

RESEARCH PAPER

Range size predicts the risk of local extinction from habitat loss

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Abstract**Aim:** The geographical range size of species is a strong predictor of vulnerability to global extinction. However, it remains unclear whether range size is also a good predictor of extinction risk at much smaller scales. Here, we reconstruct biodiversity time series to ask whether species with small ranges have declined preferentially with habitat loss at the local scale.**Location:** Global.**Time period:** 1500–2015.**Major taxa studied:** Vascular plants.**Method:** We collated 70 million occurrence records of 180,000 species of vascular plants from three biodiversity data-sharing networks. We combined these with data on changes in global land use to find locations (0.25° grid cells) with biodiversity data before and after loss of natural habitat. First, we examined the change in community median range size before and after habitat loss. Second, we quantified the probabilities of local persistence of small- and large-ranged species at different levels of habitat loss.**Results:** Community median range size was higher after habitat loss, on average. Species with small ranges had lower probabilities of persistence than species with large ranges at already moderate habitat loss ($\leq 50\%$).**Main conclusions:** The loss of natural habitat has a differential effect on the local extinction risk of species with different range sizes. Given that species with small ranges decline preferentially, habitat loss can create a linkage between temporal and spatial species turnover, in that changes within communities decrease compositional differences between communities.**KEYWORDS**

biotic homogenization, persistence, range size, spatial species turnover, temporal species turnover

1 | INTRODUCTION

The major driver of the current extinction crisis (Pimm et al., 2014) is, and is also projected to remain for the first half of the 21st century, change in land use (Maxwell, Fuller, Brooks, & Watson,

2016; Pereira et al., 2010; Sala et al., 2000). Yet, vulnerability to extinction from habitat loss is not constant across species. Among the strongest predictors of the threat of extinction in terrestrial species is small geographical range size (Gaston & Fuller, 2009; Manne, Brooks, & Pimm, 1999). In part, this is simply because

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species with small ranges have a lower number of localities at which, upon habitat loss, they either persist or go extinct. But even within a locality, small-ranged species might suffer from a higher extinction risk than widespread ones. One reason for this could be that species with small ranges tend also to have smaller local populations (Brown, 1984; Gaston et al., 2000), and with decreasing population size, the vulnerability to environmental perturbations increases (Christiansen & Fenchel, 2012; Schoener & Spiller, 1987). However, it remains poorly documented whether the threat of local extinction in species experiencing habitat loss can indeed be predicted by range size.

One corollary of an increased local extinction risk for small-ranged species would be that habitat loss creates a linkage between temporal and spatial species turnover, in that spatial turnover is reduced by temporal turnover. This is because previously differentiated local communities would increasingly resemble one another in species composition when habitat loss results in a net loss of exactly the species that drive that very differentiation (McKinney & Lockwood, 1999; Olden & Poff, 2003). Recent analyses of biodiversity time series find that temporal species turnover in local communities is occurring at rates in excess of background levels predicted by null and neutral models (Dornelas et al., 2014; Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015). It is hypothesized that this pattern is driven by biotic homogenization; that is, widespread species replace those with small ranges, and thereby, decrease spatial turnover but maintain local numbers of species (Dornelas et al., 2014). However, the empirical evidence that supports this hypothesis is scarce, all the more so for areas that are representative of habitat loss (Cardinale, Gonzalez, Allington, & Loreau, 2018; Gonzalez et al., 2016).

Moreover, evidence is lacking with regard to the amount of habitat loss that species can tolerate before becoming vulnerable to local extinction. Albeit highly relevant for conservation, we do not know whether thresholds of local habitat loss differ between species with small and large ranges. If small-ranged species are more vulnerable to even moderate habitat loss, the effect of habitat loss on biodiversity might be amplified, simply because most species have small ranges (Gaston, 1996). Although some models predict abrupt species loss when natural habitat availability falls below a threshold of 30% in the landscape (Andr n, 1994), it has recently been documented that initial intrusion in intact landscapes can substantially erode local biodiversity (Betts et al., 2017; Staude et al., 2018). This might be attributable to the local extinction of numerous small-ranged species that are already vulnerable to lower amounts of habitat loss.

Empirical applications to study temporal community changes and species persistence in human modified landscapes on a global scale have been, to date, constrained by a general paucity of representative ecological time series and high-resolution historical land-use data. However, over the last two decades, millions of digital species records have been mobilized via international data-sharing networks, providing spatio-temporal information on species occurrences (Meyer, Weigelt, & Krefl, 2016). Moreover, global change in land use has been reconstructed for the late Holocene and has recently been made available at high temporal and spatial resolution with the

LUH2vh product (<http://luh.umd.edu/data.shtml>; Hurtt et al., 2011). Integrating single point occurrences to the spatio-temporal resolution of such land-use data uncovers new vantage points for ecological research, because community time series data in areas undergoing change in land use can be reconstructed (Johnson et al., 2011).

Here, we use these data sources to compare the frequency distribution of species range sizes in vascular plant communities before and after habitat loss. We test whether this distribution shifts towards larger ranges. Next, we quantify the probability of local persistence of species with small and large ranges along a gradient of habitat loss. We hypothesize that small-ranged species are more vulnerable to local extinction from habitat loss.

2 | METHODS

2.1 | Land-use data

We used historical land-use reconstruction data provided by the Land Use Harmonization v2h product (LUHv2h; <http://luh.umd.edu/data.shtml>; Hurtt et al., 2011). Inputs of LUHv2h include HYDE 3.2 (Klein Goldewijk, Beusen, Dreht, & Vos, 2011), Food and Agriculture Organization (FAO) wood harvest data (FAO, 2008) and Landsat-based forest loss data (Hansen et al., 2013), among others (Hurtt et al., 2011). LUHv2h provides information about the annual states of 12 land-use classes at a 0.25° spatial resolution for the period 850–2015; that is, each grid cell gives a value for the percentage of cover of each of the land-use classes. Land use is divided into two classes of natural vegetation (forests or non-forests) and 10 human land uses (five cropland, two secondary vegetation, two grazing and one urban uses). Here, the natural forest and non-forest classes were aggregated into one natural habitat class. We define habitat loss as the loss of this natural habitat class. Note that the aggregate of the 10 human land uses is complementary to this natural habitat class.

2.2 | Vascular plant data

We downloaded all openly available, georeferenced data on vascular plant occurrences via the Global Biodiversity Information Facility (GBIF; <https://doi.org/10.15468/dl.chiubr>, accessed 6 December 2017), Botanical Information and Ecology Network (BIEN; R package *BIEN*; Maitner et al., 2018) and the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS; <https://doi.org/10.5519/0066354>; Hudson et al., 2014) databases. We applied geographical filters to exclude impossible, incomplete or unlikely sampling locations (R package *scrubr*; Chamberlain, 2016). Temporal filters confined biodiversity data to the period 1500–2015. Taxonomic filtering and taxon resolution and standardization included iPlant's Taxonomic Name Resolution Service (R package *taxize*; Chamberlain & Sz cs, 2013). We excluded duplicates of species, sampling location and year combination. Joining these data resulted in 73,097,393 unique records for 177,774 vascular plant species (i.e., c. 56% taxonomic coverage of c. 315,000 vascular plant species; theplantlist.org). Missing

species are most likely to be rare, small-ranged species and those endemic to regions with little documentation and data-mobilization effort. We provide R code for data retrieval and cleaning in the Supporting Information (section R code 2.1–2.4).

2.3 | Range sizes

For most species, scarcity of point occurrences at unique locations prevents the construction of meaningful species distribution models (Feeley, 2012; Guisan et al., 2007) or extent-of-occurrence range maps (Gaston & Fuller, 2009). In particular, species with restricted geographical distribution might be underrepresented when confining diversity data to species for which distribution modelling is appropriate. We thus opted for an alternative approximate but transparent approach to estimate range sizes. Initially, we gridded the c. 73 million species records to the spatial resolution of the LUHv2h data, which we had previously re-projected into an equal-area grid (Behrmann projection). Next, we simply counted the number of cells that each species occupied on that grid (Gaston, 1996). Each species thus had one range size estimate that was derived from all its occurrence records to date and measured the species' area of occupancy (Gaston & Fuller, 2009).

Owing to the incomplete spatial coverage of digital biodiversity data, we probably underestimated range size (Isaac & Pocock, 2015). Importantly, underestimation is worse for species that have parts of their ranges in areas with severe data gaps. This uneven spatial coverage is particularly problematic when comparing locations. However, this limitation did not affect our analyses, because we were comparing the temporal change within locations rather than between them.

2.4 | Communities before and after habitat loss

First, we gridded all species occurrence records to the spatial and temporal resolution of the LUHv2h data. This allowed us to identify cells that had species records before ($\geq 80\%$ of natural habitat remaining) and after (0% of natural habitat remaining) habitat loss. Each of these cells therefore gave us an individual set of species for a before and after habitat loss period. Henceforth, we refer to these species sets as communities. We further introduced a lower bound for the number of species in these communities to account for under-documentation. When cells had one community with < 10 species, either before or after habitat loss, we discarded them (see Supporting Information for discussion of thresholds and sensitivity test; Supporting Information Figure S1).

The application of the two rules for inclusion of cells (records before and after habitat loss and ≥ 10 species recorded before and after habitat loss) resulted in an inclusion of one in 1,000 cells. From the c. 90,000 cells, over which the 70 million species occurrence records were distributed, 657 cells had biodiversity data both before and after habitat loss. Of the 657 cells, 89 had ≥ 10 species recorded before and after habitat loss. The final 89 cells cover 11 out of 14 biomes (Figure 1). Their distribution reflects both change in land

use and the spatial bias typical of biodiversity records (e.g., severe gaps across Asia, Northern and Central Africa, Amazonia and Arctic Canada; Meyer et al., 2016) but also that areas of exceptionally high biodiversity might be over-represented (e.g., Atlantic Forest in SE Brazil, the Cape Provinces, Western Australia and California).

Digital biodiversity data suffer from not only spatial but also temporal bias (Meyer et al., 2016). Typically, the number of species records, and consequently, the number of species, increase progressively in time. In the LUHv2h data, natural habitat can only be lost but not gained with time; more natural habitat generally corresponds to earlier years and little natural habitat to later years. Given that documentation is higher in later years, the number of species is generally higher when little natural habitat remains (i.e., after habitat loss). In our subset of cells, the average time that passed until a cell went from ≥ 80 to 0% natural habitat was 81 years (Supporting Information Figure S2) and the average community richness was 55 and 218 species, respectively.

Nevertheless, because we do not compare the number of species but range size composition before and after habitat loss, we can account for this temporal bias by artificially keeping the number of species constant over time. For each cell, we repeatedly subsampled species from the community with the higher number of species (without replacement), so that the before and after community of a cell had the same number of species (number of sampling repetitions, $n = 100$; Figure 2). For each cell, community and n th subsample, we then calculated a summary statistic that described the composition of species range sizes before and after habitat loss. We calculated median range sizes, because range-size frequency distributions are strongly right skewed. The medians that were obtained from the 100 subsamples of the community with the higher number of species in a cell were averaged. For each cell, we then calculated the log ratio of median range size after and before habitat loss to obtain effect sizes. With a pairwise permutation test (Monte Carlo Fisher–Pitman test) we tested whether the mean of the effect sizes was different from zero.

Finally, we used a simulation approach to test whether our method introduces any bias. We simulated 1,000 before and after habitat loss communities with 50 and 200 species, respectively. For both the before and the after community, species range sizes were simulated from the same log-normal distribution. We followed the protocol above and subsampled the community with more species, in this case always the after community, 100 times. We averaged medians from the subsamples and compared this value with the median range size of the before community. If our method is indeed free of bias, effect sizes obtained from the 1,000 community comparisons should be normally distributed. We provide R code for this simulation in the Supporting Information (section R code 3.1 & 3.2).

2.5 | Probability of persistence along a habitat loss gradient

By gridding species occurrence records to the spatio-temporal resolution of the LUH2vh data, we could link each record to the

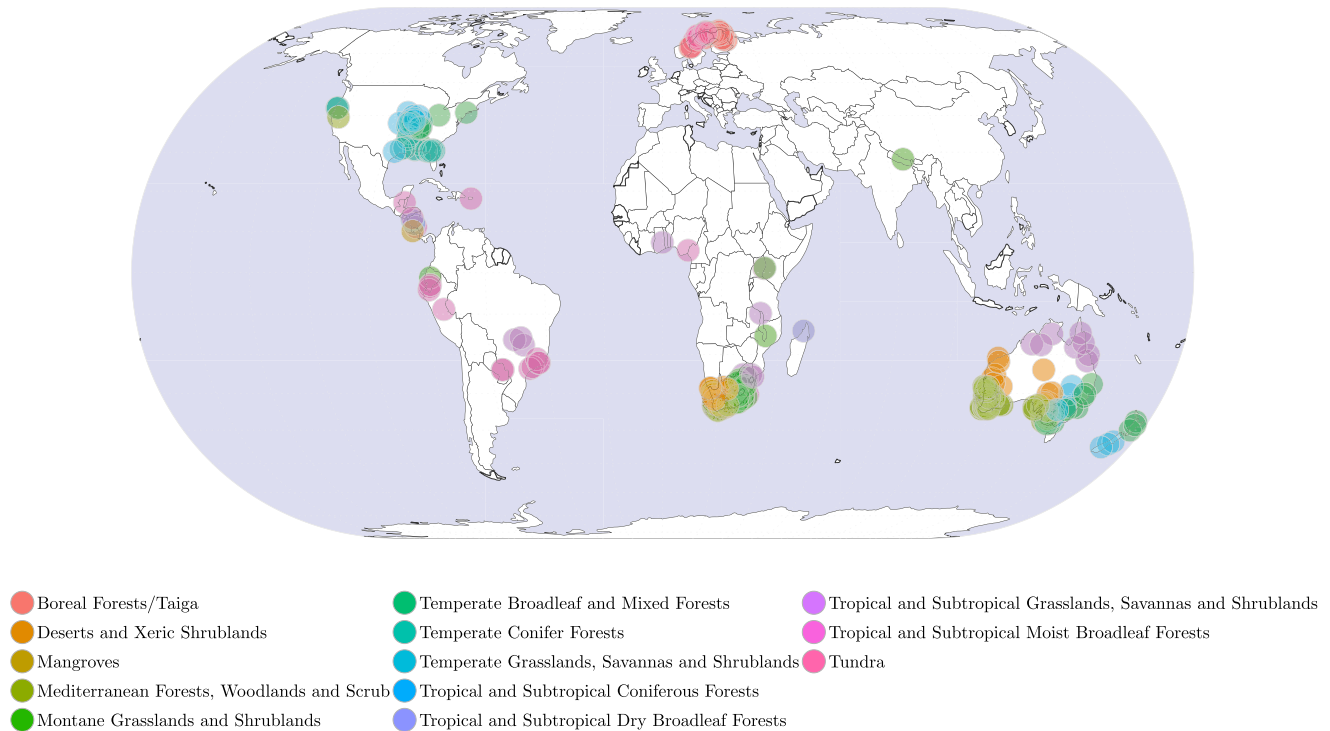


FIGURE 1 Spatial distribution of locations (0.25° cells) with biodiversity data both before (≥80% of natural habitat remaining) and after (0% of natural habitat remaining) habitat loss and with ≥ 10 plant species reported before and after habitat loss. Circles are semi-transparent and coloured according to biomes. Map is in Eckert IV projection [Colour figure can be viewed at wileyonlinelibrary.com]

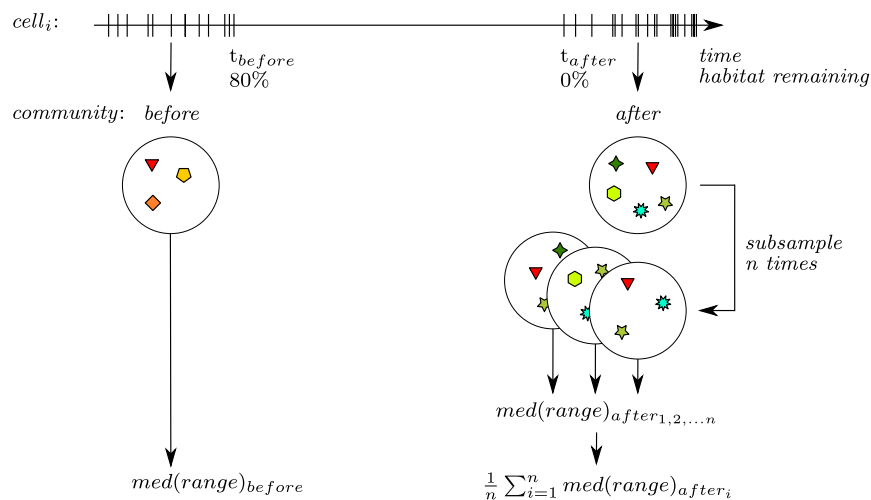


FIGURE 2 Schematic representation of our approach to comparison of species range sizes before and after habitat loss. The scheme focuses on one cell, $cell_i$. $Cell_i$ has species occurrence records before and after habitat loss. These give an individual set of species for before and after habitat loss. These sets we name communities. Communities had to have ≥ 10 species (not shown for clarity). For each community, we calculate the median (med) range size. Given that digital biodiversity records increase with time, there are typically more species in the after community. We subsample the after community 100 times. Each time, we take as many samples as there are species in the before community and calculate, for that subset, the median range size. These medians are averaged. We compare this value with the median range size from the before community [Colour figure can be viewed at wileyonlinelibrary.com]

amount of natural habitat that remained at the time (year) and location (0.25° grid cell) where it was made. Hence, for each species we could produce a list of habitat values for each cell that it occupied. We could then find, for each species, the amount of habitat that remained at its last record in a given cell (hereafter, minimum

habitat value). The minimum habitat value indicated the amount of habitat loss at the latest time when a species was still reported to be present in a cell. These values were used to calculate persistence curves for small- and large-ranged species experiencing habitat loss.

It was not possible to find minimum habitat values for all species and all cells in our data collation. This was because of insufficient sampling for many species but also because we needed to confine data to cells that had experienced habitat loss. Therefore, we set three rules for the inclusion of species and cells: (a) in each cell, a species had to be sampled at least twice; (b) in each cell, a species had to be recorded before habitat loss ($\geq 80\%$ of natural habitat remaining); and (iii) species had to occur in cells that eventually experienced habitat loss (ultimately 0% natural habitat remaining).

Applying these inclusion rules led again to a drastic reduction of data. From c. 180,000 species, 102,970 met the first rule and were sampled at least twice within one cell. Of those, 53,199 species also met the second rule and were present before habitat loss. Finally, only 2,678 species also met the third rule and occurred in cells that experienced complete loss of natural habitat. Correspondingly, cell numbers reduced from c. 90,000 to c. 43,000 (first rule), to c. 10,000 (second rule) to 365 cells (third rule). The spatial extent of these cells was largely comparable to the previous analysis (Supporting Information Figure S3). For the final subset of species and cells, we found minimum habitat values.

We then used those species' minimum habitat values to calculate probabilities of persistence as follows (for a schematic representation, see Figure 3). Species' minimum habitat values were assigned to one of five 20%-wide intervals of habitat loss. The number of species in each of these intervals was then counted. Finally, these counts were divided by the total number of species. This gave the percentage of species that persisted within a given interval of habitat loss and allowed us to plot a persistence curve. We extend this basic approach conceptually in the following two paragraphs.

Note that a species can have more than one minimum habitat value. Theoretically, a species could have as many minimum habitat

values as cells it occupies. We could simply average these to obtain one value for each species, but this would also return only one persistence curve. Instead, if we sample one minimum habitat value from each species at a time and repeat this many times, we arrive at many persistence curves, one for each sampling repetition. From these, we can still calculate an average persistence curve but also gain information about the variance of this curve. Therefore, we sampled from each species one minimum habitat value at a time, repeated this 100 times, and calculated the mean and standard deviation of the resulting 100 persistence curves.

To arrive at a separate persistence curve for small-ranged species and large-ranged species, we divided the total set of species into two classes as follows. From the range-size frequency distribution of the 2,678 species, we calculated the median range size. Species with range sizes below the median were classified as small-ranged species and species with range sizes above the median as large-ranged species (Supporting Information Figure S4). We then calculated probabilities of persistence for each range size class separately.

The central assumption of our calculation of persistence probability is that a species has become extinct after its last record. Of course, the fact that a species goes unrecorded is not proof that it has become extinct, but a necessary condition for extinction is absence from further samples. We also examined how reasonable this assumption is. We examined the number of years that had passed and the number of occurrence records that had accrued since the last time a species was reported to be present in a cell. If these numbers are low, our assumption is probably unrealistic; that is, a species is not recorded anymore because there was simply no sampling in the meantime. Moreover, low detectability in certain types of plants can make them likely to be present but not recorded in

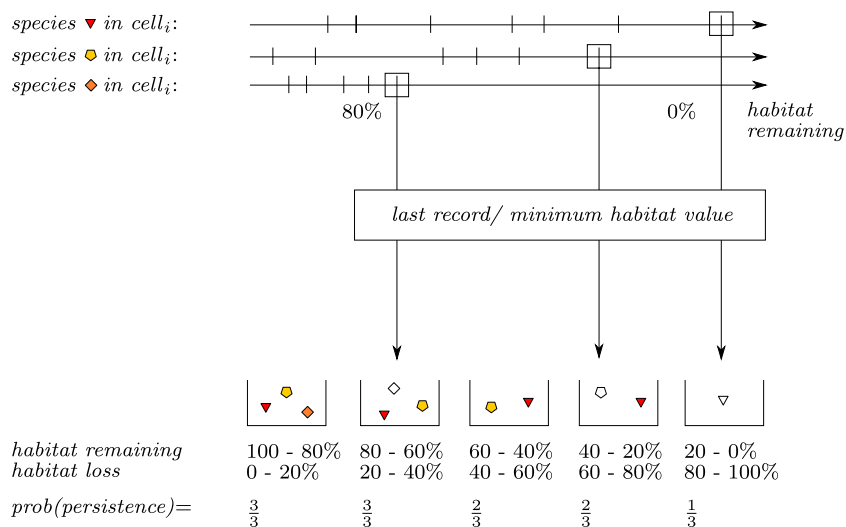


FIGURE 3 Schematic representation of our approach to calculation of persistence curves for species under habitat loss. The scheme focuses on one cell, cell_i. In this cell, the focus is on three species. All of them have been sampled at least twice, occurred before habitat loss, and importantly, cell_i experienced complete habitat loss and was sampled further. For each species, we identified its last record (minimum habitat value). We assigned the species' minimum habitat values to one of five intervals of equal length. Given that species were present before habitat loss, they also occurred in the intervals that preceded those of the last records. Given that species went unrecorded in subsequent intervals, they were absent from those. We calculated the probability of persistence as the number of species in each interval divided by the total number of species [Colour figure can be viewed at wileyonlinelibrary.com]

a census or inventory. In particular, small-ranged species that may be locally less abundant may have a lower probability of being re-sampled. This could bias our results. Therefore, we also examined whether resampling differed between small- and large-ranged species. Assuming that species are resampled at an equal and constant rate, the number of records would always be higher for species that withstood more habitat loss. Hence, we compared the number of records per percentage of habitat loss for small- and large-ranged species.

Finally, we used a simulation approach to test whether our way of calculating persistence probabilities produces any bias. The null hypothesis is that extinction, and consequently, the amount of habitat that remained at the time of extinction is random for both small- and large-ranged species. Thus, we simulated minimum habitat values from a uniform distribution. In particular, we simulated n minimum habitat values for each species, where n is the species' range size (i.e., the number of cells it occupies). We sampled one minimum habitat value from each species, calculated probabilities of persistence as above, repeated this 100 times and compared the average persistence curve of small-ranged species with the average persistence curve of large-ranged species. If our approach is free of bias, the two persistence curves should be largely the same. We provide R code for this simulation in the Supporting Information (section R Code 4.1 & 4.2).

3 | RESULTS

We studied changes in the frequency distribution of the range sizes of vascular plant species in 0.25° grid cells that experienced complete loss of natural habitat. Keeping species richness constant, the distribution of changes was towards higher median range size after habitat loss (pairwise permutation test: $Z = -2.99$, $p < .001$, $r = .22$; Figure 4a). Our approach to control for temporal bias by subsampling

communities to keep numbers of species before and after habitat loss constant did not induce any systematic bias. The distribution of effect sizes was not skewed towards positive log ratios but distributed evenly around zero (Supporting Information Figure S5a). In addition, relaxing our data selection thresholds did not change results (Supporting Information Figure S1).

Next, we studied the role of species range size in predicting vulnerability to local extinction from habitat loss. For this, we investigated the probability of persistence of small- and large-ranged species at different levels of habitat loss. Probabilities of persistence, expressed as the percentage of species of a given range size class that still occurred at, but not above, a given amount of habitat loss, indicated a generally higher vulnerability of small-ranged species to local extinction from habitat loss (Figure 4b). Small-ranged species had a steeper descending persistence curve and, moreover, a lower probability of persistence than widespread ones even at moderate levels (i.e., $\leq 50\%$) of habitat loss.

The absence of a species at higher levels of habitat loss is not proof of extinction. Therefore, we quantified the strength of this assumption. On average, 106 years passed and 806 species records accrued between the last record of a species and the last record of a cell, when species went extinct early (last reported present with $\geq 80\%$ habitat remaining). Species that persisted longer (last reported present between 60 and 80% habitat loss) had, on average, 60 years and 1,591 other species' records between their last record and the last record of a cell (Supporting Information Figure S6). Assessing potential sampling effects, we found that sampling frequencies per percentage of habitat loss were not higher for species with large ranges (Supporting Information Figure S7). Simulation results based on random extinctions of small- and large-ranged species showed that our approach did not produce any systematic bias. The simulated persistence curve of small- and large-ranged species followed the same trajectory (Supporting Information Figure S5b).

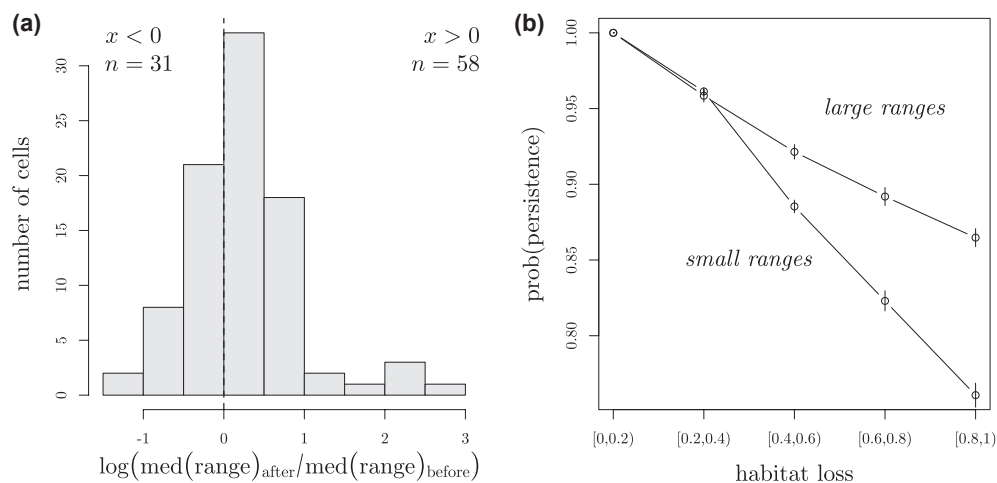


FIGURE 4 (a) Change in median range size of vascular plant communities before and after habitat loss. Positive log ratios indicate that median range size was higher after habitat loss. (b) Relationship between probability of persistence and habitat loss for species with small and large ranges. Small and large ranges include species with ranges from 1 to 63 and from 64 to 5,000 occupied cells, respectively. Error bars represent \pm two standard deviations from the mean

4 | DISCUSSION

Here, we show that habitat loss has a differential effect on the local extinction risk of vascular plant species with different range sizes. We find that the frequency distribution of range sizes in a community changes after habitat loss towards a higher median range size. In addition, we document lower persistence probabilities of small-ranged species at already moderate habitat loss. Together, this suggests that range size can be a predictor of the risk of local extinction from habitat loss. Moreover, our results imply that temporal species turnover under habitat loss can reduce spatial species turnover.

The differential vulnerabilities of species with small and large ranges to local habitat loss might have several explanations; here, we present four. First and most simply, it could follow from the effect of range size on metacommunity dynamics. Species with larger ranges are more likely to retain intact habitats that can act as a source and, via the “rescue effect”, help to uphold local persistence in sites with habitat loss (Hanski, 1991; Leibold et al., 2004). Second, it has been demonstrated for a number of taxa that range size is strongly and positively correlated with local abundance [plants (Gotelli & Simberloff, 1987), birds (Gaston & Blackburn, 1996) and mammals (Brown, 1984)]. Given that the probability of local extinction increases with decreasing population size (Christiansen & Fenchel, 2012; Schoener & Spiller, 1987), species with small ranges could be more vulnerable to habitat loss at any one site. Third, narrow habitat breadth, yet another dimension of rarity that may relate to range size (Brown, 1984), could make species with small ranges more susceptible to anthropogenic change (Rabinowitz, 1986). Fourth, habitat breadth and local abundance may influence the spatial distribution of species (Cornell, 1982). Species with relatively narrow habitat breadth and small population size are often unevenly distributed in aggregations within their range (Condit et al., 2000; Rodríguez, 2002). The more aggregated a species, the less habitat must be lost, on average, to cause local extinction. The individual importance of these potential mechanisms to make species vulnerable to local extinction still needs to be quantified.

Importantly, the higher local extinction risk from habitat loss of species with small ranges might contribute to the explanation of the systematic shifts in species composition and the scale-dependent patterns of diversity change that other studies report with long-term data. Evidence across biomes indicates no net loss in local species richness (Vellend et al., 2013), but loss of species at the continental to global scale (IPBES, 2019). If species with small ranges are preferentially declining at any one site with habitat loss, species with large ranges may also be more likely to colonize successfully, replacing small-ranged species systematically. Given that it is more likely that the entire range of small-ranged species is affected, habitat loss could then produce a homogenization pattern, where small-scale richness is largely unchanged through time, whereas larger-scale richness declines. Although our approach does not allow any inference about local-scale changes in species richness and thus species replacement, we can nevertheless infer homogenization. This is because for biotic homogenization to occur, it is sufficient that the most localized species

are systematically lost (McKinney & Lockwood, 1999; Olden & Poff, 2003) and precisely those, we find, are at higher risk of local extinction from habitat loss. This preferential decline of species with small ranges is consistent with a recent global assessment of the effects of land use on small-ranged and widespread species (Newbold et al., 2018). Those authors used space-for-time substitution to show that disturbed habitats have both reduced abundances of small-ranged species and increased abundances of widespread ones. Here, we used time series data. This allowed us, in addition to studying changes in species' range size composition, to explore how local extinction risk changes with habitat loss. To our knowledge, this is the first time that local extinction curves have been plotted against a habitat loss gradient and shown to differ for species with small and large ranges.

In the case of vascular plants, many species appear to cope well with habitat loss (Figure 4b). Recognition is growing that many species are not entirely constrained to native habitat fragments and persist in agricultural landscapes (Daily, Ehrlich, & Sanchez-Azofeifa, 2001; Mendenhall, Karp, Meyer, Hadly, & Daily, 2014); that is, habitat loss does not create a matrix entirely inhospitable to species, as is commonly assumed in studies that apply the species–area relationship from island biogeography theory to estimate the species loss attributable to change in land use. Countryside biogeography (*sensu* Mendenhall et al. (2014)), instead, considers the affinity of species for human-modified habitats, such as agriculture and forestry (Pereira, Daily, & Roughgarden, 2004), and argues that their qualities are crucial determinants of the conservation of biodiversity (Karp et al., 2012; Prugh, Hodges, Sinclair, & Brashares, 2008). Although we do not quantify the differential importance of anthropogenic habitats on the persistence of species, our results indicate that a large percentage of species can survive loss of natural habitat. Our results therefore highlight that the overextension of island biogeography theory to human-dominated ecosystems might overestimate projections of biodiversity loss driven by change in land use (Mendenhall et al., 2014).

Our approach to combine reconstructed biological time series and land-use data is novel, but also has weaknesses. The land-use harmonization product, although constrained by satellite and census data, is a model-based reconstruction from limited empirical data. It thus has differing accuracy in time and space (Ellis et al., 2013). Nonetheless, it provides the most comprehensive global land-use data available and has been widely applied in the literature. The digital biodiversity data also suffer from biases (Meyer et al., 2016). We accounted for the temporal documentation bias by subsampling communities, and simulations showed that this step did not induce any systematic bias (Supporting Information Figure S5a). We note that different before–after time periods were compared for this analysis (Supporting Information Figure S2). Therefore, cells that lost habitat early on would have had a longer time for extinctions to occur over and also a longer time to accrue opportunistic records. However, comparison of different time periods would not alone lead to higher community median range sizes, on average, after habitat loss.

For the calculation of persistence probabilities, we found no sampling bias towards species with larger ranges in our data subset (Supporting

Information Figure S7). This could reflect the ter Steege effect, which describes the fact that botanists tend to avoid collecting large-ranged species that they have already collected in the general vicinity (ter Steege, Haripersaud, Bánki, & Schieving, 2011), but it is more likely that this is because we set strict inclusion rules for species and cells, meaning that our data subset includes rather well-sampled species. But this might also mean that we are neglecting truly rare species (Supporting Information Figure S4), potentially weakening the effect of range size in our analysis. Nonetheless, persistence curves differed between relatively small- and large-ranged species. Importantly, we can exclude the possibility that our approach produced these differences. Under simulated random extinctions, the persistence curves of small- and large-ranged species did not differ (Supporting Information Figure S5b).

In addition, we find that the assumption that a species goes extinct after its last record is justifiable for our data subset, because in general, many other species records were made in the meantime (Supporting Information Figure S6). Finally, we note that locations of this analysis are spatially biased. For example, no cell in Asia or tropical Africa met the inclusion criteria of the before–after comparison. This spatial bias is typical for digital biodiversity data, and only with increasing data-mobilization efforts in these regions will analyses based on such data become truly globally representative. Although we acknowledge that data biases are inherent to our data, we contend that they do not nullify the implications of our results. Given that small-ranged species are at higher risk of local extinction, temporal species turnover is biased towards species with larger ranges in local communities undergoing habitat loss.

Although it is expected that species with smaller ranges will be more vulnerable to global extinction from habitat loss than widespread ones, because the drivers of threat are more likely to affect the entire range of these species (Collen et al., 2016), we emphasize that there is a lack of studies that quantify this expectation at different spatial scales. Here, we find that relatively small-ranged species are more vulnerable to extinction from habitat loss even at a local scale. This will necessarily cause a disproportionate effect of range size on the risk of extinction at broader spatial scales. Understanding and quantifying the mechanisms that determine local extinction risk from anthropogenic change, how these depend on spatial scale and how local extinction risk, in turn, can be used to predict the consequences of range loss will be imperative for the conservation of species.

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DATA AVAILABILITY STATEMENT

Species' point occurrence data are openly available from GBIF (<https://doi.org/10.15468/dl.chiubr>), BIEN (via R package BIEN) and PREDICTS (<https://doi.org/10.5519/0066354>). Global land-use data are openly available from LUH2 (<http://luh.umd.edu/data.shtml>). We provide the R markdown file for data retrieval and cleaning, and all simulations, in the Supporting Information.

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BIOSKETCHES

Ingmar R. Staude is a PhD student working under the supervision of **Henrique M. Pereira** and **Laetitia M. Navarro** in the Biodiversity Conservation group of iDiv. His research focuses on the causes and prediction of species extinction.

SUPPORTING INFORMATION

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

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