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ARTICLE

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Habitat loss and simplification lower arthropod richness but not diversity

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Abstract

Habitat loss is rarely truly random and often occurs selectively with respect to the plant species comprising the habitat. Such selective habitat removal that decreases plant species diversity, that is, habitat simplification or homogenization, may have two negative effects on other species. First, the reduction in plant community size (number of individuals) represents habitat loss for species at higher trophic levels who use plants as habitat. Second, when plants are removed selectively, the resulting habitat simplification decreases the diversity of resources available to species at higher trophic levels. It follows that habitat loss combined with simplification will reduce biodiversity more than habitat loss without simplification. To test this, we experimentally implemented two types of habitat loss at the plant community level and compared biodiversity of resident arthropods between habitat loss types. In the first type of habitat loss, we reduced habitats by 50% nonselectively, maintaining original relative abundance and diversity of plant species and therefore habitat and resource diversity for arthropods. In the second type of habitat loss, we reduced habitats by 50% selectively, removing all but one common plant species, dramatically simplifying habitat and resources for arthropods. We replicated this experiment across three common plant species: *Asclepias tuberosa*, *Solidago altissima*, and *Baptisia alba*. While habitat loss with simplification reduced arthropod species richness compared with habitat loss without simplification, neither type of habitat loss affected diversity, measured as effective number of species (ENS), or species evenness as compared with controls. Instead, differences in ENS and evenness were explained by the identity of the common plant species. Our results indicate that the quality of remaining habitat, in our case plant species identity, may be more important for multi-trophic diversity than habitat diversity per se.

KEYWORDS

biodiversity, biotic homogenization, effective number of species, habitat loss, habitat simplification, species evenness, species richness

INTRODUCTION

Biodiversity is declining globally (Barnosky et al., 2011; Butchart et al., 2010; Cardinale et al., 2012; Ceballos et al., 2015; Dirzo & Raven, 2003), in large part because of habitat loss (Brooks et al., 2002; Chase et al., 2020; Pimm et al., 2014; Yin et al., 2021). When addressing the effects of habitat loss on biodiversity decline, it is often implicitly or explicitly assumed that habitat is lost nonselectively with respect to organisms comprising the habitat (Bonin et al., 2011; Chaudhary et al., 2015; Keil et al., 2015; Ney-Nifle & Mangel, 2000). While this is sometimes true, habitat loss is often aggregated, resulting in habitats experiencing simultaneous area reduction and nonrandom loss of biodiversity (Seabloom et al., 2002; Thiollay, 1997). This nonrandom aggregation may also occur with respect to species comprising the habitat, that is, the primary producers at the base of the trophic pyramid. One example of such a situation is selective logging of forests in which some tree species are preferentially removed over others, leaving a less diverse plant community (Broadbent et al., 2008; Edwards & Laurance, 2013; Ernst et al., 2006; Thiollay, 1992). Another example is increased land use intensity, including grazing, mowing, and fertilization. In grasslands, these activities selectively affect rare or specialist flora, decreasing the relative abundance of those species and increasing the relative abundance of generalist species in the habitat (Chisté et al., 2018; Gossner et al., 2016). Given the primacy of habitat loss and modification as drivers of biodiversity loss, more explorations of how selective versus nonselective habitat loss affects biodiversity are likely to be critical to biodiversity conservation and management.

It is generally well understood that selective forms of disturbance lead to greater ecosystem-wide biodiversity loss than random disturbances (Almeida et al., 2021; García-Valdés et al., 2018; Smith et al., 2009). Niche theory and the diversity-begets-diversity principle underlie this phenomenon: loss of biodiversity at lower trophic levels is also loss of habitat diversity for organisms at higher trophic levels (Miao et al., 2021; Thiollay, 1997). According to the diversity-begets-diversity principle, which postulates that diverse resources and niches provided by taxonomic diversity stimulate evolution or the recruitment of additional diversity (Emerson & Kolm, 2005; Kerr & Packer, 1997; Tilman et al., 2014; Whittaker, 1972), a loss of lower trophic level diversity should result in a trophic cascade of biodiversity decline (Allan et al., 2014; Soliveres et al., 2016). Because plants provide multiple resources for species in higher trophic levels, plant communities are themselves habitat for the species that rely on plant structure, resource composition, and therefore diversity. For example, when host plant communities become dominated by one or a few similar species, the diversity of available arthropod niches is reduced, thus reducing arthropod diversity (Ebeling et al., 2020). We therefore expect disturbances that simplify habitat by decreasing both the amount of habitat and number of available niches within a habitat to affect the biodiversity of resident species occupying those niches more dramatically than disturbances that nonselectively decrease habitat.

In this experiment, we manipulated habitat amount (number of individual plants) and composition (plant identity) at the level of plant communities and assessed the concomitant effects of habitat loss and simplification on associated arthropod community biodiversity. Our goal was to determine how much more biodiversity loss should be expected when habitat loss is combined with habitat simplification, as compared to nonselective habitat loss alone. Our experimental study system reflects natural habitats in that the number, richness, and diversity of host plants determine habitat size and niche availability for organisms at higher trophic levels. The pattern of habitat quality and quantity being largely determined by producers has been observed and widely discussed in forest ecosystems (Larrieu et al., 2018; Patiño et al., 2018; Przepióra & Ciach, 2022). Examining how selective and nonselective habitat loss affects biodiversity in small, controlled habitats gives us insight into how selective forces versus nonselective forces may influence biodiversity in natural habitats of conservation concern, thus informing more effective predictions of biodiversity loss following habitat loss.

Our experimental habitats each contained one common and four rare plant species, reflecting the often-uneven abundance distributions of natural habitats (Preston, 1962). The three different common plant species we selected (*Asclepias tuberosa*, *Solidago altissima*, and *Baptisia alba*) each come from a different taxonomic family and vary in the types of arthropod communities they support. We implemented two different types of habitat loss and compared arthropod biodiversity between them. In the first type, we reduced the size of habitats by 50% nonselectively, while maintaining the original plant species richness and relative abundance patterns (hereafter, habitat loss). In the second type, we reduced habitats by 50% selectively, removing all but one plant species, dramatically reducing species richness and evenness of the habitat (hereafter, habitat simplification). Comparing these habitats to a control treatment, which experienced neither habitat loss nor simplification, allowed us to assess the effects of habitat loss with and without reduction of diversity on biodiversity decline.

METHODS

Habitat establishment

We constructed 45 experimental habitats in 1-m^2 fabric plant growth bags in a grid arrangement (Appendix S1: Figure S1) with ~5 m between bags in a fenced field within a larger forest-old field complex in the Davidson College Ecological Preserve in Davidson, NC. Each bag was filled with a commercial topsoil mixture and covered with a layer of bark mulch. In May and June 2018, we planted 16 individual plants in each bag. Eight of the 16 plants in each habitat were one of our designated common species, *B. alba*, *A. tuberosa*, or *S. altissima*. The remaining eight plants in each habitat were evenly split among four other species, each of which was represented twice within the habitat. These four rare species were systematically selected from a pool of six possible plant species such that each plant species was equally represented across replicates in the experiment: *Echinacea purpurea*, *Monarda fistulosa*, *Opuntia humifusa*, *B. alba*, *A. tuberosa*, or *S. altissima*. Thus, habitats had a rotating assemblage of five species, one of which comprised 50% of the plants in the habitat (Figure 1; Appendix S1: Table S2). All six plant species are native to the region and were chosen for their phylogenetic diversity (six families) and expected variation in arthropod assemblages. We collected *S. altissima* ramets from wild, local populations, and purchased all other species as seedlings from Prairie Moon Nursery (Winona, MN).

Maintenance

We weeded bags year-round and maintained the original number of individual plants as described above. To maintain the relative abundance distributions of the species in each habitat and to make visual arthropod sampling possible, we maintained stem numbers for each individual plant starting four weeks before sampling as follows: *S. altissima*: three stems; *B. alba*: two stems; *E. purpurea*: three stems; *M. fistulosa*: five stems; *A. tuberosa*: five stems. Given its different growth form, we did not maintain *O. humifusa* to a specific stem number, but rather to prevent encroachment on adjacent plants.

Experimental design and treatment implementation

To address our prediction that habitat simplification would lead to greater biodiversity loss than habitat loss, we implemented three treatments in the summer of 2019 ($n = 15$ habitats per treatment; Figure 1). We fully crossed the three treatments (control, 50% habitat loss, and 50% habitat loss with simplification) with the three common plant species (*B. alba*, *A. tuberosa*, or *S. altissima*), yielding nine individual treatment–common plant combinations. These nine combinations were replicated five times across different background plant communities, for a total of 45 experimental habitats (Appendix S1: Table S2). For the control treatment, we left habitats undisturbed, other

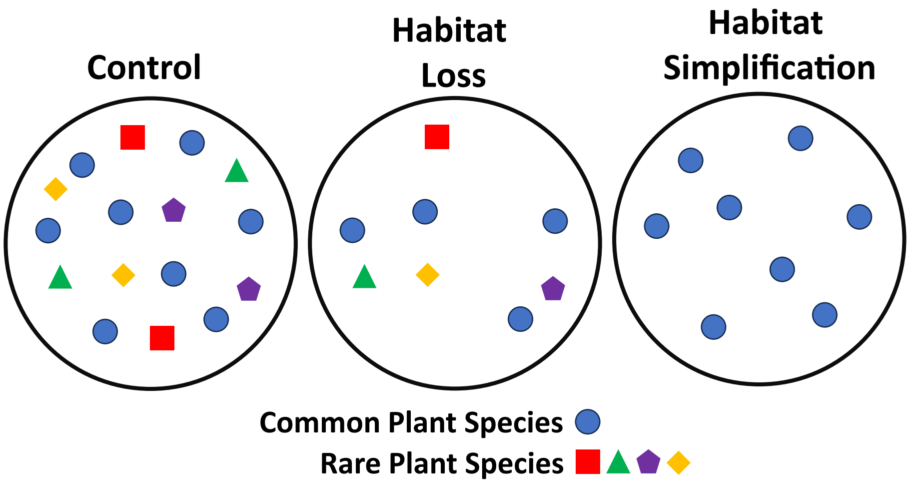

FIGURE 1 Schematic describing experimental treatments in this study. Large circles represent experimental habitats, ~1 m^2 in area. Colored shapes within each circle represent individual plants, with shape and color designating plant species as shown in the legend. Plant species richness and diversity were identical in the control and habitat loss treatments, but habitat simplification reduced plant species richness and diversity compared with the control treatment.

than maintenance of stem density as described above. For the habitat loss treatment, we randomly chose half the common species individuals and one individual of each rare plant species for removal from the habitat. By reducing only the amount of habitat, but not the plant species diversity, we simulated nonselective habitat loss. For the habitat simplification treatment, we removed all rare species plants, leaving only common species plants. Remaining plant community structure posttreatment is fully described in Appendix S1: Table S3. By reducing both the amount of habitat and the plant species diversity in the habitat, we simulated selective habitat loss and habitat simplification. In both habitat loss treatments, we removed 50% of the individual plants, and therefore ~50% of habitat area.

Sampling and arthropod classification

Because we were most interested in identifying the first pulse of changes to arthropod diversity directly caused by our treatments, and not by subsequent changes to the habitat following disturbance, we focused on biodiversity changes immediately following treatment implementation. Treatment implementation and subsequent sampling occurred in five blocks, each containing nine habitats with all possible common plant species–treatment combinations represented once in the block. We implemented treatments for each block two weeks prior to sampling that block. Sampling occurred from June 10, 2019 through July 3, 2019. We systematically and fully sampled each habitat in each block twice on two consecutive days, with the goals of nondestructively identifying all resident species and recording accurate relative abundance values for each species. The group of researchers sampling the habitats rotated on alternating days to ensure that each habitat was viewed by as many people as possible. This sampling method resulted in double-counting of experimental units by two groups of researchers on two different days. Although this approach resulted in double-counting of arthropods, this does not affect our measures of diversity or our analyses, which focus on relative rather than absolute arthropod abundance.

Our sampling was nondestructive; we conducted exhaustive visual surveys of macroinvertebrate abundance on each individual plant. We avoided double-counting within each observation period by systematically observing one stem at a time from bottom to top or top to bottom. We also avoided touching the plants during surveying to discourage arthropods from moving between plants during our observations. We observed plants systematically until every stem had been surveyed, and all visible arthropods had been counted. In addition to untimed exhaustive visual sampling, we conducted timed pollinator surveys (10 min per habitat) at midday for each habitat. We collected descriptive data and took photographs of species that could not be identified in the field. We categorized macroinvertebrates to either the lowest identifiable taxonomic unit or to morphospecies (hereafter "species") using field guides, BugGuide.net, identification keys, expert advice, and an existing reference collection. We provide a complete list of observed taxa (Appendix S1: Table S1). Species that could not be assigned to known taxa were given distinct morphospecies names that were paired with descriptions and photographs to allow for consistent identification (i.e., "Un_ID_Hemip1").

DATA ANALYSIS

Calculating arthropod diversity: Species richness, ENS, and evenness

The goal of our analysis was to determine how arthropod biodiversity was affected by different types of habitat loss. In our analysis, we focused on three biodiversity measures: arthropod species richness (i.e., number of taxa), diversity measured as effective number of species (ENS), and species evenness. We calculated ENS as the exponential of the Shannon–Weiner diversity index for arthropods in each habitat. ENS is the number of equally abundant arthropod species that would need to be in the habitat to yield the actual Shannon–Weiner diversity index of arthropods in the habitat. We calculated arthropod evenness as the Shannon–Weiner index for each habitat divided by the natural log of arthropod species richness for each habitat.

Statistical analysis

We used generalized linear mixed models to determine how habitat loss treatment and common plant species affected arthropod richness and diversity. In R version 4.1.1, using the lme4 package (Bates et al., 2015), we created four potential models for explaining the variation in arthropod diversity between habitats for each dependent variable: species richness (Appendix S1: Table S4), ENS (Appendix S1: Table S5), and species evenness (Appendix S1: Table S6). The full model for each dependent variable included treatment, common species, and their interaction as fixed effects, with sampling block as a random effect. The other three models respectively dropped the interaction, common species, and treatment terms. For the ENS models, we weighted variance for common species to account for heteroscedasticity of that variable using nlme::varIdent (Pinheiro et al., 2021), according to criteria outlined by Zuur et al. (2009). We calculated Akaike information criterion (AIC) for all models and selected models with the lowest AIC values as the best explanation of variation in the dependent variable. We then checked our selected models for normality of residuals and heteroscedasticity by plotting residuals versus fitted values, inspecting qqplots, and plotting residuals versus levels of each fixed effect. Once the best fit models for ENS and species richness had been identified, we assessed the relative effects of levels within important fixed effects using post hoc pairwise comparisons using the emmeans package (Lenth, 2021) (Appendix S1: Tables S7–S12).

RESULTS

Selective habitat loss reduces arthropod richness compared with nonselective habitat loss

Both habitat loss and habitat simplification reduced arthropod species richness compared with the undisturbed control habitats. Additionally, habitat simplification reduced arthropod species richness to a greater degree than habitat loss alone (Figure 2A). The differences in species richness between treatments can be visualized in species-abundance distribution plots (Figure 3A), with the variation in length of the distribution tails between treatments showing variation in species richness. These results are consistent with our prediction that habitat simplification will more dramatically affect biodiversity, in this case, richness, than habitat loss without simplification.

Habitat loss does not affect biodiversity as measured by ENS and evenness

We detected no difference in average ENS or evenness between habitats that experienced simplification, habitat loss, or no disturbance (Appendix S1: Figures S2 and S3). Neither of the best fit models explaining variation in ENS and evenness between habitats contained treatment as an effect (Appendix S1: Tables S5 and S6). This suggests that while habitat loss and simplification affect the species richness component of diversity, they do not affect the evenness component of diversity. This result is supported by the species-abundance distribution plots, which show a similar ratio of rare to common arthropod species across treatments (Figure 3A). This surprising result not only contradicts our prediction that habitat simplification would reduce biodiversity compared to habitat loss, but also challenges general expectations in ecology that habitat loss results in loss of biodiversity, and that loss of diversity cascades between trophic levels.

Common plant species affects ENS by changing habitat richness and evenness

We found that arthropod diversity, as measured by ENS, was affected by the common plant species in the habitat. Specifically, *S. altissima*-common habitats had higher arthropod ENS than *A. tuberosa* and *B. alba*-common habitats and *A. tuberosa*-common habitats had higher ENS than *B. alba*-common habitats (Figure 2C).

Because ENS is influenced by both richness and evenness, it can be affected by changes to species richness, species evenness, or both. The variation in ENS between *S. altissima* and *A. tuberosa*-common habitats cannot be explained by species richness, as we found no difference in species richness between *S. altissima* and *A. tuberosa*-common habitats (Figure 2B). Instead, evidence suggests that the difference in ENS between *S. altissima* and *A. tuberosa*-common habitats is explained by changes in evenness. *S. altissima* habitats have higher average arthropod evenness, which is consistent with the higher ENS of those habitats. *A. tuberosa*-common habitats, on the other hand, have a lower average arthropod evenness (Figure 2D), which is consistent with the lower ENS of those habitats (Figure 2C).

Though *B. alba*-common habitats do have a lower ENS relative to *S. altissima* and *A. tuberosa*-common habitats, the evenness of *B. alba*-common habitats is not different from those of *S. altissima* or *A. tuberosa* (Figure 2D). The species richness of *B. alba*-common habitats, however, is lower than either of the other two (Figure 2B). This suggests that the low ENS of *B. alba*-common habitats can be explained by a decrease in arthropod richness, rather than a decrease in arthropod evenness in those habitats.

These patterns are also evident in the species-abundance distribution plots for each common plant species (Figure 3B). The shorter tail of the species-abundance distribution for *B. alba* plot reflects the lower species richness in *B. alba*-common habitats compared to *A. tuberosa* and *S. altissima*, which are each longer tailed. Additionally, the difference in distribution shape between the *A. tuberosa* and *S. altissima* plots show differences in ratios of rare to abundant arthropod species. These patterns reflect the differences in evenness between *A. tuberosa* and *S. altissima*-common habitats.

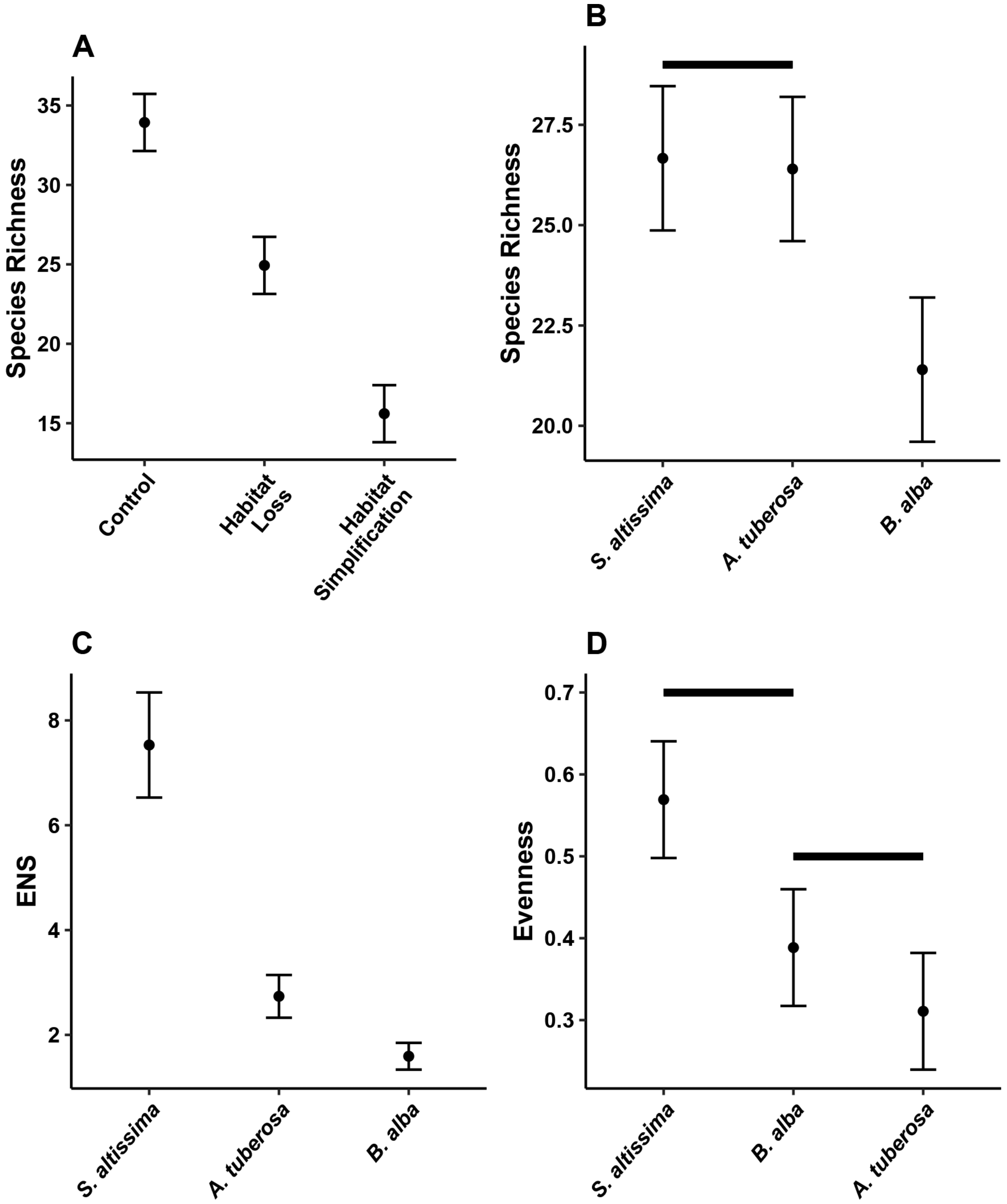

FIGURE 2 Mean arthropod species richness for (A) each treatment and (B) each common plant species. Habitat loss and simplification treatments both have reduced species richness compared with control ($p < 0.0001$, SE = 1.56), and habitat simplification has reduced species richness compared with habitat loss without simplification ($p < 0.0001$, SE = 1.56). There is no difference in species richness between *Solidago altissima* and *Asclepias tuberosa*-common habitats ($p = 0.866$, SE = 1.56). *Baptisia alba*-common habitats have lower species richness than habitats with either of the other two common species ($p < 0.01$, SE = 1.56). (C) Mean arthropod effective number of species (ENS) and (D) evenness for each common plant species. *A. tuberosa* ($p < 0.0001$, SE = 1.02) and *B. alba*-common habitats ($p < 0.0001$, SE = 0.969) both have lower ENS than *S. altissima*-common habitats, and *B. alba*-common habitats have lower ENS than *A. tuberosa*-common habitats ($p = 0.0009$, SE = 0.318). There was no effect of treatment on arthropod evenness (Appendix S1: Table S10, Figure S2). *A. tuberosa*-common habitats have lower arthropod evenness than *S. altissima*-common habitats ($p = 0.0019$, SE = 0.0775). Arthropod evenness in *B. alba*-common habitats is not different from either *A. tuberosa* ($p = 0.322$, SE = 0.0775) or *S. altissima*-common habitats ($p = 0.0252$, SE = 0.0775). There was no effect of treatment on arthropod evenness (Appendix S1: Table S12, Figure S3). All means are marginal means from best fit model, and all error bars represent 1 SE. Black bars above points indicate when means are not statistically different.

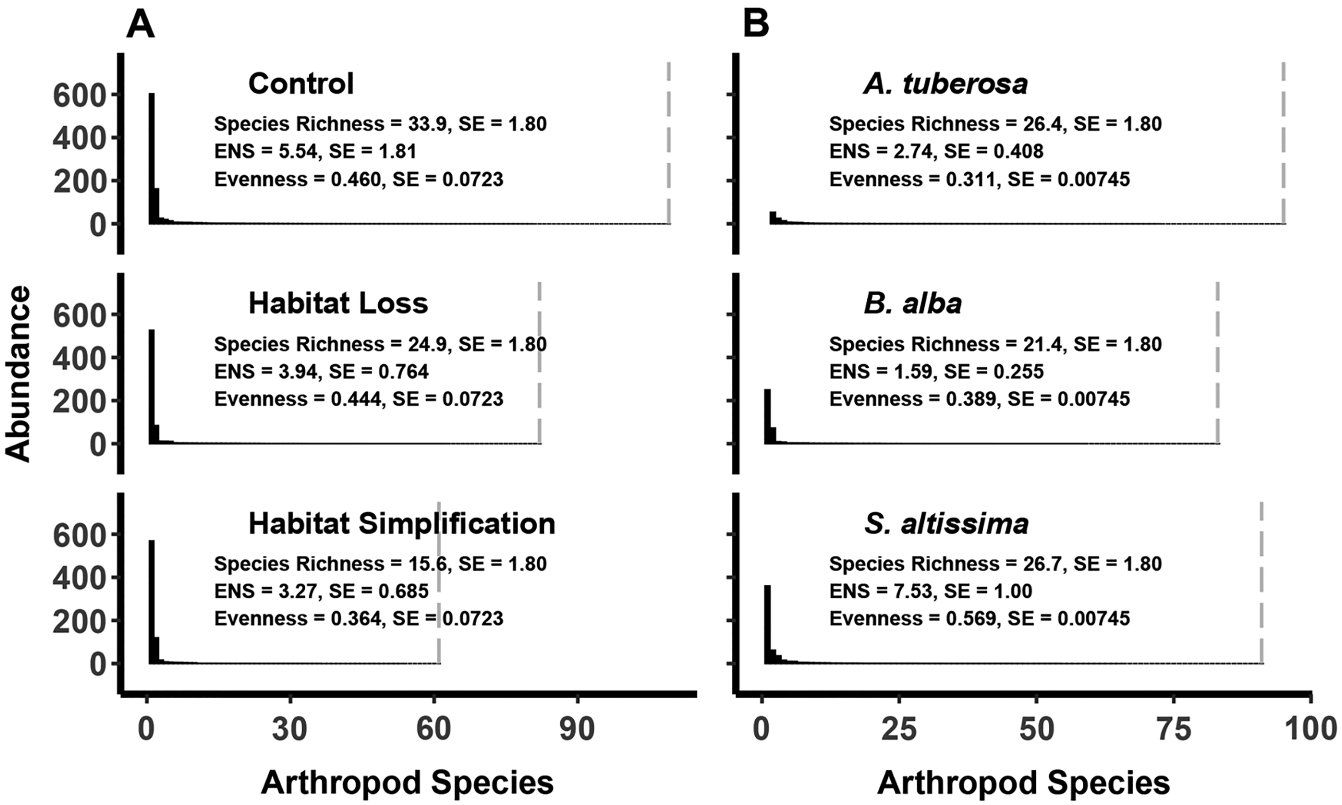

FIGURE 3 Plot of average arthropod species-abundance distribution across (A) treatments and (B) common species regions. Abundances for each arthropod species are averaged across habitats in the region. Arthropod species identity on the x-axis is ranked from most to least abundant (i.e., the most abundant species is different in each panel). Marginal mean (from best fit model) species richness, evenness, and effective number of species (ENS) with SE are listed for each region. Marginal means and SE for ENS and evenness in (A) were computed from full models, as best fit models for ENS and evenness did not contain treatment. Gray vertical lines highlight the end of the distribution (i.e., the rarest species).

DISCUSSION

Habitat loss often targets specific producer species, thus simplifying the habitat for consumers and other taxa by reducing plant diversity. Most methods of predicting the effects of habitat loss on biodiversity, however, treat habitat loss as nonselective with respect to species. In contrast, our prediction was based on expectations that habitat simplification would homogenize available resources within the habitat, restricting both the richness and evenness of species that could be supported by the habitat. In alignment with this prediction, we detected a difference in arthropod species richness between habitat loss with and without simplification, with simplification decreasing richness more dramatically. However, we surprisingly did not detect any differences in diversity, that is, ENS, between habitat simplification and habitat loss in our experiment. This difference between our richness and ENS results indicates that loss of plant habitat decreases the number of arthropod species but does not fundamentally change the species-abundance relationship or species evenness (i.e., the ratio of rare to abundant species) of the arthropods.

Loss of any species affects species richness, that is, declines in species richness can result from losing rare or abundant species, and the abundance distribution of a community does not have to change for species richness to be reduced. However, evenness is only affected by changes in the overall abundance distribution of species in a community. ENS is affected by changes to both the number of species and the abundance distribution. Therefore, the fact that both types of habitat loss affected richness and not ENS indicates that both habitat loss and simplification primarily affected rare species but did not change the overall arthropod abundance distributions in the habitats.

When habitat is lost randomly (i.e., without simplification), rare species are stochastically more likely to be lost, simply as a function of their rarity (Almeida et al., 2021; Goodsell & Connell, 2002; Hedrick et al., 1996; Raup, 1992; Smith & Almeida, 2020). As a result, it is less surprising that habitat loss without simplification, a putatively stochastic disturbance, should have affected only rare species, thus primarily reducing richness but not ENS. Habitat loss with simplification, on the other hand, a putatively deterministic disturbance, should affect both rare and abundant arthropod species thus changing ENS. Yet, in our experiment, it did not. We attribute this outcome to the dramatic variation in quality of the common plant species in our experiment, which apparently overwhelmed any variation in habitat diversity between treatments. In other words, which habitat type (plant species indentity) was left after habitat simplification was more important than the effect of simplification per se.

We found that the abundance distribution of arthropods on *A. tuberosa* is less even (many rare species, few common species) than on *S. altissima*. We propose that this outcome was caused by the presence of a few highly abundant specialists arthropods on *A. tuberosa*, the presence of which lowers evenness of the whole habitat, regardless of what other plants are in the habitat. In contrast, the relatively even abundance distribution of arthropods on *S. altissima* helps maintain a high overall evenness in the whole habitat, even in the face of significant habitat loss and selective removal of plant species.

We suggest that this difference in resources provided by the different common plant species overpowers the differences in plant taxonomic diversity between habitat loss and habitat simplification in their effect on ENS. In other words, which plant species are present and common is more important than how diverse the plant community is. Ours is not the first study to indicate that taxonomic homogenization may be less relevant for biodiversity at other trophic levels than functional or structural homogenization, in alignment with niche theory (Brose, 2003; De Deyn et al., 2004; Geppert et al., 2021), but our controlled experiment is unique in documenting that phenomenon in a habitat loss context.

Our results have important implications for considerations of biotic homogenization as a mechanism of biodiversity loss. Biotic homogenization, the process by which a combination of extirpations and invasions increases functional and taxonomic similarity across communities over time, occurs globally across biological scales because of anthropogenic activities (Olden & Rooney, 2006). Many biotic homogenization studies have documented habitats where regions are taxonomically but not functionally homogenized (Abadie et al., 2011; Mouton et al., 2020; Sonnier et al., 2014; but see Villéger et al., 2014; White et al., 2018). It has also been suggested that loss of species in a biotic homogenization scenario does not necessarily equate to loss of function (Baiser & Lockwood, 2011). Our results build on these findings by indicating that even highly homogenized habitats with low producer-level diversity may still support a relatively high diversity of species at higher trophic levels, depending on the identity of the plant species that is common in the homogenized habitats. In the case of our experiment, the presence of important host plant species such as *S. altissima* that support both high richness and evenness of arthropod species may mitigate homogenizing effects of selective habitat loss on biodiversity at higher trophic levels.

Although *A. tuberosa* and *B. alba* respectively are associated with lower evenness and richness of the habitats where they are common, it cannot be overlooked that they contribute unique arthropod species to the overall landscape. By focusing too heavily on diversity and conserving host species like *S. altissima* that have diverse arthropod assemblages, we could lose unique, highly coevolved relationships such as the ones *B. alba* and *A. tuberosa* have with their specialist arthropods. This loss of specialization could ultimately decrease community resilience, ecosystem function, and synchronization between disturbed communities (Clavel et al., 2011). Additionally, regimes of conserving plant species that support more generalist arthropods could lead to large scale functional homogenization in the long term (Clavel et al., 2011).

An important consideration for our results is that our experiment occurred within the native ranges of all the plant species used, and thus within a rich pool of preadapted arthropod species. Loss of rare plant species in a habitat dominated by one or a few non-native plant species might affect biodiversity differently, a relevant concern as decline in native habitat (habitat loss) and dominance of non-native species often happen simultaneously (MacDougall & Turkington, 2005). One reason *S. altissima* maintains such a high richness and evenness of arthropods is that it recruits both specialist and generalist arthropod species. However, when *S. altissima* is outside of its native range, it recruits primarily generalist arthropod species and does not provide habitat suitable for specialist arthropods (Jobin et al., 1996; Kajzer-Bonk et al., 2016; Ustinova, 2019). This phenomenon is not exclusive to *S. altissima*; exotic species tend to interact more with generalists than specialists (Morriën et al., 2010; Peralta et al., 2020). Using non-native plant species as dominant species in our experiment could therefore have yielded different results. In this case, habitat simplification would be more likely to decrease the ratio of native to non-native plants in the habitat, and we would therefore expect it to have a greater effect on both arthropod richness and ENS.

Our results also show the importance of addressing both richness and evenness in studies on biodiversity. Ecologists often choose richness as a proxy for total biodiversity (Haddad et al., 2009; Soliveres et al., 2016) or focus on loss of species rather than changes in relative species abundance (Brooks et al., 2002). Additionally, review articles synthesizing biodiversity research often fail to distinguish between conclusions drawn from studies using different biodiversity measures (Cardinale et al., 2012; Tilman et al., 2014). These practices overlook the fact that biodiversity measures are fundamentally different in how they value rarity (Hill, 1973). In this study, if we had ignored evenness, we would have underestimated important effects of common plant species identity on arthropod biodiversity. By contrast, if we had ignored richness, we would have failed to detect any effects of habitat loss on arthropod biodiversity. This is because species richness places higher value on rare species, which were more affected by habitat loss and simplification. On the other hand, evenness (and thus ENS, as it incorporates evenness) places higher value on abundant species, which were more affected by the identity of the common plant species. Our results empirically demonstrate that choosing to measure either species richness or species evenness precludes important conclusions by changing the value placed on rare species in the study.

Our research highlights important nuances in the relationship between habitat loss and biodiversity. First, we show that the manner of habitat loss matters, that is, does it include simplification? Additionally, we show that the identity of the most common plant species in the habitat matters. And finally, we showed that even the way we measure biodiversity, that is, the value we give to rare species, matters. Blanket statements and one-size-fits-all conclusions about how habitat loss affects biodiversity can undermine conservation efforts by ignoring relevant ecological scenarios such as the one we describe. The effect of habitat loss on biodiversity is context dependent and should be treated as such in research and conservation efforts.

AUTHOR CONTRIBUTIONS

Study conception and design: Ryan Almeida, Kevin G. Smith, Erin V. Scott, Sam McKlin, and Alston Lee Lippert. *Data collection*: Erin V. Scott, Ryan Almeida, Jake Clary, Carlos Vargas, Will Hidell, and Kevin G. Smith. *Analysis and interpretation of results*: Erin V. Scott, Ryan Almeida, Susana Wadgymar, and Kevin G. Smith. *Draft, review, and edit manuscript*: Erin V. Scott, Kevin G. Smith. All authors reviewed the results and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Scott, 2024) are available from Zenodo: 10.5281/zenodo.10927289.

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REFERENCES

Abadie, J.-C., N. Machon, A. Muratet, and E. Porcher. 2011. “Landscape Disturbance Causes Small-Scale Functional Homogenization, but Limited Taxonomic Homogenization, in Plant Communities: Local Homogenization of Plant Communities.” *Journal of Ecology* 99(5): 1134–42. https://doi.org/10.1111/j.1365-2745.2011.01851.x.

Allan, E., O. Bossdorf, C. F. Dormann, D. Prati, M. M. Gossner, T. Tscharntke, N. Blüthgen, et al. 2014. “Interannual Variation in Land-Use Intensity Enhances Grassland Multidiversity.” *Proceedings of the National Academy of Sciences* 111(1): 308–313. https://doi.org/10.1073/pnas.1312213111.

Almeida, R. J., A. A. G. Berro, A. Lippert, J. Clary, S. McKlin, E. V. Scott, and K. G. Smith. 2021. “Selective Extinctions Resulting from Random Habitat Destruction Lead to Under-Estimates of Local and Regional Biodiversity Loss in a Manipulative Field Experiment.” *Global Change Biology* 27(4): 793–803. https://doi.org/10.1111/gcb.15464.

Baiser, B., and J. L. Lockwood. 2011. “The Relationship between Functional and Taxonomic Homogenization: Functional and Taxonomic Homogenization.” *Global Ecology and Biogeography* 20(1): 134–144. https://doi.org/10.1111/j.1466-8238.2010.00583.x.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, et al. 2011. “Has the Earth’s Sixth Mass Extinction Already Arrived?” *Nature* 471(7336): 51–57. https://doi.org/10.1038/nature09678.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. “Fitting Linear Mixed-Effects Models Using Lme4.” *Journal of Statistical Software* 67(1): 1–48. https://doi.org/10.18637/jss.v067.i01.

Bonin, M. C., G. R. Almany, and G. P. Jones. 2011. “Contrasting Effects of Habitat Loss and Fragmentation on Coral-Associated Reef Fishes.” *Ecology* 92(7): 1503–12. https://doi.org/10.1890/10-0627.1.

Broadbent, E. N., G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, and J. N. Silva. 2008. “Forest Fragmentation and Edge Effects from Deforestation and Selective Logging in the Brazilian Amazon.” *Biological Conservation* 141(7): 1745–57. https://doi.org/10.1016/j.biocon.2008.04.024.

Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, et al. 2002. “Habitat Loss and Extinction in the Hotspots of Biodiversity.” *Conservation Biology* 16(4): 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x.

Brose, U. 2003. “Bottom-Up Control of Carabid Beetle Communities in Early Successional Wetlands: Mediated by Vegetation Structure or Plant Diversity?” *Oecologia* 135(3): 407–413. https://doi.org/10.1007/s00442-003-1222-7.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, et al. 2010. “Global Biodiversity: Indicators of Recent Declines.” *Science* 328(5982): 1164–68. https://doi.org/10.1126/science.1187512.

Cardinale, B. J., J. Emmett Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, et al. 2012. "Biodiversity Loss and Its Impact on Humanity." *Nature* 486(7401): 59–67. https://doi.org/10.1038/nature11148.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. "Accelerated Modern Human–Induced Species Losses: Entering the Sixth Mass Extinction." *Science Advances* 1(5): e1400253. https://doi.org/10.1126/sciadv.1400253.

Chase, J. M., S. A. Blowes, T. M. Knight, K. Gerstner, and F. May. 2020. "Ecosystem Decay Exacerbates Biodiversity Loss with Habitat Loss." *Nature* 584(7820): 238–243. https://doi.org/10.1038/s41586-020-2531-2.

Chaudhary, A., F. Verones, L. de Baan, and S. Hellweg. 2015. "Quantifying Land Use Impacts on Biodiversity: Combining Species–Area Models and Vulnerability Indicators." *Environmental Science & Technology* 49(16): 9987–95. https://doi.org/10.1021/acs.est.5b02507.

Chisté, M. N., K. Mody, G. Kunz, J. Gunczy, and N. Blüthgen. 2018. "Intensive Land Use Drives Small-Scale Homogenization of Plant- and Leafhopper Communities and Promotes Generalists." *Oecologia* 186(2): 529–540. https://doi.org/10.1007/s00442-017-4031-0.

Clavel, J., R. Julliard, and V. Devictor. 2011. "Worldwide Decline of Specialist Species: Toward a Global Functional Homogenization?" *Frontiers in Ecology and the Environment* 9(4): 222–28. https://doi.org/10.1890/080216.

De Deyn, G. B., C. E. Raaijmakers, J. van Ruijven, F. Berendse, and W. H. van der Putten. 2004. "Plant Species Identity and Diversity Effects on Different Trophic Levels of Nematodes in the Soil Food Web." *Oikos* 106(3): 576–586. https://doi.org/10.1111/j.0030-1299.2004.13265.x.

Dirzo, R., and P. H. Raven. 2003. "Global State of Biodiversity and Loss." *Annual Review of Environment and Resources* 28(1): 137–167. https://doi.org/10.1146/annurev.energy.28.050302.105532.

Ebeling, A., E. W. Lind, S. T. Meyer, A. D. Barnes, E. T. Borer, N. Eisenhauer, and W. W. Weisser. 2020. "Contrasting Effects of Plant Diversity on Β- and Γ-Diversity of Grassland Invertebrates." *Ecology* 101(7): e03057. https://doi.org/10.1002/ecy.3057.

Edwards, D. P., and W. F. Laurance. 2013. "Biodiversity Despite Selective Logging." *Science* 339(6120): 646–47. https://doi.org/10.1126/science.339.6120.646-b.

Emerson, B. C., and N. Kolm. 2005. "Species Diversity Can Drive Speciation." *Nature* 434(7036): 1015–17. https://doi.org/10.1038/nature03450.

Ernst, R., K. Eduard Linsenmair, and M.-O. Rödel. 2006. "Diversity Erosion beyond the Species Level: Dramatic Loss of Functional Diversity after Selective Logging in Two Tropical Amphibian Communities." *Biological Conservation* 133(2): 143–155. https://doi.org/10.1016/j.biocon.2006.05.028.

García-Valdés, R., H. Bugmann, and X. Morin. 2018. "Climate Change-Driven Extinctions of Tree Species Affect Forest Functioning More than Random Extinctions." *Diversity and Distributions* 24(7): 906–918. https://doi.org/10.1111/ddi.12744.

Geppert, C., G. La Bella, F. Boscutti, F. Sanna, F. Marangoni, and L. Marini. 2021. "Effects of Temperature and Plant Diversity on Orthopterans and Leafhoppers in Calcareous Dry Grasslands." *Journal of Insect Conservation* 25(2): 287–296. https://doi.org/10.1007/s10841-021-00300-3.

Goodsell, P., and S. Connell. 2002. "Can Habitat Loss Be Treated Independently of Habitat Configuration? Implications for Rare and Common Taxa in Fragmented Landscapes." *Marine Ecology Progress Series* 239: 37–44. https://doi.org/10.3354/meps239037.

Gossner, M. M., T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, et al. 2016. "Land-Use Intensification Causes Multitrophic Homogenization of Grassland Communities." *Nature* 540(7632): 266–69. https://doi.org/10.1038/nature20575.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops, and D. Tilman. 2009. "Plant Species Loss Decreases Arthropod Diversity and Shifts Trophic Structure." *Ecology Letters* 12(10): 1029–39. https://doi.org/10.1111/j.1461-0248.2009.01356.x.

Hedrick, P. W., R. C. Lacy, F. W. Allendorf, and M. E. Soule. 1996. "Directions in Conservation Biology: Comments on Caughley." *Conservation Biology* 10(5): 1312–20. https://doi.org/10.1046/j.1523-1739.1996.10051312.x.

Hill, M. O. 1973. "Diversity and Evenness: A Unifying Notation and Its Consequences." *Ecology* 54(2): 427–432. https://doi.org/10.2307/1934352.

Jobin, A., U. Schaffner, and W. Nentwig. 1996. "The Structure of the Phytophagous Insect Fauna on the Introduced Weed *Solidago altissima* in Switzerland." *Entomologia Experimentalis et Applicata* 79(1): 33–42. https://doi.org/10.1111/j.1570-7458.1996.tb00806.x.

Kajzer-Bonk, J., D. Szpiłyk, and M. Woyciechowski. 2016. "Invasive Goldenrods Affect Abundance and Diversity of Grassland Ant Communities (Hymenoptera: Formicidae)." *Journal of Insect Conservation* 20(1): 99–105. https://doi.org/10.1007/s10841-016-9843-4.

Keil, P., D. Storch, and W. Jetz. 2015. "On the Decline of Biodiversity Due to Area Loss." *Nature Communications* 6(1): 8837. https://doi.org/10.1038/ncomms9837.

Kerr, J. T., and L. Packer. 1997. "Habitat Heterogeneity as a Determinant of Mammal Species Richness in High-Energy Regions." *Nature* 385(6613): 252–54. https://doi.org/10.1038/385252a0.

Larrieu, L., Y. Paillet, S. Winter, R. Bütler, D. Kraus, F. Krumm, T. Lachat, A. K. Michel, B. Regnery, and K. Vandekerkhove. 2018. "Tree Related Microhabitats in Temperate and Mediterranean European Forests: A Hierarchical Typology for Inventory Standardization." *Ecological Indicators* 84(January): 194–207. https://doi.org/10.1016/j.ecolind.2017.08.051.

Lenth, R. V. 2021. "Emmeans: Estimated Marginal Means, Aka Least-Squares Means." https://cran.r-project.org/web/packages/emmeans/index.html

MacDougall, A. S., and R. Turkington. 2005. "Are Invasive Species the Drivers or Passengers of Change in Degraded Ecosystems?" *Ecology* 86(1): 42–55. https://doi.org/10.1890/04-0669.

Miao, B.-G., Y.-Q. Peng, D.-R. Yang, B. Guénard, and C. Liu. 2021. "Diversity Begets Diversity: Low Resource Heterogeneity Reduces the Diversity of Nut-Nesting Ants in Rubber Plantations." *Insect Science* 29(3): 932–941. https://doi.org/10.1111/1744-7917.12964.

Morriën, E., T. Engelkes, M. Macel, A. Meisner, and W. H. Van der Putten. 2010. "Climate Change and Invasion by

Intracontinental Range-Expanding Exotic Plants: The Role of Biotic Interactions.” *Annals of Botany* 105(6): 843–48. https://doi.org/10.1093/aob/mcq064.

Mouton, T. L., J. D. Tonkin, F. Stephenson, P. Verburg, and M. Floury. 2020. “Increasing Climate-Driven Taxonomic Homogenization but Functional Differentiation among River Macroinvertebrate Assemblages.” *Global Change Biology* 26(12): 6904–15. https://doi.org/10.1111/gcb.15389.

Ney-Nifle, M., and M. Mangel. 2000. “Habitat Loss and Changes in the Species-Area Relationship.” *Conservation Biology* 14(3): 893–98. https://doi.org/10.1046/j.1523-1739.2000.98163.x.

Olden, J. D., and T. P. Rooney. 2006. “On Defining and Quantifying Biotic Homogenization: Defining Biotic Homogenization.” *Global Ecology and Biogeography* 15(2): 113–120. https://doi.org/10.1111/j.1466-822X.2006.00214.x.

Patiño, J., C. Gómez-Rodríguez, A. Pupo-Correia, M. Sequeira, and A. Vanderpoorten. 2018. “Trees as Habitat Islands: Temporal Variation in Alpha and Beta Diversity in Epiphytic Laurel Forest Bryophyte Communities.” *Journal of Biogeography* 45(8): 1727–38. https://doi.org/10.1111/jbi.13359.

Peralta, G., G. L. W. Perry, D. P. Vázquez, D. Matthias Dehling, and J. M. Tylianakis. 2020. “Strength of Niche Processes for Species Interactions Is Lower for Generalists and Exotic Species.” *Journal of Animal Ecology* 89(9): 2145–55. https://doi.org/10.1111/1365-2656.13274.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. “The Biodiversity of Species and Their Rates of Extinction, Distribution, and Protection.” *Science* 344(6187): 1246752. https://doi.org/10.1126/science.1246752.

Pinheiro, J., D. Bates, S. Debroy, D. Sarkar, and R Core Team. 2021. “{nlme}: Linear and Nonlinear Mixed Effects Models.” https://cran.r-project.org/web/packages/nlme/index.html

Preston, F. W. 1962. “The Canonical Distribution of Commonness and Rarity: Part I.” *Ecology* 43(2): 185. https://doi.org/10.2307/1931976.

Przepióra, F., and M. Ciach. 2022. “Tree Microhabitats in Natural Temperate Riparian Forests: An Ultra-Rich Biological Complex in a Globally Vanishing Habitat.” *Science of the Total Environment* 803(January): 149881. https://doi.org/10.1016/j.scitotenv.2021.149881.

Raup, D. M. 1992. *Extinction: Bad Genes or Bad Luck?* New York: Norton.

Scott, E. V. 2024. “erscott65/Habitat-Loss: Habitat Loss Code and Data (v1.0.0).” Zenodo. https://doi.org/10.5281/zenodo.10927290.

Seabloom, E. W., A. P. Dobson, and D. M. Stoms. 2002. “Extinction Rates under Nonrandom Patterns of Habitat Loss.” *Proceedings of the National Academy of Sciences* 99(17): 11229–34. https://doi.org/10.1073/pnas.162064899.

Smith, K. G., and R. J. Almeida. 2020. “When Are Extinctions Simply Bad Luck? Rarefaction as a Framework for Disentangling Selective and Stochastic Extinctions.” *Journal of Applied Ecology* 57(1): 101–110. https://doi.org/10.1111/1365-2664.13510.

Smith, K. G., K. R. Lips, and J. M. Chase. 2009. “Selecting for Extinction: Nonrandom Disease-Associated Extinction Homogenizes Amphibian Biotas.” *Ecology Letters* 12(10): 1069–78. https://doi.org/10.1111/j.1461-0248.2009.01363.x.

Soliveres, S., F. van der Plas, P. Manning, D. Prati, M. M. Gossner, S. C. Renner, F. Alt, et al. 2016. “Biodiversity at Multiple Trophic Levels Is Needed for Ecosystem Multifunctionality.” *Nature* 536(7617): 456–59. https://doi.org/10.1038/nature19092.

Sonnier, G., S. E. Johnson, K. L. Amatangelo, D. A. Rogers, and D. M. Waller. 2014. “Is Taxonomic Homogenization Linked to Functional Homogenization in Temperate Forests? Functional Homogenization of Forests.” *Global Ecology and Biogeography* 23(8): 894–902. https://doi.org/10.1111/geb.12164.

Thiollay, J.-M. 1992. “Influence of Selective Logging on Bird Species Diversity in a Guianan Rain Forest.” *Conservation Biology* 6(1): 47–63. https://doi.org/10.1046/j.1523-1739.1992.610047.x.

Thiollay, J.-M. 1997. “Disturbance, Selective Logging and Bird Diversity: A Neotropical Forest Study.” *Biodiversity and Conservation* 6(8): 1155–73. https://doi.org/10.1023/A:1018388202698.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. “Biodiversity and Ecosystem Functioning.” *Annual Review of Ecology, Evolution, and Systematics* 45(1): 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917.

Ustinova, E. N. 2019. “The Ability of Terrestrial Mollusks of Moscow Oblast to Feed on Invasive Species of the Genus Solidago (*S. canadensis* and *S. gigantea*).” *Russian Journal of Biological Invasions* 10(4): 387–393. https://doi.org/10.1134/S2075111719040106.

Villéger, S., G. Grenouillet, and S. Brosse. 2014. “Functional Homogenization Exceeds Taxonomic Homogenization among European Uropean Fish Assemblages.” *Global Ecology and Biogeography* 23(12): 1450–60. https://doi.org/10.1111/geb.12226.

White, H. J., W. Ian Montgomery, L. Storchová, D. Hořák, and J. J. Lennon. 2018. “Does Functional Homogenization Accompany Taxonomic Homogenization of British Birds and How Do Biotic Factors and Climate Affect These Processes?” *Ecology and Evolution* 8(15): 7365–77. https://doi.org/10.1002/ece3.4267.

Whittaker, R. H. 1972. “Evolution and Measurement of Species Diversity.” *Taxon* 21(2–3): 213–251. https://doi.org/10.2307/1218190.

Yin, D., Q. Ye, and M. W. Cadotte. 2021. “Habitat Loss-Biodiversity Relationships Are Influenced by Assembly Processes and the Spatial Configuration of Area Loss.” *Forest Ecology and Management* 496: 119452. https://doi.org/10.1016/j.foreco.2021.119452.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Statistics for Biology and Health. New York: Springer New York. https://doi.org/10.1007/978-0-387-87458-6.

SUPPORTING INFORMATION

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