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Species richness change across spatial scales

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Humans have elevated global extinction rates and thus lowered global scale species richness. However, there is no a priori reason to expect that losses of global species richness should always, or even often, trickle down to losses of species richness at regional and local scales, even though this relationship is often assumed. Here, we show that scale can modulate our estimates of species richness change through time in the face of anthropogenic pressures, but not in a unidirectional way. Instead, the magnitude of species richness change through time can increase, decrease, reverse, or be unimodal across spatial scales. Using several case studies, we show different forms of scale-dependent richness change through time in the face of anthropogenic pressures. For example, Central American corals show a homogenization pattern, where small scale richness is largely unchanged through time, while larger scale richness change is highly negative. Alternatively, birds in North America showed a differentiation effect, where species richness was again largely unchanged through time at small scales, but was more positive at larger scales. Finally, we collated data from a heterogeneous set of studies of different taxa measured through time from sites ranging from small plots to entire continents, and found highly variable patterns that nevertheless imply complex scale-dependence in several taxa. In summary, understanding how biodiversity is

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changing in the Anthropocene requires an explicit recognition of the influence of spatial scale, and we conclude with some recommendations for how to better incorporate scale into our estimates of change.

Synthesis

There is no doubt that human activities have driven hundreds to thousands of species extinct, with recent reports (e.g. IPBES) suggesting a million more at imminent risk. While it is often implicitly assumed that this global biodiversity loss must be reflected at smaller scales, this is not always (or even often) true. Instead, even within the same taxa, species richness can decline locally but increase regionally, vice versa, or have more complex scaling relationships. We highlight the critical need for a scale-explicit quantification of species richness change and its potential drivers to achieve deeper understanding of biodiversity in the Anthropocene.

Introduction

Biodiversity is changing through time at a rapid pace, and anthropogenic factors such as land-use intensification and climate change are directly and indirectly responsible (Pereira et al. 2012, Pimm et al. 2014, Ceballos et al. 2015). Such biodiversity change has profound influence on the functioning and stability of natural ecosystems and the people who depend on them (Cardinale et al. 2012, Isbell et al. 2017), precipitating a number of international collaborations and policies to understand and manage these changes (e.g. Aichi targets of the United Nations' Convention on Biodiversity; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES); Tittensor et al. 2014, Diaz et al. 2015). Exactly how this change is manifest, however, has been the subject of some debate. At the global scale, historical and modern anthropogenic factors have directly and indirectly caused the extinction of many taxa (Barnosky et al. 2011, Pimm et al. 2014, Alroy 2015, McCauley et al. 2015), leading to a decline in global-scale species richness. While it is sometimes assumed that global extinctions are reflected across all spatial scales, this is not always, or even often, the case. Instead, exactly how species richness changes at scales smaller than the globe is more nuanced and has been the subject of some debate (see Primack et al. 2018 for an overview).

Change in the numbers of species through time at scales smaller than the globe (i.e. in the absence of speciation) will depend on the balance between losses and gains of species from one point in time to the next (Sax et al. 2002, Jackson and Sax 2010, Batt et al. 2017, Dornelas et al. 2019). In this article, we do not enter into the debate about whether fine-scale species richness is changing in the face of human activities (Vellend et al. 2013, 2017a, Dornelas et al. 2014, Gonzalez et al. 2016, Cardinale et al. 2018), but rather simply acknowledge that the observed pattern of change is variable, with some intriguing biogeographic and taxonomic variation (Newbold et al. 2015, Blowes et al. 2018). Nor do we distinguish among types of species involved in any change (e.g. native versus non-native, specialist versus generalist), even though turnover in species composition is more responsive to environmental change than species richness change (Dornelas et al. 2014, Supp and Ernest 2014,

Hill et al. 2016, Hillebrand et al. 2018). Instead, our main purpose is to emphasize that species losses and gains though time are asymmetric across spatial scales. It only takes one individual of a new species to result in a gain, but requires the loss of all individuals of a species to lead to a loss. Given this asymmetry, it is likely that the magnitude of species richness change through time, and even its direction (i.e. losses observed at some scales and gains at other scales) will be strongly influenced by the spatial scale under investigation (Cassey et al 2006).

Rates of loss of species from a given area via extirpations can be lower or higher than the global rate, and can be highly non-linear across scales (Hughes et al. 1997, Keil et al. 2018). Gains are likewise highly scale-dependent and result from the recolonization of previously extirpated species (McAlpine et al. 2016), range expansions (via climate change and human modification of habitat) (Batt et al. 2017), and/or introductions of species into their non-native ranges (Sax et al. 2002). As a result, biodiversity change, and especially the change in species richness through time, can often be scale-dependent (Sax and Gaines 2008, Cassey et al. 2006, McGill et al. 2015, Vellend et al. 2017b).

There have been numerous case studies illustrating the critical role of scale for understanding species richness change (Hill and Hamer 2004, Dumbrell et al. 2008, Keil et al. 2011, Carvalheiro et al. 2013, Chase et al. 2018, Jarzyna and Jetz 2018). However, the incorporation of spatial scale in modulating species richness change through time in the context of anthropogenic pressure has not been well considered in previous meta-analyses (Vellend et al. 2013, Dornelas et al. 2014, Newbold et al. 2015, Blowes et al. 2018; but see Elahi et al. 2015), even though the spatial extent of studies included varies by orders of magnitude (Cardinale et al. 2018). Nor has spatial scale been incorporated into conservation and scenario modelling in the context of biodiversity–policy initiatives (Isbell et al. 2017, Purvis et al. 2018). Furthermore, when spatial scale is considered, it is often implicitly assumed that species richness change varies with scale in a relatively straightforward way, so that change observed at one scale can be used to predict change at another scale. As we will argue below, this expectation can often prove to be incomplete or wrong.

In the context of species richness change in the face of human impact, scale-dependence has been most often discussed regarding changes in site-to-site species composition,

known as β-diversity (Socolar et al. 2016). For example, biotic homogenization (McKinney and Lockwood 1999, Olden and Rooney 2006) leading to a reduction in β-diversity, could be one explanation for why smaller-scale patterns of species richness (i.e. α-diversity) may not change (or even increase) despite larger-scale (i.e. γ-diversity) extinctions via Whittaker's (1960) diversity partition, $\gamma = \alpha \times \beta$. However, the opposite pattern, an increase in β-diversity through time leading to biotic differentiation, is increasingly recognized as a frequent result of human impact (Socolar et al. 2016). This can occur, for example, via increases in habitat heterogeneity (e.g. multiple types of land-use in a landscape), introductions of species that remain relatively localized, or the loss of common/shared species among locations (Winter et al. 2009, de Castro Solar et al. 2015, de Carvalho et al. 2016).

Because both biotic homogenization and differentiation may be common, the direction of scale-dependence of species richness change following human impacts will be variable. As we illustrate below, the magnitude of species richness change can increase with scale under biotic homogenization, but decrease with scale under biotic differentiation. Thus, simply including the scale of observation as a covariate in synthetic analyses of species richness change would only yield interpretable results if one of these processes (and thus directions of scale-dependence) predominates.

In what follows, we first discuss the theoretical expectations for how patterns of species richness change through time, particularly in response to human pressures, and critically illustrate how these depend on the spatial scale of observation. We show that scale alters our observations of species richness change in a more complex way than typically assumed. Next, we illustrate this nuance with a series of case studies that show disparate scale-dependent responses of species richness change. Finally, we compile data from a number of sources that measured change through time across multiple taxa and scales. In summary, we show that the seemingly simple question of how species richness is changing through time in the face of anthropogenic change is not only scale dependent, but that this scale-dependence itself is more complex than typically assumed, and will require a great deal more work explicitly detailing the influence of scale in order to fully understand and synthesize patterns.

Theoretical framework for the scale-dependence of biodiversity change

The null expectation in the absence of any strong environmental change is that there should be no net change in species richness through time (despite species turnover) as a result of balanced colonizations and extinctions (MacArthur and Wilson 1967, Brown et al. 2001). At the global scale, and across very long time periods, this stasis would also depend critically on speciation and extinction events, but we do not consider this further. A number of factors associated with human impacts can alter this null expectation,

including shifts in local environmental conditions (e.g. land use, environmental change), and regional shifts in the size and composition of the species pool (e.g. via introductions or extirpations) (Brown et al. 2001, Jackson and Sax 2010).

We use two qualitatively distinct model scenarios to illustrate the following: 1) that scale-dependence in species richness change is typical. 2) That the nature of scale-dependence in species richness change depends critically on model structure and parameter values. Details of the two model structures are presented in Supplementary material Appendix 1.

In the first model scenario, the metacommunity is altered by some hypothetical change such as that due to human impacts, but has not returned to equilibrium when richness is measured following the change. Here, there was strong scale-dependence between the average change in species richness through time and the spatial scale of observation, but this was strongly dependent on the structure of dispersal among localities (Fig. 1A). When dispersal was relatively high (intermediate and global), we often observed a hump-shaped relationship between species richness change and scale (see also Cassey et al. 2006, which had a similar model structure). However, the position of this hump-shape (whether richness increased or decreased in total) depended critically on the rates of local extirpations. When dispersal was more localized, scale-dependence was weaker and tended to be unidirectional towards more negative effects at larger scales (Fig. 1A).

In the second set of simulations, we allowed communities to return to a quasi-equilibrium following the hypothetical change. Here, the direction of change and its scale dependence were quite different. First, when we assumed that only the carrying capacity of the local community was changed by the perturbation, there were only increases or declines in equilibrium species richness through time, but these changes were not strongly scale-dependent (Fig. 1B). However, when species colonization rates were also altered, we observed strong scale-dependence in equilibrium species richness change (Fig. 1B). When colonization rates were increased, local species richness increased, but this effect declined with scale (sometimes leading to decreases at the largest scales) as a result of biotic homogenization. Conversely, decreases in colonization rates tended to decrease local species richness, but the magnitude of this decreased with increasing spatial scale (sometimes leading to increases at the largest scale) as a result of biotic differentiation.

By no means are these modelling scenarios complete, but even within our brief presentation, it is easy to see the breadth of possibilities of how species richness can change, and how that change can be scale-dependent, following some environmental perturbation. Nevertheless, there are some important general caveats to the simple simulations we have shown here. First, we assumed that environmental conditions are identical throughout the metacommunity, and that this does not change through time (e.g. is not influenced by human activities). However, in reality the environmental changes that result from human interventions not only directly influence species colonizations and
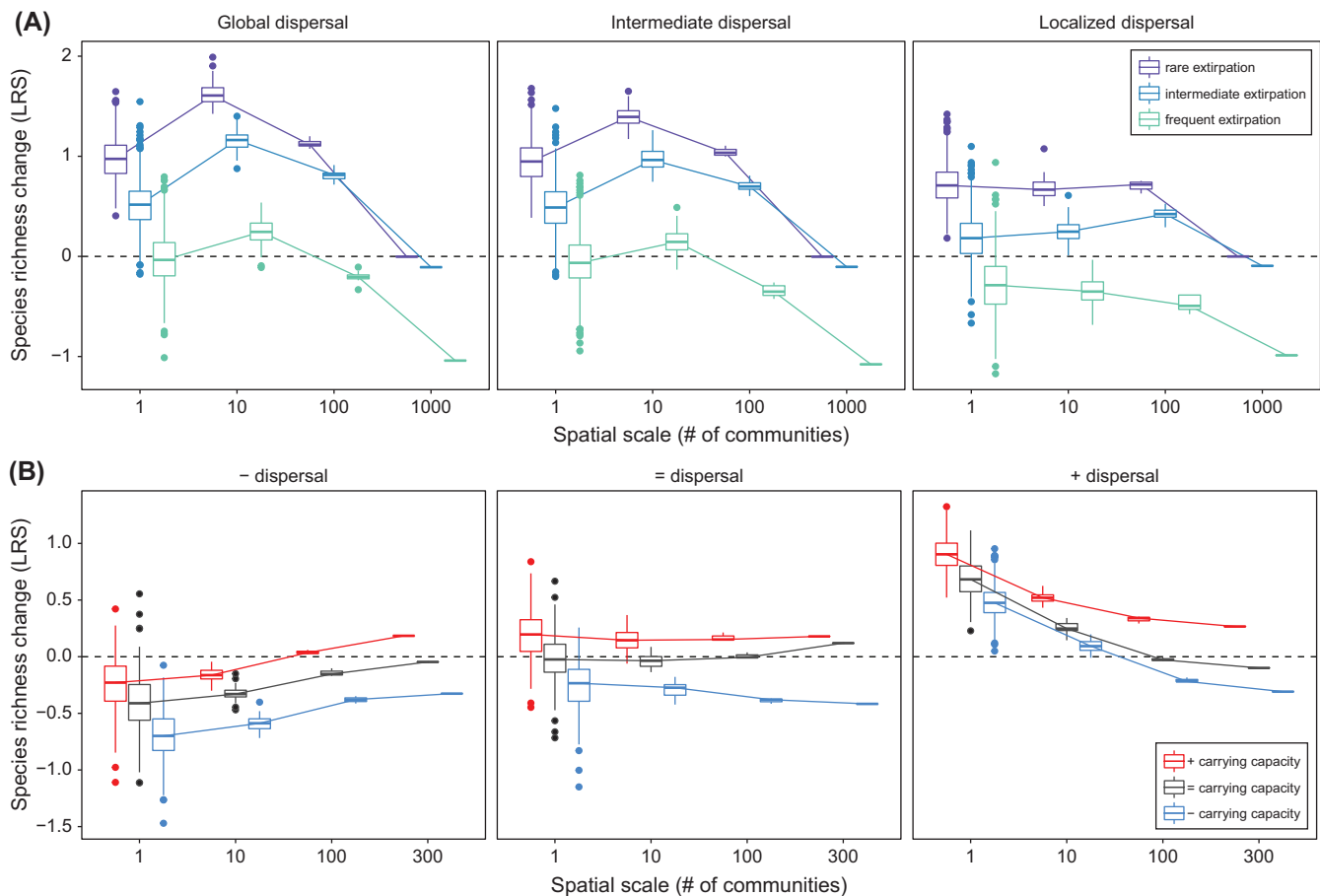
Figure 1. Species richness change at four spatial scales in the two simulation models. (A) shows the non-equilibrium model and (B) shows the equilibrium model. In (A), scenarios of dispersal scale are arranged by column (global – dispersal is equally likely between all local communities; intermediate – dispersal is somewhat constrained within nested spatial scales; localized – dispersal is highly constrained within nested spatial scales). The colors contrast three different scenarios of local extirpation frequency (rare, intermediate and frequent). In (B), scenarios of dispersal change are arranged by column (decreased, no change and reduced dispersal compared to the pre-equilibrium conditions). The colors contrast different scenarios of carrying capacity change. In both panels, box plots show the range of variation at a given spatial scale in the simulation. Boxplots are offset to avoid overlap, but all scenarios were conducted at the same spatial scales in each model. The solid lines connect the median values for each spatial scale. Both panels show results from a single representative run of the simulation.

extinctions, but do so indirectly by altering habitat characteristics. This can either increase habitat heterogeneity (more likely leading to differentiation) or decrease habitat heterogeneity (more likely leading to homogenization), which would alter the expected magnitude and direction of scale-dependent species richness change (Socolar et al. 2016). In addition, species in our models have no trait differences, whereas environmental changes such as those caused by human-modified landscapes are often associated with losses of narrowly distributed specialist species and gains in widely distributed generalist species, which could tip the balance towards biotic homogenization and greater losses at larger scales (Mckinney and Lockwood 1999, Eskildsen et al. 2015, Gossner et al. 2016). Such complexities would provide valuable information about the nuance in these relationships expected for specific real-world cases. However, fitting any of the model predictions to specific cases is beyond what we hope to accomplish here.

Recognizing that the modelling scenarios we presented in Fig. 1 represent only a small fraction of the possibilities for how human activities can alter patterns of species richness and its scaling, we provide a more generalized framework that is necessarily more phenomenological in Box 1 (similar to, but more general than that presented by Chase et al. 2018). Specifically, we draw hypothetical species–area relationships (SARs) for a given system, comparing between two time periods (before and after some hypothetical environmental or human-caused change). By comparing the difference between the two SARs at any given scale, we can quickly see 1) how scale-dependence can emerge depending on how the parameters of the SAR change between time periods, and 2) that the direction of scale-dependence will critically depend on the nature in which SARs are influenced.

Box 1. Conceptual overview of scale-dependent species richness change through time

We illustrate how species richness can change through time by varying parameters of the power-law species-area relationship (SAR), $S = cA^z$ (where S is species richness, A is area, and c and z are constants) and simple derivatives of it, between two time periods. This can also be directly linked to the concept of diversity partitioning (γ-diversity $= \alpha$-diversity $\times \beta$-diversity) and the influence of biotic homogenization and differentiation through time (Crist and Veech 2006, Scheiner et al. 2011, Socolar et al. 2016).

The figure below illustrates several qualitatively distinct ways in which the balance of species gains and losses ($=$ net change in richness) through time can change from local to global scales. In each case in the figure below, the solid line represents the SAR from one point in time, and the dashed line represents the SAR from a different point in time. The largest scales in these comparisons need not be global, and instead can represent differences in regional species richness, which can decrease via range contractions or local extirpations, or increase via introductions or range expansions. For completeness, the two time periods (A and B) can be reversible; time A can be 'pre-impact' and time B can be 'post-impact', or vice versa.

In each of the first four cases of the figure, we vary the two parameters (c and z) in the SAR between the two time periods, and compare the log response ratio difference in species richness between the two time periods. In the final case, we changed the power law form of the SAR to have a saturating shape (i.e. $S = c + AS_{max}/(k + A)$, where S_{max} is the saturation value for species richness, and k is the area at $S = 0.5S_{max}$). (Note, we are not arguing that SAR curves should be saturating, but rather use this shape simply to illustrate how homogenization and differentiation can simultaneously operate at different scales). By simply changing the parameters of these models, we show how species richness change can increase, decrease or remain the same through time, and how the magnitude of this change can increase, decrease or be unimodal across spatial scales.
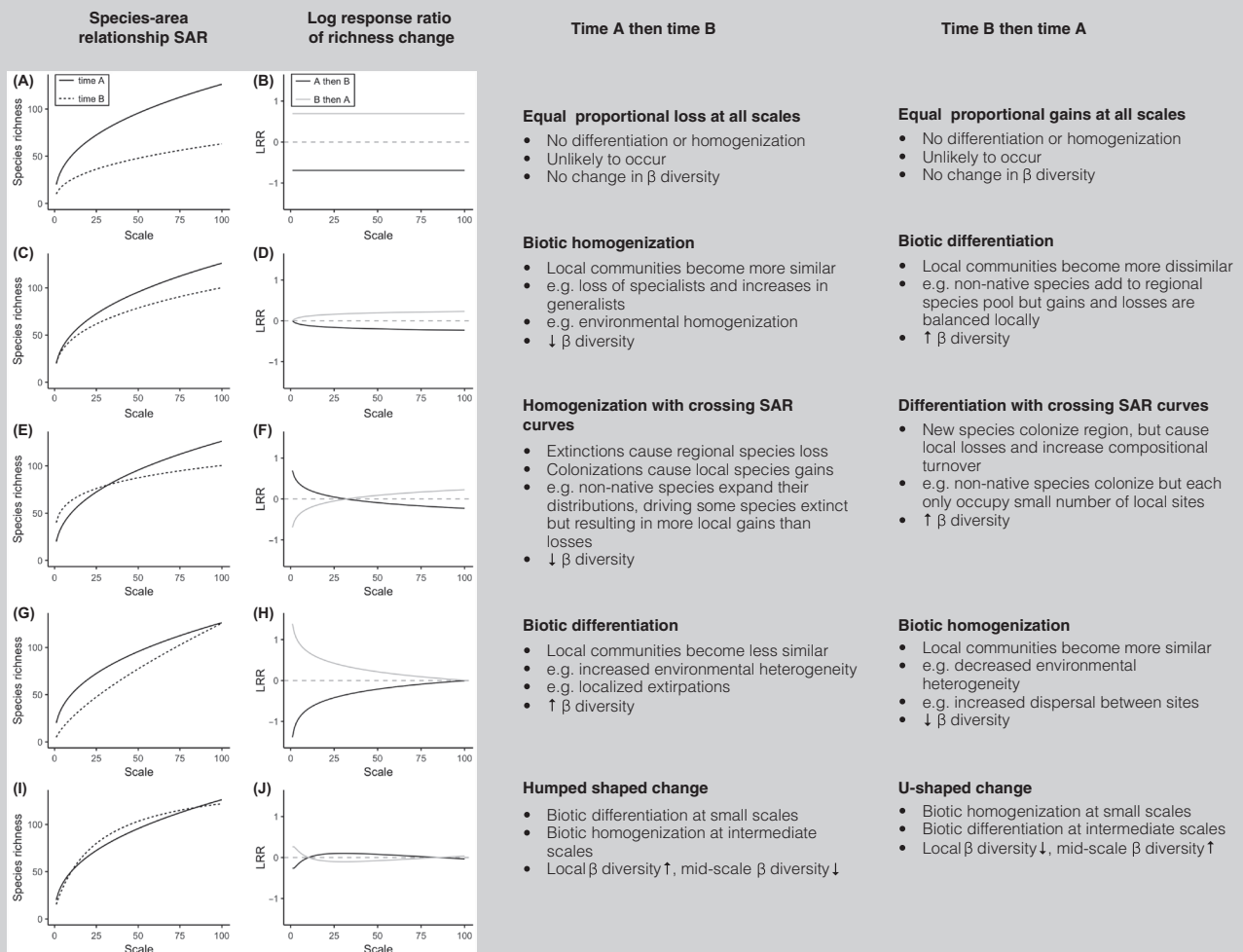
Conceptual figure illustrating different hypothetical scenarios of biodiversity change and their relationship with spatial scale: equal proportional change (A–B), greater regional than local change (C–D), crossing SARs (E–F), greater local than regional change (G–H), and double crossing SARs (I–J). The left column (A, C, E, F, I) shows species-area relationships (SARs) at time A (solid line) and time B (dashed line). The right column (B, D, F, H, J) shows the log response ratio (LRR) of this change (i.e. log(S_{after}/S_{before})), where the black line corresponds to the scenario of time A then B and the grey line is time B then A.

Case studies illustrating scale-dependence of biodiversity change over time

We next illustrate case studies where patterns of scale-dependence were consistent with several of the hypothetical scenarios discussed above. While lacking generality, these case studies have the strength that the data are consistently gathered and directly comparable across nested scales across at least two time periods. Such nested observations collected with uniform methods is critical for quantifying true scale-dependent species richness change, but is only available for a limited number of case studies. For each system, we compared species richness from two time periods. Then we examined how species richness changed through time at different spatial grains (sampling points or geographic units) nested within that larger extent.

An overview of the case studies is provided in Table 1. Two of these case studies – corals near Central America and North American breeding birds – are based on surveys done at local scales to evaluate species richness change over a period of years to decades. The other two case studies – passerine birds from the Hawaiian archipelago and European plants – are based on checklists of species from smaller regions (e.g. islands, countries) that were nested to create checklists for the encompassing regions to evaluate scale-dependent changes due to human activities over centuries. In each case, we had information on species composition in addition to numbers of species present, gained and/or lost, and so we could nest the data at different spatial scales. For each case study, we plot the patterns and used quadratic ordinary least squares regression with 10 and 90% quantiles for visualization (in Supplementary material Appendix 2, we provide some discussion of more formal statistical analyses).

Central American corals

Reef-forming scleractinian corals were sampled across multiple reefs along the Pacific coast of Panama annually (full data and analyses presented in Gomez et al. 2017). In Fig. 2A, we present data from multiple reefs over a 5-year period (2005–2009) where significant change in water temperature anomalies led to variable change in coral abundance and evenness. Nested sampling was organized as follows: 1) several one m^2 permanent quadrats were the smallest unit, and these were censused visually each year; 2) ten of these quadrats were along 10 m transects; 3) three transects (= 30 quadrats) were in the upper slope of a reef and three transects (= 30 quadrats) were in the lower slope of a reef; 4) the six transects from a

reef were combined (= 60 quadrats) to achieve a 'reef-scale' estimate; 5) five reefs (= 300 quadrats) were censused in the gulf of Chiriqui and six reefs (= 360 quadrats) were censused in the gulf of Panama to achieve 'gulf-scale' estimates; 6) all quadrats from all 11 reefs (= 660 quadrats) were combined for the largest scale estimate (see Gomez et al. 2017 for further sampling methods and other details).

When we analyzed change in coral species richness over a five-year period, we found a scale-dependent effect (Fig. 2A). At the smallest scales (quadrats, transects and reefs) some sites gained species while others lost species, but on average, there was no net change in species richness (regression quantiles overlap with zero). However, at the largest scales (entire survey), there was a trend for more species losses than gains (quantiles having no overlap with zero net change). This pattern is expected from the classic 'homogenization' scenario discussed in Box 1. Indeed, while local scale gains and losses were generally equalized, at the scale of the entire survey, more narrowly distributed species such as *Pavona frondifera* and *Pavona gigantea* were more likely to disappear from the surveyed quadrats, while widespread species such as *Pocillopora damicornis* and *Pavona clavus* became even more widespread.

North American breeding birds

Terrestrial birds were sampled annually from routes (~40.23 km with point counts every 0.8 km) spread across the United States and Canada as part of the North American Breeding Bird Survey (BBS) (for details see Sauer et al. 2017). For this analysis, we used routes over a span of 30 years (1982–2011) that met quality tests in each of these years, resulting in a total of 393 routes (we did not use older data because the number of quality routes drops quickly). We binned the data into six 5-year periods to minimize noise and detectability issues. In order to nest surveys, we used routes in a rectangular area found between 95°W to 70°W and 30°N to 50°N. To nest areas, we subdivided the area into squares of 1, 2, 4, 8, 16° and the entire 25×20° area. For each grid cell size, we examined how many routes were found in each cell, choose an appropriate rarefaction level (capturing most but not all cells) and then used sample-based rarefaction so that all cells included in the analysis were sampled equally. Specifically, we rarefied to 1, 3, 6, 32, 150 and 393 routes for the 1, 2, 4, 8, 16° and full region grid sizes. The area shown on the x-axis in Fig. 3B is based on the total directly sampled area rather than the size of the grid cells using 14.14 km^2 per BBS route (circles of 300 m radius at 50 point counts along

Table 1. Brief summary of case studies.

| Geographic region and taxa	Range of scales	Data type	Temporal range	Reference
Central American corals	1-m^2 plots nested within transects across sites and regions	surveys	5 years	Gomez et al. 2017
North American Breeding Bird Survey (BBS)	~40 km routes nested within 20×25° grid	surveys	30 years	Sauer et al. 2017
Hawaiian Passerine birds	single island to entire archipelago	checklists	~200 years	Pyle and Pyle 2017
Plants in Europe	single country to whole continent	checklists	~500 years	Essl et al. 2013
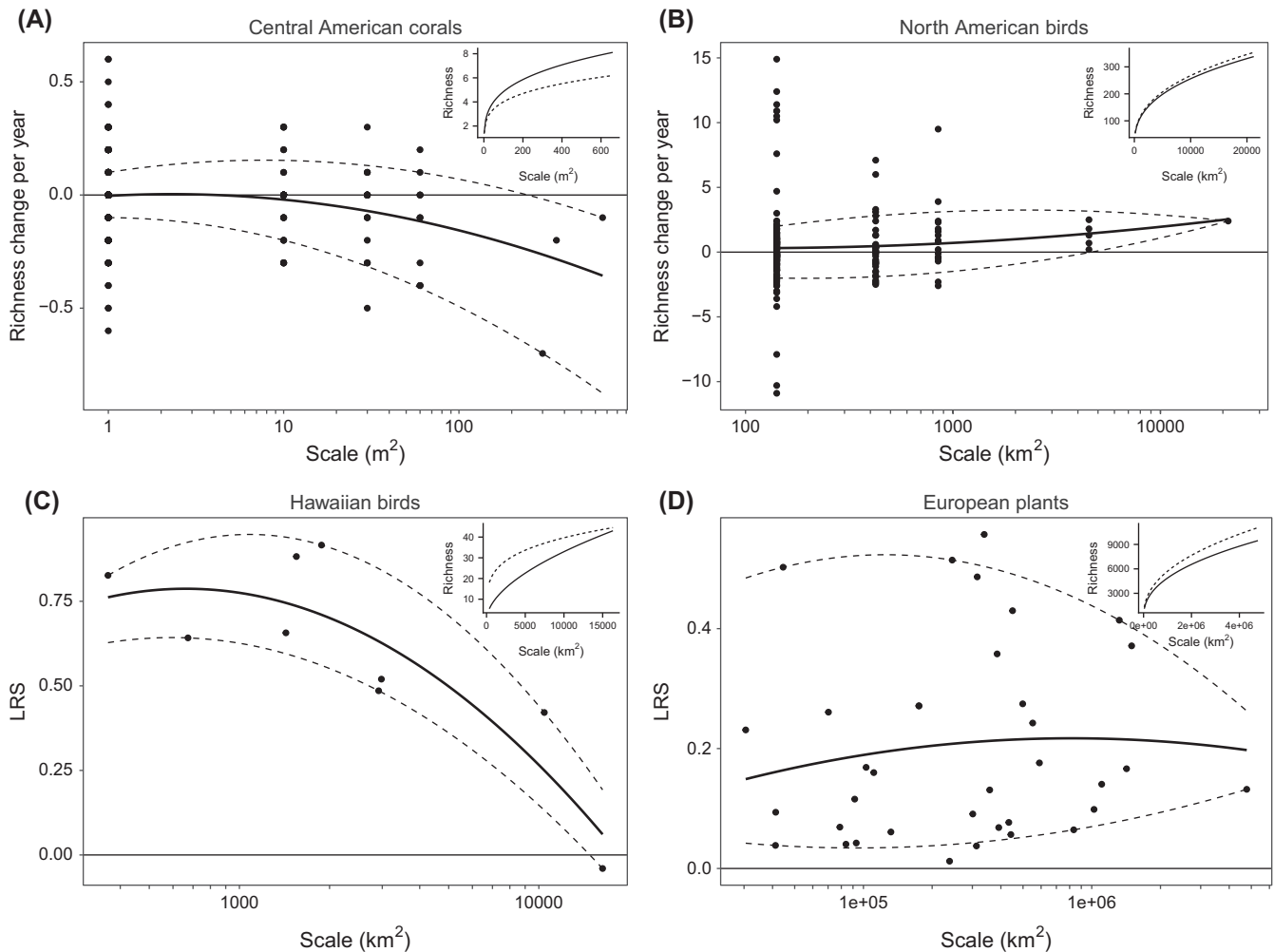
Figure 2. Results from case studies where species richness change was measured on a yearly basis from surveys (A–B), or as the log ratio of species richness change (LRS) from checklists before/after intense human activities (C–D). A brief description of each case study is in Table 1, and more detail methods are given in Supplementary material Appendix 2. Points are nested so that the smallest scale is nested within the next largest scale. For surveys (A–B), scales are discrete, while for the check-lists (C–D), scales are more continuous because countries and islands differ in size. In each case, the solid line is the fit from a quadratic ordinary least squares regression and the dashed lines are the 10 and 90% quantiles from this model. Richness change patterns for: (A) Central American corals over 5 years, where 1-m^2 quadrats are nested within transects, sites and entire regions; (B) North American Breeding Bird Survey (BBS) over 30 years where routes were aggregated into increasing degree grid sizes (the scale on the x-axis is the sum of the areas on each route); (C) Hawaiian bird species since European colonization (~200 years) of the archipelago taken from checklists of native, extinct and exotic species. Leftmost points represent change on individual islands, whereas points to the right represent change on increasing nested combinations of islands (the point at the farthest right represents the entire archipelago). (D) European plant species richness over several centuries of increasing human impact (~500 years) by including native, extinct and alien species lists from countries and nesting those within sub-regions, regions and the European continent. Insets show the corresponding SAR curves from the start (solid line) and end (dashed line) of the time-series comparisons estimated using non linear regression with the form $y = a + x^z$.

each route). We fit trend lines over the six time periods and recorded the slopes to generate estimates of yearly species richness change within a transect.

In the BBS, we found a pattern opposite to that observed in the corals (Fig. 2B). Rather than homogenization, we find a pattern more consistent with the idea of compositional differentiation through time in Box 1. Specifically, at the smaller spatial scales, there is again a considerable amount of variation whereby some sites have gains and others have losses in species richness, but overall no net change

(regression quantiles overlap with zero). This result is largely consistent with the results of Schipper et al. (2016), who also found many sites with increases and decreases when they analyzed BBS data at this scale, but detected a slight increase in species richness overall (use of different subsets of the data in both space and time could explain this discrepancy). However, when we nested data at larger spatial scales, we find a stronger and more consistent pattern of species richness increase over the last 30 years (regression quantiles greater than zero). This result is consistent with the idea that
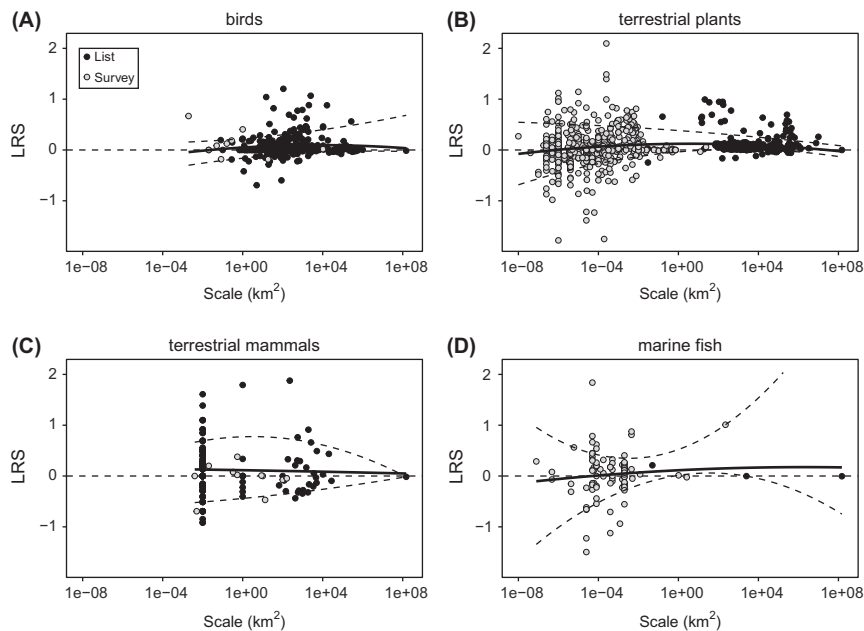
Figure 3. These figures show a plot of LRS (log ratio of species richness) versus log spatial scale, indicating trends (positive is an increase, negative a decrease in richness). Light circles are survey-based data. Dark circles are checklist-based data. Data are presented for (A) terrestrial birds, (B) terrestrial plants, (C) terrestrial mammals and (D) marine fishes. In each case, the solid line is the fit from a quadratic ordinary least squares regression and the dashed lines are the 10 and 90% quantiles.

conversion of relatively homogeneous habitats (e.g. forests, agriculture) into more heterogeneous landscapes favor different species, which combined with introductions of exotic taxa raise larger-scale species richness (Schipper et al. 2016, Jarzyna and Jetz 2018). Note, although our approach examining scale-dependent diversity responses was similar to that reported by Jarzyna and Jetz (2018) also using the BBS dataset, our results differed slightly from theirs. Specifically, Jarzyna and Jetz (2018) found increases in species richness from their smallest scales (50 km²) which increased at the scale of the entire continent, consistent with the pattern of differentiation we found at this scale. However, when Jarzyna and Jetz (2018) extended their analysis to include global extinctions, this necessarily led to a subsequent decline in richness from the continental to global scale, more in line with the hump-shaped predictions in Box 1.

Hawaiian Passerine birds

The bird fauna of the Hawaiian archipelago is a classic example of unique adaptive radiations as a result of their remoteness, as well as devastating extinctions at the hands of humans, both directly via hunting, and indirectly via the introductions of many exotic species. We compiled data from Pyle and Pyle (2017), comparing species that invaded and went extinct since colonization of Europeans (~200 years; we do not consider extinction that occurred due to humans prior to European contact) and included only data from passerines from the six largest islands (Kauai, Oahu, Lanai, Molokai, Maui, Hawaii) to avoid undue influence from marine species (see also Sax et al. 2002). This case

study is based on checklist data rather than survey data, but islands can be nested within the archipelago for a scale-explicit analysis, as presented in Fig. 2C. Here, we analyzed data for three nested scales: 1) the scale of a single island (islands differ considerably in area and so vary along the x-axis); 2) by combining the two most northerly islands (Oahu and Kauai), the three central islands which make up the Maui Nui complex that was connected ~200 000 years ago (Maui, Lanai and Molokai) (we did not nest the largest island, Hawaii, at this scale because it is so large); 3) by combining all six islands into a single archipelago-wide estimate. For each scale, we calculated the log-ratio of species richness change (hereafter LRS).

At the scale of each island, we find large increases in species richness over the considered time period (i.e. lower confidence interval is well above zero). Indeed, it is well known that introductions of bird species far exceed extinctions on these islands, leading to a net increase in species richness at the hands of humans (Sax et al. 2002, Lockwood 2006). However, when we nested islands into groups, this pattern became less dramatic. Even though individual islands gained many more species (average of 19 species) than they lost (average of 6.5 species), this pattern was reversed at the scale of the entire archipelago with a slight reduction in species richness over time (29 species went extinct archipelago-wide, while 27 species invaded). This pattern was consistent with the 'flip-flop' scenario in Box 1, whereby gains of invaders were widespread (average range of invading species was 4.07 islands), but these gains were tempered at larger scales because of homogenization, due to the extinctions of small-ranged (island endemic) species (average range of extinct species was 1.2 islands).

European plants

We used species lists of plant extirpations (based on national Red Lists) and invasions (from the DAISIE database) from Europe, compiled at the country level (see Winter et al. 2009, Essl et al. 2013 for details). We analyzed data at three nested scales based on proximity and natural geographic boundaries (Supplementary material Appendix 2 Table A1): 1) country; 2) subregions consisting of geographically proximate countries; 3) regions consisting of proximate subregions; and 4) the entire continent. For each scale, we calculated the LRS based on the country level species lists.

In this case, we found that species richness increased through time, but that the overall pattern of species richness change across nested scales did not show a clear signal (Fig. 2D). If this pattern is likely, it would be consistent with the scenario discussed in Box 1, where there is no homogenization or differentiation, and thus no scale-dependence in species richness change. However, there is considerably more variance and higher increases in species richness at intermediate scales (relative to lower or higher scales), suggesting a possible hump-shaped relationship more consistent with the scenario in Box 1 (with so few groupings at larger scales, there is not enough power for such an analysis).

Towards a synthesis of temporal change in species richness across scales

We hope that we have made it evident that spatial (and temporal) scale is a critical feature that influences the magnitude and direction of species richness change. Any syntheses of species richness change, thus, will be greatly enhanced by an explicit consideration of scale. However, it remains unclear how straightforward it will be to incorporate scale into future analyses and meta-analyses.

One hypothesis is that we would be unlikely to observe any signature of scale in a compilation of heterogeneous data collected on disparate taxa and systems. This is because, as we illustrated above, there are a range of possibilities for how scale-dependence can emerge depending on features that are likely to vary among studies, taxa and systems. For example, dispersal or introduction rates, which vary greatly among taxa (e.g. birds versus mollusks) and systems (e.g. islands versus mainlands), influence the magnitude of species richness change through time, as well as the scale-dependence of this change. Likewise, the magnitude and direction of species richness change and its scale-dependence will depend on whether a system returns to a quasi-equilibrium following disturbance or human impact (Fig. 1). If all, or even some, of these possibilities were equally likely, they would obscure any clear pattern from observations across taxa, systems and scales since the contrasting results would cancel each other out.

Alternatively, it could be that across studies and scales, there is a predominant signature of scale-dependence that emerges. For example, many authors have suggested that

small (or negligible) changes in species richness at small scales are exacerbated at larger scales via biotic homogenization due to regional and global extinctions (McKinney and Lockwood 1999, Sax and Gaines 2008, Cardinale et al. 2018). However, other authors have suggested that the overarching pattern of species richness change should be hump-shaped with scale first increasing from to intermediate scales due to the spread of non-native species, and then decreasing from intermediate to large scales due to extinctions (Cassey et al. 2006, Thomas 2013, Vellend et al. 2017b, Primack et al. 2018).

In what follows, we present the outline of an approach that may help address whether there is general consistency in the scaling relationships of species richness change through time. Importantly, however, our compilation and analysis are by no means complete, but rather just the beginning of a much more intensive investigation which we hope may be inspired by this Forum piece. Our exploration began with the collation of a large dataset of species richness change through time from local to global scales and across several taxa (for details, see Supplementary material Appendix 3). Specifically, we combined two types of data. 1) At typically small spatial scales, we pooled three databases (Elahi et al. 2015, Vellend et al. 2017a, Dornelas et al. 2018) that consisted of local measurements of species richness from a variety of ecosystems through time. These data all involved some form of repeated surveys of individuals over time. 2) At regional scales, we compiled a database consisting of studies where species richness could be discerned from two points in time – typically a long time period spanning the range of smaller versus higher levels of human impact. These were typically species checklists from nature parks and natural areas, geopolitical regions (e.g. states, countries), or other biogeographic boundaries (e.g. continents, islands). Such checklist compilations have often been used to determine long-term trends of introductions/extinctions (Sax et al. 2002, Winter et al. 2009, Essl et al. 2013). These two distinct sources of data raise clear issues discussed below.

For each time-series from this combined dataset, we calculated the log ratio of species richness (LRS) between the first and last observation of species richness ($\log(S_T/S_1)$; intermediate time points were ignored) and estimated the spatial extent of the study. We coarsely separated data into taxonomic and habitat groupings (e.g. terrestrial plants, marine fish) which were analyzed separately. This is because we felt that combining taxa and ecosystem types into an overall analysis was not sensible because these groups are not expected to respond to spatial scale in the same way. For example, owing to differences in body size, dispersal capacity and other features, we would expect colonization rates, extinction rates and other features of the taxa to dramatically influence whether, and how, scale-dependence emerges (Supplementary material Appendix 1). However, even within taxa, we expect a great deal of heterogeneity depending on the landscape in which observations are made (e.g. the diverging patterns observed among birds in North America [Fig. 2B] and Hawaii [Fig. 2C]). Since our intention is simply to expose the nature of the scale-dependence

problem, we performed only exploratory analysis of these data, which we discuss in more detail in Supplementary material Appendix 3.

In Fig. 3, we illustrate how the LRS varied as a function of the spatial scale on which the study took place for four taxa for which we had enough data to provide meaningful illustration – terrestrial plants, terrestrial birds, terrestrial mammals and marine fish (other taxa for which we had data are also presented in Supplementary material Appendix 3). A few interesting patterns emerge. First, the variation in LRS was quite high at smaller scales, but with an average change centered on zero, in line with previous meta-analysis (Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015, Blowes et al. 2018). Second, for most taxa, increases were more prevalent than decreases at intermediate to large scales. This is consistent with the notion that increases in habitat heterogeneity and/or species invasions lead to increases in species richness at these intermediate to large (roughly regional) scales (Sax et al. 2002, Winter et al. 2009, Jarzyna and Jetz 2018). Indeed, when we combined data from all studies and made scale binary, where studies on local scales are defined as those $\leq 10\,km^2$ and those on regional scales are defined as those $>10\,km^2$, a Wilcox non-parametric test shows that the LRS is significantly higher at the regional scale (i.e. an average gain of species) than for studies at the local scale (i.e. no net change) ($p < 0.001$). While the choice of $10\,km^2$ as a cutoff is arbitrary and may vary depending on the body size and dispersal ability of different taxa, the same results emerge if this cutoff is varied by several orders of magnitude. This is consistent with the idea that even if small-scale species richness change is zero or negative, biotic differentiation due to habitat heterogeneity and/or alien species can lead to smaller negative effects and/or positive effects at larger spatial scales. In addition, for both terrestrial birds (Fig. 3A) and terrestrial plants (Fig. 3B), we see patterns consistent with the notion of a hump-shaped scale-dependent relationship with significantly negative quadratic terms with LRS first increasing, and then declining again at the largest spatial scales where regional and global extinctions play a stronger role (see also Jarzyna and Jetz 2018; Supplementary material Appendix 3). We did not observe any clear signals for the other taxa, though acknowledge that data limitations are likely a reason.

We emphasize that these data and analyses are meant to be illustrative of the problem of incorporating scale into synthetic analyses of species richness change, and how one might approach it, rather than to provide any definitive conclusions. Even if a signal of the influence of scale can be discerned from Fig. 3, there is a great deal of variation that is not captured by simple patterns. Furthermore, at present we do not attempt to disentangle differences in methodology and/or time scale for each study. For example, larger scale studies are typically based on checklist data and occur over longer time periods, and thus confound spatial and temporal scales (Supplementary material Appendix 4 Fig. A1). Despite these complexities, we hope this analysis accomplishes two goals: 1) illustrate why different studies performed with

different methods and at different scales can give very different answers to a seemingly simple question of whether (and how) species richness changes through time; 2) emphasize that scale-dependent species richness change will require a more sophisticated approach to studying species richness change in order to understand past species richness change, and potentially predict future changes.

Conclusions

There is no a priori reason to expect that losses of species richness at the global scale trickles down to losses of species richness at regional and local scales, nor is there an a priori reason to expect that any changes (or lack thereof) in richness at local scales should be reflected in regional and global trends. Here, we have presented a three-pronged narrative regarding the issue of scale-dependent richness changes using simulation models, case studies and a collation of heterogeneous data. We show that the nature of scale-dependence need not be as simple as usually depicted, and that instead, any change in species richness can remain the same across scales, can increase with scale, can decrease with scale, or can be unimodal with scale. A deeper understanding of the features of how and which species respond to changing conditions is necessary in order to more fully understand and predict this scale-dependence.

From our analyses above, it seems clear that incorporating scale into analyses of species richness and its change will be much more complex than simply incorporating the scale of the study as a covariable into synthetic analyses. Instead, we advocate that it will be necessary to establish new analytic tools that can explicitly measure the scaling of diversity, and how that scaling changes through time, along the lines of the species–area relationships (SARs) discussed in Box 1. This will likely require the gathering and analysis of nested scale-explicit data, such as from the case studies above, or the development of novel analytical tools that can capture changes in species richness in a scale-explicit way. For example, Keil and Chase (2019) have recently shown how scale-heterogeneous data can be combined into a single predictive framework on how species richness changes due to environmental and biogeographic factors using the concept of SARs. While their approach focused on patterns at a single point in time, it could be extended to include comparisons of SARs between time periods to evaluate the nature of scale-dependent species richness change. There is no doubt that this is a much more difficult endeavor than what has been accomplished to date, but one which we argue is essential if we hope to understand and predict how species richness is changing, and will continue to change, at the hands of human activity.

In our discussion, we have almost exclusively focused on changes in species richness through time. This is because species richness is the most frequently used metric to evaluate patterns of biodiversity and its change, especially in response to anthropogenic impacts. This makes some sense, as species richness is the ultimate currency in which many scientists and

conservation managers are most interested. However, species richness is a notoriously unreliable metric of change, often being quite insensitive to dramatic changes in the abundance and composition of species in a community (Dornelas et al. 2014, Supp and Ernest 2014, Hill et al. 2016, Santini et al. 2017, Hillebrand et al. 2018). Therefore, it is important to keep in mind that quantifying species richness change (or lack thereof) is only one measure of a much more complex phenomenon of biodiversity change through time and space. Additionally, we have only focused on change in taxonomic patterns of richness, and it is possible that other facets of diversity, such as functional and phylogenetic diversity, can differ in how they change across scales in response to environmental change (Knapp et al. 2017). Nevertheless, it is also clear that scale can strongly influence measures of taxonomic diversity other than species richness (Lande 1996, Dauby and Hardy 2012), as well as functional and phylogenetic metrics (Morlon et al. 2011, Smith et al. 2013, Jarzyna and Jetz 2018). Thus, adapting this scale-explicit perspective would be highly relevant for other measures of biodiversity and its change, as well as the ecosystem-level services associated with this biodiversity.

Because species richness scales non-linearly with increasing area, and because environmental changes such as those caused by human activities can influence species colonizations and extinctions differentially, we should often expect a complex response of species richness change to human activities across scales. As a result, we argue that scientists interested in biodiversity change and its potential consequences should change their perspectives from one focused primarily on measures of species richness and a largely agnostic perspective on scale, to one focused more explicitly on understanding how and why species richness changes across spatial and temporal scales. To do so will require a more concerted effort to monitor and analyze biodiversity and its change in a more scale-explicit way.

Data deposition

Code for the simulation and figures are available in <https://github.com/sChange-workshop/BiodivScale> and a static version deposited at <https://doi.org/10.5281/zenodo.2652582>. Data are available on Dryad <https://doi.org/10.5061/dryad.2jk717g> (Chase et al. 2019).

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