BIODIVERSITY

The geography of biodiversity change in marine and terrestrial assemblages

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Human activities are fundamentally altering biodiversity. Projections of declines at the global scale are contrasted by highly variable trends at local scales, suggesting that biodiversity change may be spatially structured. Here, we examined spatial variation in species richness and composition change using more than 50,000 biodiversity time series from 239 studies and found clear geographic variation in biodiversity change. Rapid compositional change is prevalent, with marine biomes exceeding and terrestrial biomes trailing the overall trend. Assemblage richness is not changing on average, although locations exhibiting increasing and decreasing trends of up to about 20% per year were found in some marine studies. At local scales, widespread compositional reorganization is most often decoupled from richness change, and biodiversity change is strongest and most variable in the oceans.

Humans are reshaping biodiversity patterns. Against a background of elevated extinction rates (*1*, *2*), local biodiversity change results from multiple interacting drivers that influence the abundance and distribution of species. Different regions of the globe are projected to experience different trends in biodiversity change, particularly those caused by variations in the strength of drivers such as land-use intensity (*3*) and climate change (*4*). There are widespread changes in the identities of species that live in any one location (species composition), whereas shifts in the numbers of species (species richness) show mixed patterns, with increasing, decreasing, or static trends (*5*–*9*). However, the spatial distribution of the locations most affected is unknown. Here, we map biodiversity change, in terms of species richness and composition, to uncover the geography of biodiversity change. Our analysis compares assemblage time series across the marine, terrestrial, and freshwater realms, different biomes, and latitudinal bands (i.e., polar, temperate, and tropical).

Both biodiversity and its change are unevenly distributed on the planet (*10*, *11*) and unevenly sampled (*12*–*15*). Species densities typically decline drastically from the tropics to the poles, and the identities of species differ across continents and oceans. Hence, knowing which locations are undergoing different types of net change in biodiversity is critical to understanding how biodiversity is changing globally. Detecting geographic variation in biodiversity trends will not only improve our understanding of how global biodiversity is changing but will also inform conservation prioritization. Specifically, by identifying the regions of the planet that are changing more, we will be better placed to make informed decisions about the spatial distribution of biodiversity vulnerability and about where to prioritize reactive (such as restoration) and proactive (protection) conservation actions (*16*). In addition, quantifying this spatial distribution will refine hypotheses about the drivers of biodiversity change.

Spatial patterns in biodiversity change are the combined result of species changing their distributions, entering and leaving local communities, going extinct, or speciating. These processes are affected by many drivers, which themselves are spatially heterogeneous (*17*, *18*) and differ between the marine and terrestrial realms (*19*). For example, spatial overlap between climate change and other drivers of change is greater in the marine realm than in the terrestrial realm (*19*). Moreover, species sensitivities to climate change (i.e., temperature increases) are also greater in the marine realm (*20*, *21*). When coupled with ecological differences between realms, such as fewer barriers to dispersal and greater colonization rates in marine ecosystems (*22*, *23*), these differences may result in greater compositional change in marine compared with terrestrial assemblages (*21*). Therefore, we predict that biodiversity in the marine realm has changed more than it has in the terrestrial realm. Changes in community composition are not necessarily associated with changes in species richness if species gains and losses are approximately balanced (*5*–*9*, *24*, *25*). However, in regions where land-use intensity is high (*26*) or where range sizes contract in response to climate change (*27*), species extirpations could result in a decrease in species richness. Conversely, in regions subject to high rates of species introductions (*28*–*31*) or high connectivity, or where ranges expand (*32*, *33*) or species are broadly favored by land-use change (*34*), species richness could increase. Hence, we expect there to be variation in biodiversity change across different biomes and geographical regions of the planet. There may also be latitudinal differences in biodiversity change. For example, tropical regions are entering climatic conditions with no present-day equivalents (*35*), and intensification of land-use change is more recent than in temperate regions (*36*); therefore, richness loss may be more prevalent and more extreme in tropical latitudes. Here, we investigated whether biodiversity change differs in magnitude between the realms and if strong geographic patterns exist in the changes to species richness and composition across realms, latitudes, or regions.

We examined geographic variation in patterns of change in both species richness and composition using local assemblage time series from across the globe (*37*, *38*) (fig. S1). The BioTIME database is currently the largest compilation of assemblage time series, and our analysis included 239 independent studies (table S1). Because spatial extent varied considerably among studies, we used a gridding method (96-km^2 hexagonal cells) (*39*) to partition the 126 studies that had multiple sampling locations and large spatial extents (*38*); 113 studies were not partitioned because they were contained within a single grid cell. This resulted in 51,932 individual

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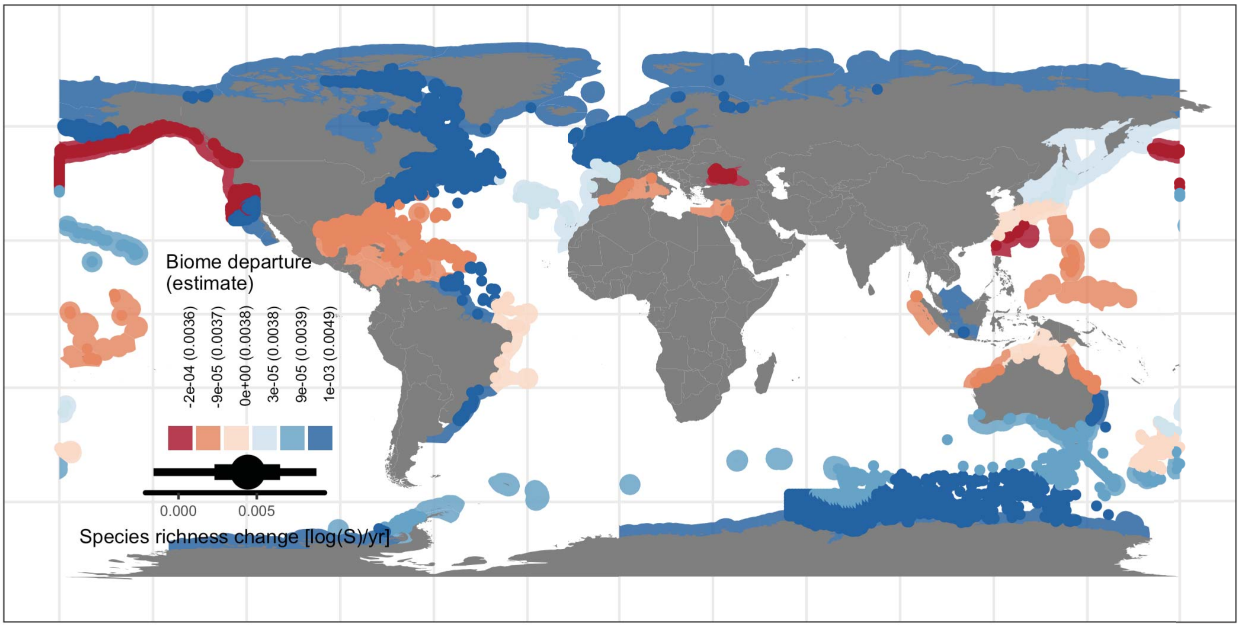
local assemblage time series, with each time series composed of samples from only one study. This means that important study-level considerations (e.g., sampling method) were consistent within each time series. After further filtering by sampling completeness and standardization by sample-based rarefaction (*38*), these time series became the lowest level in our hierarchical models of temporal trends. Temporal extent and start date vary substantially within these data: time series span from the late 1800s to the present, though most data come from the past 40 years (fig. S2), and we examined the sensitivity of our results to this heterogeneity.

A Marine



B Terrestrial and freshwater

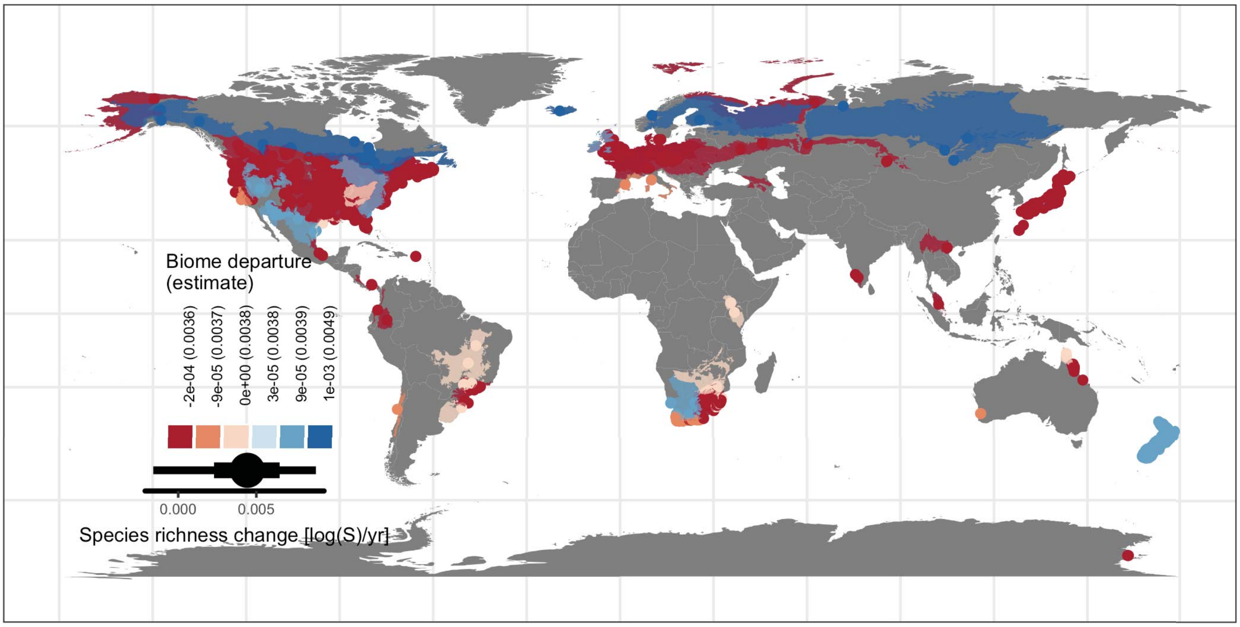


Fig. 1. Species richness change maps showing departures from the overall trend for marine and terrestrial biomes. Inset shows the overall trend in assemblage species richness change; bar depicts 50% (thick) and 90% (thin) credible intervals. Shading on the map represents positive (blue; faster increases in species richness than average) and negative (red; slower increases in species richness than average) departures for each biome from the overall average species richness change (0.004 log species per year). Numbers in the inset denote the departure and the biome-level (overall + departure) estimate in parentheses. The 90% credible intervals for all biome-level estimates overlap zero. (**A**) Marine biomes (n = 33) show both positive and negative departures from the overall trend, with more negative departures in the tropics, whereas there are no latitudinal trends in (**B**) terrestrial (n = 10) and freshwater (n = 5) biomes, which also show both positive and negative departures from the overall trend.

Biodiversity trends across the globe

To examine geographic patterns in biodiversity change, we quantified realm, latitudinal, and regional departures from the overall trends of richness and composition change using hierarchical generalized linear models. We first nested the cell-level time series within the 239 original studies to control for effects of sampling methods and nonindependence of cell-level time series that came from a single study. Throughout our analysis, we controlled for not having the same taxa sampled everywhere by including taxon in our models. Our first model, the biome-taxon model, nested studies into nine taxonomic-habitat groupings that were further nested within 48 biomes [defined by the Ecoregions of the World datasets available from *The Nature Conservancy* website; http://maps.tnc.org/gis_data.html, TNC terrestrial regions dataset (*40*–*43*)]; this resulted in 321 biome-taxon study combinations grouped within 105 specific biome-taxon combinations. The 48 biomes, including 33 marine (*41*), 10 terrestrial (*44*), and 5 freshwater (*42*), represent geographic regions of the world and allowed us to characterize spatial patterns as biome-level departures from the overall trend of biodiversity change for each realm. The taxonomic-habitat groupings, dictated by specifications in the original studies, were amphibians, benthos, birds, fish, invertebrates, mammals, marine invertebrates and plants, plants, and multiple taxa, and were included to contrast and control for differences in trends among taxa within the different biomes. We examined the robustness of our biome-taxon models, and the spatial patterns they identified, by fitting two complementary hierarchical models with simpler geographic structures. Here, we focus on the simplest model (referred to as the realm-latitude-taxon model) and present a model of intermediate complexity in the supplement (*38*). All models grouped cells within studies at the lowest level, and the realm-latitude-taxon model grouped studies into 29 specific combinations of realm (marine, terrestrial, freshwater), latitude (polar, temperate, tropical), and taxonomic-habitat group, allowing us to characterize variation in biodiversity change for taxon groups across broad latitudinal bands within each realm. The different geographic structure meant that this model included 271 studies when we applied our threshold of three cell-level time series per realm-latitude-taxon group (*38*). Results of all models were qualitatively consistent, both in terms of the overall trends they estimated and at the lowest levels (i.e., at the study and cell levels: fig. S3), suggesting that our inferences are largely robust to differences in how we searched for geographic patterns. Additionally, we found our results relatively insensitive to the heterogeneity in temporal extent of the data and did not detect systematic effects of the number of years sampled, temporal duration, start year, or the initial species richness on the estimates of rates of change (figs. S7 and S8).

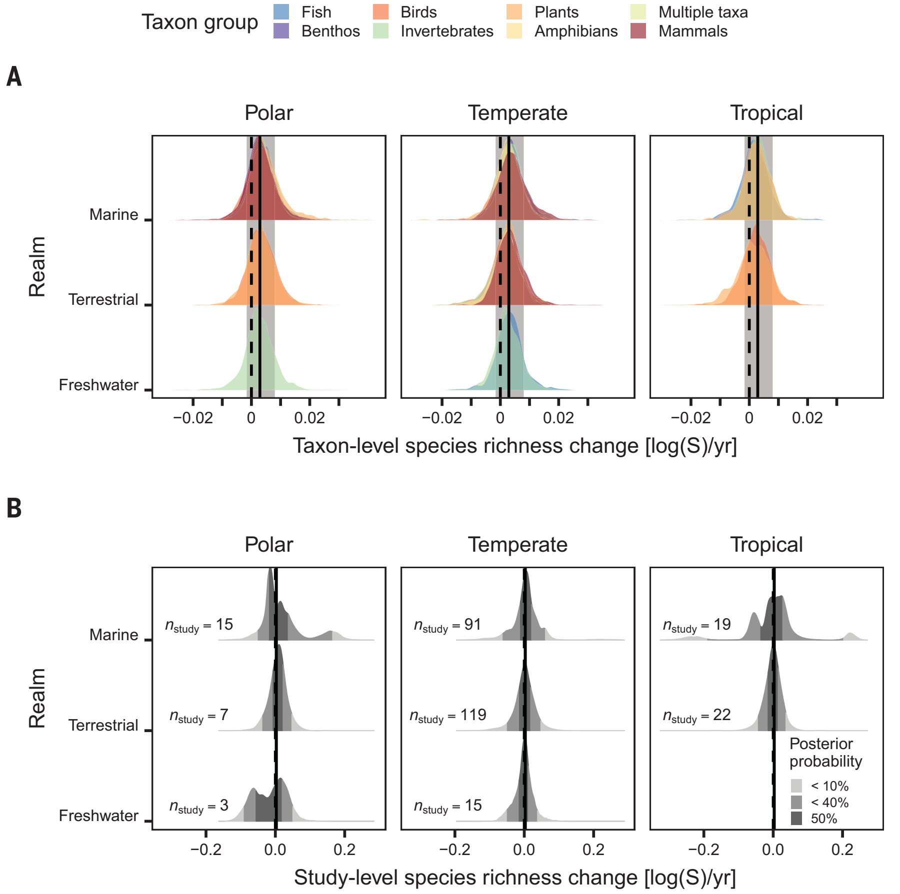
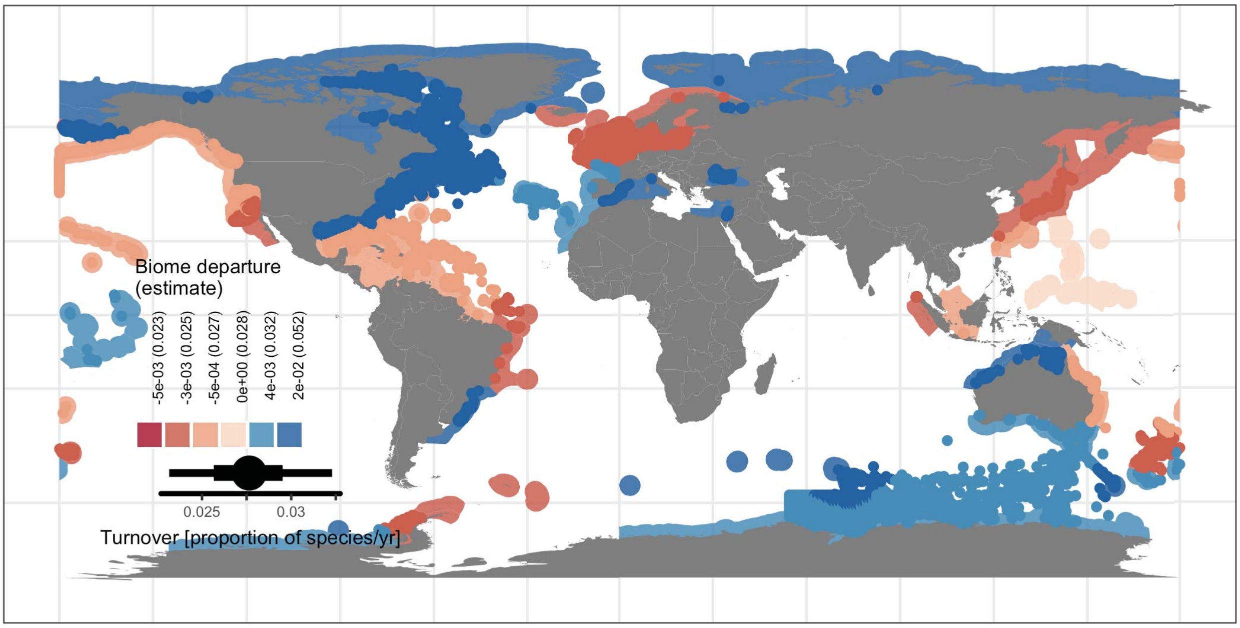


Fig. 2. Posterior distributions of species richness change for the realm-latitude-taxon model. The overall trend in assemblage richness change (solid vertical bar) does not differ from zero (gray shading depicts the 90% credible interval) for the realm-latitude-taxon study model. (**A**) Density ridges of the taxon-level slope coefficients (color represents the taxonomic group). (**B**) Density ridges of the posterior distributions of the study-level slope coefficients within a given combination of realm and latitudinal band estimated with the realm-latitude-taxon model.

Our biome-taxon model results show that variation in biodiversity change is greater in the marine versus the terrestrial and freshwater realms. The overall average of richness change was not statistically distinguishable from zero globally or for any individual biome (Fig. 1). The magnitude of positive departures from the overall trend was greater among marine biomes (range of median biome departure: −0.0003 to 0.001, $n = 33$; Fig. 1A) compared with terrestrial and freshwater biomes (−0.0007 to 0.0001, $n = 15$; Fig. 1B), but richness trends did not vary substantially among biomes ($\sigma_{\text{Biome}} = 0.004$) or for taxon groups within biomes ($\sigma_{\text{Biome-taxon}} = 0.003$). Instead, the main level of variation was at the study level ($\sigma_{\text{Biome-taxon-study}} = 0.04$), where specific studies exhibited species richness increases or decreases of up to 20% per year in the marine realm and up to 10% in the terrestrial realm (fig. S9). Twenty-three marine, five terrestrial, and two freshwater studies showed significant species richness losses, whereas 31 marine and nine terrestrial studies showed significant gains. These results were consistent with the realm-latitude-taxon model that showed change centered on zero for all latitudinal bands (Fig. 2A), with the greatest variation observed in the marine realm at the study level, particularly in polar and tropical latitudes (Fig. 2B). Data limitations from tropical systems remain in our assemblage time-series data (e.g., no tropical freshwater assemblages), precluding some direct comparison between realms (see also fig. S1). The high rates of change that we observed in the marine tropics (Fig. 2B) are consistent with predictions that tropical marine species will be relatively sensitive to extreme heat events because they are closer to their physiological limits (*20*, *21*), in addition to overexploitation, pollution, and other threats occurring in the marine tropics (*36*).

A Marine



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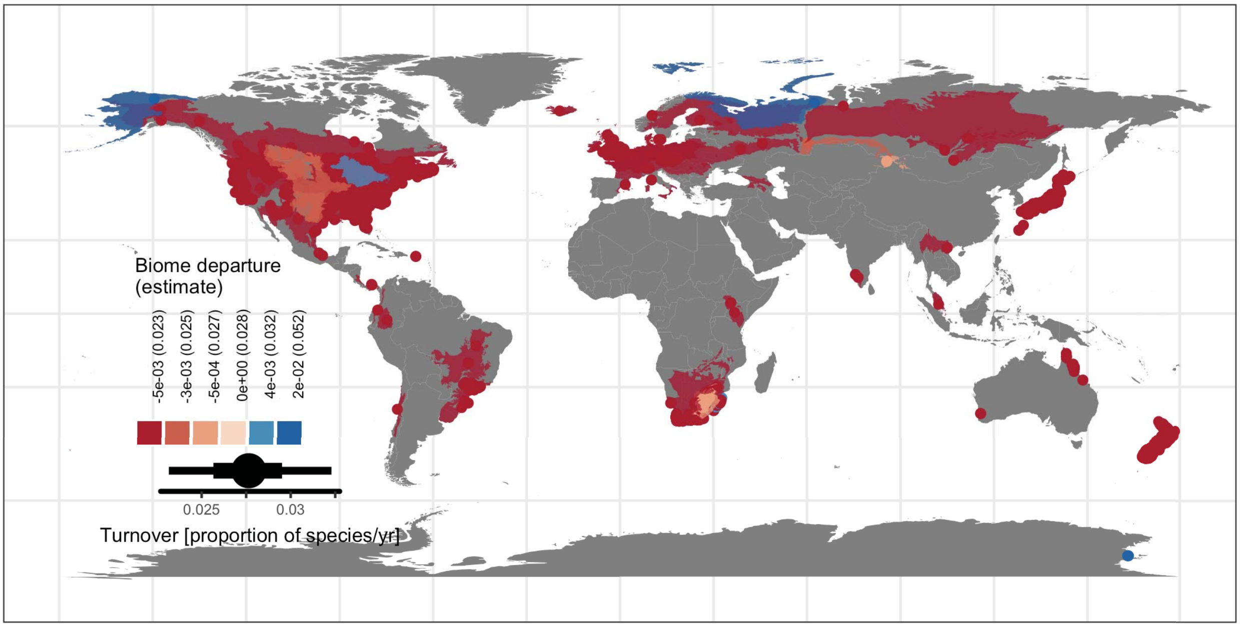

Fig. 3. Species turnover component maps showing departures from the overall trend for marine and terrestrial biomes. Assemblages across the globe are experiencing high rates of species replacement (median ~28% of species replaced per decade). Shading represents positive (blue; faster turnover than average) and negative (red, slower turnover than average) departures from the overall trend for each biome; numbers in the inset denote the departure and the biome level (overall + departure) estimate in parentheses. (**A**) Rates of arriving species replacing original species have both faster (blue) and slower rates of turnover (red) from the overall trend in marine biomes, but included the biomes with the highest turnover rates: the 90% credible intervals in the warm temperate northwestern Atlantic, warm temperate southwestern Atlantic, and the northwest Australian shelf biomes were greater than the overall trend, whereas (**B**) terrestrial and freshwater biomes have mostly slower rates of turnover than the overall trend (red shading), and the 90% credible intervals for temperate broadleaf and mixed forests, temperate conifer forests, and tropical and subtropical moist broadleaf forests were lower than the overall trend.

To examine changes in species composition, we partitioned total Jaccard dissimilarity, calculated as the dissimilarity between the initial year and each subsequent year of a time series, into the additive components of turnover and nestedness (*45*). These trends describe directional compositional change relative to the initial assemblage, and the decomposition determines whether changes in community composition were caused by the original species in assemblages being replaced by other species (turnover) or if assemblages were becoming smaller subsets of themselves or growing to include additional species alongside the original species (nestedness). Overall, we found that rates of turnover were positive and much greater (0.028; 90% credible interval: 0.023 to 0.032; Fig. 3) than the rates of change in nestedness (0.006; 0.006 to 0.007; fig. S12). Compositional change was dominated by species replacement within assemblages, with ~28% of species being replaced per decade. Variation at the biome level was much greater for turnover (σ_{Biome} = 0.01) compared with species richness, resulting in stronger geographic patterns and revealing further differences between marine and terrestrial realms (Fig. 4). Three marine biomes (warm temperate northwest and southwest Atlantic and the northwest Australian shelf) had rates of turnover greater than the overall trend. By contrast, three terrestrial biomes (temperate broadleaf and mixed forests, temperate conifer forests, and tropical and subtropical moist broadleaf forests) had rates of turnover slower than the global trend, and most terrestrial biomes showed negative departures from the global average (Fig. 3B). Positive departures from the overall trend in terrestrial and freshwater biomes were found in aquatic systems: large lakes, mangroves, and polar freshwaters. These trends of directional compositional change are highly unlikely to have arisen simply from random assemblages being drawn from relatively constant regional species pools. Simulations show that such a process has a median slope of zero for both turnover and nestedness change (*38*) (fig. S10). Additionally, we found that higher rates of compositional change in marine and freshwater biomes were associated with a higher proportion of assemblages undergoing complete turnover (fig. S13) and were robust to our choice of error distribution (fig. S14) and whether comparisons were made with the initial assemblage or between assemblages at consecutive time points (*38*) (figs. S15 and S16).

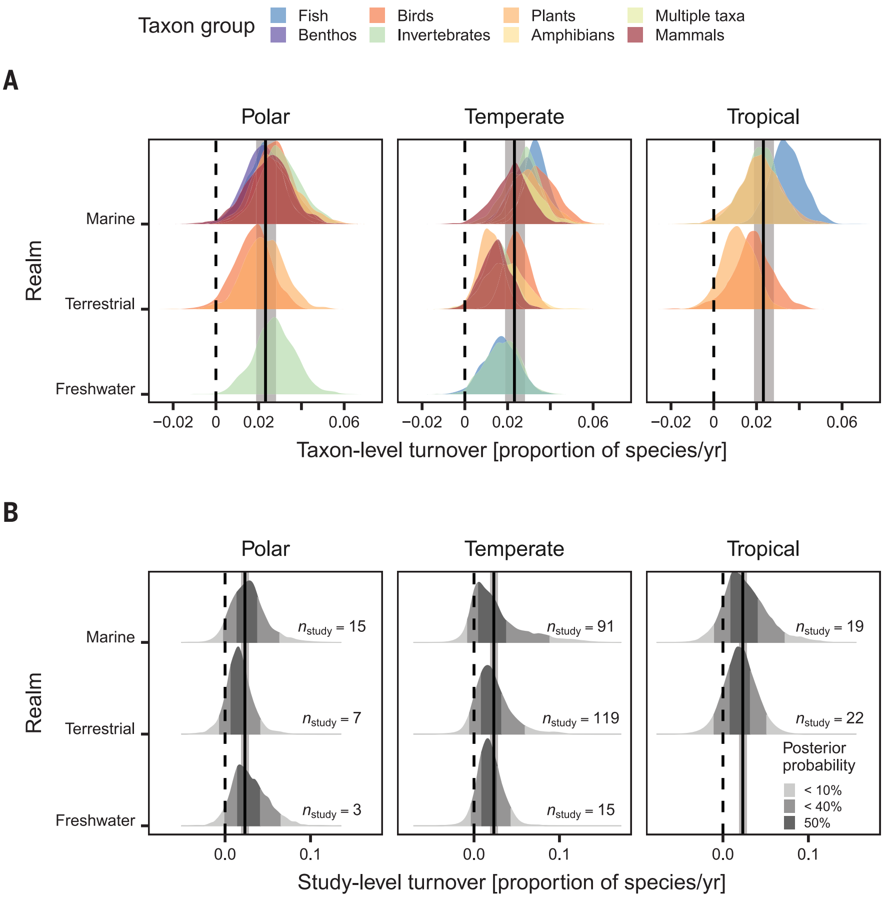

Fig. 4. Posterior distributions of turnover for the realm-latitude-taxon model. The overall trend in turnover change per year is greater than zero (solid black line; gray shading depicts the 90% credible interval) for the realm-latitude-taxon-study model. (**A**) Density ridges of the taxon-level slope coefficients (color represents the taxonomic group). (**B**) Density ridges of the study-level slope coefficients within a given combination of realm and latitudinal band estimated with the realm-latitude-taxon model.

Linking richness and composition change

To examine the relationship between changes in species richness and changes in composition, we plotted the dominant component of composition change (turnover or nestedness) for each biome-taxon-study combination against species richness change (*46*) (Fig. 5, A and B). When turnover is the dominant component, this relationship shows how quickly different species are replacing original species and whether these arrivals are associated with changes to the number of species. At the study level, rates of turnover exceeded nestedness change for >97% of biome-taxon-study combinations (313/321; Fig. 5, B and C). Among these studies, ~23% (57/313) exhibited trends different from zero for both turnover and species richness rates (Fig. 5C), with a relatively balanced distribution of 23 cases of species richness losses and 34 cases with gains. We did not adjust for multiple comparisons, though they are less of a problem when comparing partially pooled estimates from hierarchical models (*47*). When nestedness is the dominant component, this relationship shows how fast assemblages are changing to become smaller subsets or growing to include additional species alongside the species initially observed. Among the eight biome-taxon-study combinations where nestedness exceeded turnover change (8/321; Fig. 5, B and C), only two showed rates of nestedness and richness trends different from zero, with one losing and one gaining species. Our combined results for turnover and species richness change support recent studies reporting that different components of biodiversity change, such as composition shifts and species richness, are largely uncoupled (*5*, *7*–*9*). In fact, we found that high rates of turnover were associated with the full spectrum of richness changes.

Discussion

Compositional change dominated by species turnover is the most conspicuous and prevalent form of biodiversity change across the globe and was characterized by strong geographic structure. Only marine biomes were found to have faster rates of compositional change than the overall trend, whereas only terrestrial biomes were observed to trail the overall compositional trend. Moreover, marine studies exhibited greater variation in rates of compositional turnover. We also found that most studies, across all biomes and realms, showed considerable replacement of species through time without associated species richness changes. This finding, using the largest global dataset to date, is consistent with the assertion that species richness trends are often uncoupled from species replacement, and thus are insufficient alone for fully capturing how biodiversity might change (*9*). The consistent pattern of species replacement is likely underpinned by a diverse suite of drivers affecting different study sites, regions, and realms. Such reorganization independent of changes to the number of species is also consistent with the presence of regulatory mechanisms for species richness. Community regulation of species richness is widespread (*48*) and may be driven, for example, by shared resources (*24*). Contemporary pressures such as introduced species (*29*–*31*), replacement of localized specialists by widespread generalists (*49*, *50*), range shifts in response to environmental change (*22*, *51*), or local warming (*52*, *53*) may also help to explain our finding of widespread composition change associated with variable richness change at the study level.

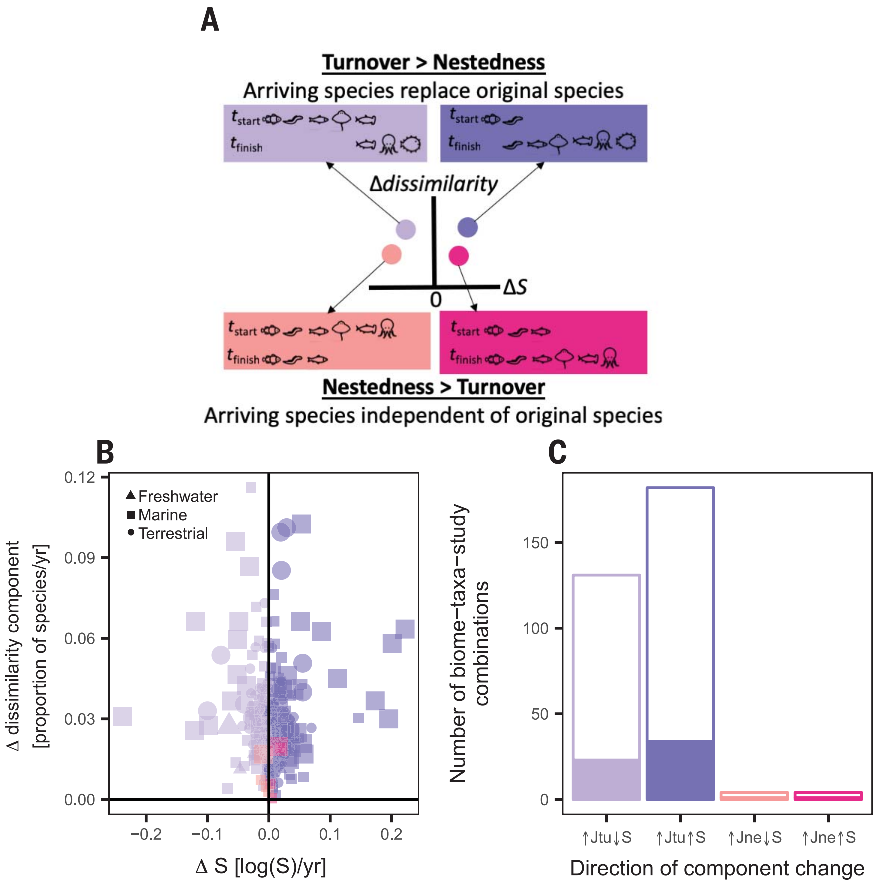

Fig. 5. Conceptual and empirical relationships between changes in species richness and changes in species composition. (**A**) Conceptual model relating the turnover and nestedness components of species composition change (Δ*dissimilarity*) to changes in species richness (Δ*S*). When the turnover component is larger than the nestedness component, different species entering assemblages replace the original species (purple shaded boxes). Conversely, when the nestedness component is larger than the turnover component, some original species of the assemblage remain and the numbers of different species entering the assemblage are largely independent of the original species (pink shaded boxes). The change in species richness documents the net change in the numbers of species in the assemblage (and ignores their identity as either original or additional species). (**B**) Scatterplot showing the dissimilarity trend as a function of the species richness trend. Each point represents a biome-taxon-study level estimate, point shape indicates realm, and larger points indicate that both composition and richness trends differed from zero with 90% probability (credible intervals are not shown for clarity). (**C**) Number of studies for each combination of change in species richness and species composition measured as either the turnover (Jtu) or nestedness (Jne) component of Jaccard dissimilarity. Filled sections of each bar represent the number of biome-taxon-study combinations where the 90% credible intervals for both species richness (*S*) and composition change (Jtu or Jne) did not overlap zero.

Rates of species richness change and turnover were higher in absolute magnitude and more variable in the marine realm, with maximum turnover rates in marine biomes twice those observed for terrestrial biomes. Higher rates of turnover in the marine realm are consistent with predictions for species responses on the basis of greater sensitivities to increased temperatures (*20*, *21*) coupled with fewer barriers to dispersal in marine systems (*22*, *23*), though attribution to specific drivers is beyond the scope of analyses presented here. Further, if assemblages are more spatially heterogeneous in marine compared with terrestrial systems, then this too may contribute to our finding of higher temporal turnover in marine assemblages (*54*). Although we did not find strong contrasting trends for specific taxonomic groups within biomes, environmental differences between the realms (unrelated to dispersal and connectivity) or life history differences among taxa could also underpin some of the patterns in turnover detected at the realm and regional scales. For example, in the temperate marine realm, mammals had lower turnover than invertebrates, which is consistent with other findings showing that long-lived taxa exhibit less rapid temporal turnover (*54*).

Amid widespread variation in biodiversity trends, we found that tropical marine regions have a higher proportion of studies exhibiting biodiversity change at the extremes of richness gains, losses, and turnover (Figs. 2B and 4 and fig. S9). Hence, although we find higher magnitude changes in the tropics, this result contrasts with our prediction that we would find mostly richness losses. The tropics, which harbor most of the biological diversity on the planet, are also generally considered to be the place where biodiversity is the most threatened (*36*). Moreover, in the context of climate change, there are likely fewer species available to replace those species lost in tropical zones that have entered no-analog warm-temperature conditions (*55*, *56*). If these trends are maintained, then this could lead to a market restructuring of biodiversity, with potentially severe consequences for ecosystem functioning across biomes and changes to the latitudinal diversity gradient, substantially altering the planet's biogeography. However, such a pattern of biotic attrition would be expected to be accompanied by a larger contribution of the nestedness component to community compositional change than we found here (Fig. 5 and fig. S12). BioTIME includes relatively few tropical datasets (*37*), despite being the largest compilation of biodiversity time series currently available, and further data collection in these areas is needed to be able to confidently assess trends in the tropics. Furthermore, biodiversity monitoring overall is lacking for many regions of the planet, e.g., the deep ocean. The geographical variation that we uncovered highlights the critical importance of improving the spatial coverage of biodiversity monitoring to better estimate global biodiversity change.

We identified hotspots of biodiversity change, that is, key areas that represent extremes for biodiversity trends. As conservation has moved toward systematically identifying regions in need of protection (*57*), global maps of conservation priorities according to different criteria have been developed (*16*, *58*). Our study provides an important criterion for targeting conservation action: a global map of current rates of biodiversity change. In addition to the marine tropics, marine biomes in the western Atlantic and northwest Australia are undergoing rates of replacement higher than the global average. Therefore, these regions are currently undergoing the most substantial rates of change and should be prioritized for reactive conservation measures. By contrast, several forest biomes (e.g., temperate broadleaf and mixed, temperate conifer) have slower rates of replacement than the global average. Because these regions appear to be undergoing less change, we speculate that proactive conservation measures are likely to be more appropriate. Specific conservation actions always need to be tailored to the locations and taxa, but our study provides the global and regional context in which individual locations are immersed.

The global heterogeneity in biodiversity change is underpinned by geographic variation. We find that spatial variation in species gains and losses is greater than taxonomic variation. This spatial variation suggests that statements about biodiversity loss need to be conditional on context and location. On average, local species richness change across the globe does not differ from zero, but there are many locations gaining or losing species. Species replacement is ubiquitous and also spatially structured. Determining whether the spatial variation uncovered is related to differences among communities in their degree of exposure and vulnerability to drivers of biodiversity change is an important next step. Nevertheless, our results show that, although the entire planet is undergoing biodiversity change, the direction and magnitude of change differs across geographic regions.

REFERENCES AND NOTES

1. S. L. Pimm *et al.*, *Science* **344**, 1246752 (2014).
2. V. Proença, H. M. Pereira, "Comparing extinction rates: Past, present and future," in *Encyclopedia of Biodiversity*, S. A. Levin, Ed. (Elsevier, ed. 2, 2013), pp. 167–176.
3. H. M. Pereira *et al.*, *Science* **330**, 1496–1501 (2010).
4. J. García Molinos *et al.*, *Nat. Clim. Chang.* **6**, 83–88 (2016).
5. M. Dornelas *et al.*, *Science* **344**, 296–299 (2014).
6. M. Vellend *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **110**, 19456–19459 (2013).
7. S. R. Supp, S. K. M. Ernest, *Ecology* **95**, 1717–1723 (2014).
8. R. Elahi *et al.*, *Curr. Biol.* **25**, 1938–1943 (2015).
9. H. Hillebrand *et al.*, *J. Appl. Ecol.* **55**, 169–184 (2018).
10. E. R. Pianka, *Am. Nat.* **100**, 33–46 (1966).
11. M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge Univ. Press, 1995).
12. A. Gonzalez *et al.*, *Ecology* **97**, 1949–1960 (2016).
13. M. Vellend *et al.*, *Ecology* **98**, 583–590 (2017).
14. L. Tydecks, J. M. Jeschke, M. Wolf, G. Singer, K. Tockner, *PLOS ONE* **13**, e0199327 (2018).
15. C. Meyer, P. Weigelt, H. Kreft, *Ecol. Lett.* **19**, 992–1006 (2016).
16. T. M. Brooks *et al.*, *Science* **313**, 58–61 (2006).
17. C. J. Ellis, *Syst. Biodivers.* **9**, 307–317 (2011).
18. B. S. Halpern *et al.*, *Nat. Commun.* **6**, 7615 (2015).
19. D. E. Bowler *et al.*, *bioRxiv* 432880 [Preprint]. 2 October 2018.
20. J. M. Sunday, A. E. Bates, N. K. Dulvy, *Nat. Clim. Chang.* **2**, 686–690 (2012).
21. M. L. Pinsky, A. M. Eikeset, D. J. McCauley, J. L. Payne, J. M. Sunday, *Nature* **569**, 108–111 (2019).
22. E. S. Poloczanska *et al.*, *Nat. Clim. Chang.* **3**, 919–925 (2013).
23. R. M. May, *Philos. Trans. R. Soc. London B Biol. Sci.* **343**, 105–111 (1994).
24. J. H. Brown, S. K. M. Ernest, J. M. Parody, J. P. Haskell, *Oecologia* **126**, 321–332 (2001).
25. M. Dornelas *et al.*, *Ecol. Lett.* **22**, 847–854 (2019).
26. T. Newbold *et al.*, *Nature* **520**, 45–50 (2015).
27. R. K. Colwell, G. Brehm, C. L. Cardelús, A. C. Gilman, J. T. Longino, *Science* **322**, 258–261 (2008).
28. M. van Kleunen *et al.*, *Nature* **525**, 100–103 (2015).
29. D. F. Sax, S. D. Gaines, *Trends Ecol. Evol.* **18**, 561–566 (2003).
30. M. Winter *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 21721–21725 (2009).
31. M. Winter *et al.*, *Glob. Ecol. Biogeogr.* **19**, 332–342 (2010).
32. C. Parmesan, G. Yohe, *Nature* **421**, 37–42 (2003).
33. J. Lenoir, J. C. Svenning, *Ecography* **38**, 15–28 (2015).
34. L. Fahrig, *Annu. Rev. Ecol. Evol. Syst.* **48**, 1–23 (2017).
35. J. W. Williams, S. T. Jackson, J. E. Kutzbach, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 5738–5742 (2007).
36. J. Barlow *et al.*, *Nature* **559**, 517–526 (2018).
37. M. Dornelas *et al.*, *Glob. Ecol. Biogeogr.* **27**, 760–786 (2018).
38. See supplementary materials.
39. R. Barnes, dggridR: Discrete global grids. R package version 2.0.3 (2018); https://CRAN.R-project.org/package=dggridR.
40. D. M. Olson, E. Dinerstein, *Ann. Mo. Bot. Gard.* **89**, 199–224 (2002).
41. M. D. Spalding *et al.*, *Bioscience* **57**, 573–583 (2007).
42. R. Abell *et al.*, *A.I.B.S. Bull.* **58**, 403–414 (2008).
43. The Nature Conservancy, *Terrestrial Ecoregions Dataset: Vector Digital Data.* (2009); http://maps.tnc.org/gis_data.html.
44. D. M. Olson *et al.*, *Bioscience* **51**, 933–938 (2001).
45. A. Baselga, *Glob. Ecol. Biogeogr.* **19**, 134–143 (2010).
46. C. Albouy, F. Guilhaumon, M. B. Araújo, D. Mouillot, F. Leprieur, *Glob. Chang. Biol.* **18**, 2995–3003 (2012).
47. A. Gelman, J. Hill, M. Yajima, *J. Res. Educ. Eff.* **5**, 189–211 (2012).
48. N. J. Gotelli *et al.*, *Sci. Adv.* **3**, e1700315 (2017).
49. I. Le Viol *et al.*, *Biol. Lett.* **8**, 780–782 (2012).
50. L. Alvarez-Filip, M. J. Paddack, B. Collen, D. R. Robertson, I. M. Côté, *PLOS ONE* **10**, e0126004 (2015).
51. R. D. Batt, J. W. Morley, R. L. Selden, M. W. Tingley, M. L. Pinsky, *Ecol. Lett.* **20**, 1148–1157 (2017).
52. P. H. Flanagan, O. P. Jensen, J. W. Morley, M. L. Pinsky, *Ecography* **42**, 214–224 (2019).
53. H. Hillebrand, J. Soininen, P. Snoeijs, *Glob. Change Biol.* **16**, 1181–1193 (2010).
54. S. L. Collins *et al.*, *Ecology* **99**, 858–865 (2018).
55. M. T. Burrows *et al.*, *Nature* **507**, 492–495 (2014).
56. M. L. Pinsky, B. Worm, M. J. Fogarty, J. L. Sarmiento, S. A. Levin, *Science* **341**, 1239–1242 (2013).
57. C. R. Margules, R. L. Pressey, *Nature* **405**, 243–253 (2000).
58. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, *Nature* **403**, 853–858 (2000).
59. S. A. Blowes *et al.*, Code for: The geography of biodiversity change in marine and terrestrial assemblages, Zenodo (2019); https://doi.org/10.5281/zenodo.1473860.

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SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/366/6463/339/suppl/DC1
Materials and Methods
Figs. S1 to S18
Table S1
References (*60*–*481*)

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Science

The geography of biodiversity change in marine and terrestrial assemblages

Shane A. Blowes, Sarah R. Supp, Laura H. Antão, Amanda Bates, Helge Bruelheide, Jonathan M. Chase, Faye Moyes, Anne Magurran, Brian McGill, Isla H. Myers-Smith, Marten Winter, Anne D. Bjorkman, Diana E. Bowler, Jarrett E. K. Byrnes, Andrew Gonzalez, Jes Hines, Forest Isbell, Holly P. Jones, Laetitia M. Navarro, Patrick L. Thompson, Mark Vellend, Conor Waldock and Maria Dornelas

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Spatial structure of species change

Biodiversity is undergoing rapid change driven by climate change and other human influences. Blowes *et al.* analyze the global patterns in temporal change in biodiversity using a large quantity of time-series data from different regions (see the Perspective by Eriksson and Hillebrand). Their findings reveal clear spatial patterns in richness and composition change, where marine taxa exhibit the highest rates of change. The marine tropics, in particular, emerge as hotspots of species richness losses. Given that human activities are affecting biodiversity in magnitudes and directions that differ across the planet, these findings will provide a much needed biogeographic understanding of biodiversity change that can help inform conservation prioritization.

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