi.org/10.1242/jeb.01588>.
- Matthews, T.J., Aspin, T.W.H., Ulrich, W., Basela, A., Kubota, Y., Proios, K., Triantis, K. A., Whittaker, R.J., Strona, G., 2019. Can additive beta diversity be reliably partitioned into nestedness and turnover components? *Glob. Ecol. Biogeogr.* 28 (8), 1146–1154. <https://doi.org/10.1111/geb.12921>.
- May, F., Rosenbaum, B., Schurr, F.M., Chase, J.M., 2019. The geometry of habitat fragmentation: effects of species distribution patterns on extinction risk due to habitat conversion. *Ecol. Evol.* 9 (5), 2775–2790. <https://doi.org/10.1002/ece3.4951>.
- McGill, B.J., 2019. The what, how and why of doing macroecology. *Glob. Ecol. Biogeogr.* 28 (1), 6–17. <https://doi.org/10.1111/geb.12855>.
- Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L., Stanley, E.H., 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. *BioScience* 54 (4), 310–320. [https://doi.org/10.1641/0006-3568\(2004\)054\[0310.SETSOP\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0310.SETSOP]2.0.CO;2).
- Newman, E.A., Kennedy, M.C., Falk, D.A., McKenzie, D., 2019. Scaling and complexity in landscape ecology. *Front. Ecol. Evol.* 7, 293. <https://doi.org/10.3389/fevo.2019.00293>.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solyomos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M.D., Durand, S., Weedon, J., 2022. *vegan: Community Ecology Package (2.6-4)* [Computer software]. <https://cran.r-project.org/web/packages/vegan/index.html>.
- O'Neill, R.V., 1979. Transmutations across hierarchical levels. In: Innis, G.S., O'Neill, R. V. (Eds.), *Systems Analysis of Ecosystems*. International Cooperative Publishing House, pp. 58–78.
- Preston, F.W., 1960. Time and space and the variation of species. *Ecology* 41 (4), 611–627. <https://doi.org/10.2307/1931793>.
- Prugh, L.R., Hodges, K.E., Sinclair, A.R.E., Brashares, J.S., 2008. Effect of habitat area and isolation on fragmented animal populations. *Proc. Natl. Acad. Sci.* 105 (52), 20770–20775. <https://doi.org/10.1073/pnas.0806080105>.
- Quinn, J.F., Harrison, S.P., 1988. Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. *Oecologia* 75 (1), 132–140. <https://doi.org/10.1007/BF00378826>.
- R Core Team, 2023. *R: A Language and Environment for Statistical Computing* [Computer Software]. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Ren, P., Didham, R.K., Murphy, M.V., Zeng, D., Si, X., Ding, P., 2023. Forest edges increase pollinator network robustness to extinction with declining area. *Nat. Ecol. Evol.* 7, 393–404. <https://doi.org/10.1038/s41559-022-01973-y>.
- Riva, F., Fahrig, L., 2022. The disproportionately high value of small patches for biodiversity conservation. *Conserv. Lett.* 15 (3), e12881 <https://doi.org/10.1111/conl.12881>.
- Riva, F., Fahrig, L., 2023. Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. *Ecol. Lett.* 26 (2), 268–277. <https://doi.org/10.1111/ele.14145>.
- Riva, F., Martin, C.J., Millard, K., Fahrig, L., 2022. Loss of the world's smallest forests. *Glob. Chang. Biol.* 28 (24), 7164–7166. <https://doi.org/10.1111/geb.16449>.

- Riva, F., Barbero, F., Balletto, E., Bonelli, S., 2023a. Combining environmental niche models, multi-grain analyses, and species traits identifies pervasive effects of land use on butterfly biodiversity across Italy. *Glob. Chang. Biol.* 29 (7), 1715–1728. <https://doi.org/10.1111/gcb.16615>.
- Riva, F., Graco-Roza, C., Daskalova, G.N., Hudgins, E.J., Lewthwaite, J.M.M., Newman, E.A., Ryo, M., Mammola, S., 2023b. Toward a cohesive understanding of ecological complexity. *Sci. Adv.* 9 (25), eabq4207. <https://doi.org/10.1126/sciadv.abq4207>.
- Riva, F., Koper, N., Fahrig, L., 2024. Overcoming confusion and stigma in habitat fragmentation research. *Biol. Rev.*, Early View. <https://doi.org/10.1111/brv.13073>.
- Simberloff, D.S., Abele, L.G., 1976. Island biogeography theory and conservation practice. *Science* 191 (4224), 285–286. <https://doi.org/10.1126/science.191.4224.285>.
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol. Lett.* 17 (7), 866–880. <https://doi.org/10.1111/ele.12277>.
- Vanneste, T., Depauw, L., De Lombaerde, E., Meeussen, C., Govaert, S., De Pauw, K., Sanczuk, P., Bollmann, K., Brunet, J., Calders, K., Cousins, S.A.O., Diekmann, M., Gasperini, C., Graae, B.J., Hedwall, P.-O., Iacopetti, G., Lenoir, J., Lindmo, S., Orczewska, A., De Frenne, P., 2024. Trade-offs in biodiversity and ecosystem services between edges and interiors in European forests. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-024-02335-6>.
- Weber, D., Schwieder, M., Ritter, L., Koch, T., Psomas, A., Huber, N., Ginzler, C., Boch, S., 2023. Grassland-use intensity maps for Switzerland based on satellite time series: challenges and opportunities for ecological applications. *Remote Sens. Ecol. Conserv.*, Early View rse2.372. <https://doi.org/10.1002/rse2.372>.
- Wickham, H., 2011. ggplot2. *WIREs Comput. Stat.* 3 (2), 180–185. <https://doi.org/10.1002/wics.147>.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Funct. Ecol.* 3 (4), 385–397. <https://doi.org/10.2307/2389612>.
- Willmer, J.N.G., Püttker, T., Prevedello, J.A., 2022. Global impacts of edge effects on species richness. *Biol. Conserv.* 272, 109654 <https://doi.org/10.1016/j.biocon.2022.109654>.
- Yan, Y., Jarvie, S., Zhang, Q., Han, P., Liu, Q., Zhang, S., Liu, P., 2023. Habitat heterogeneity determines species richness on small habitat islands in a fragmented landscape. *J. Biogeogr.* 50 (5), 976–986. <https://doi.org/10.1111/jbi.14594>.