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The Geography of Ecological Niche Evolution in Mammals

Highlights

- Evolutionary convergences scale up from species to entire biota of mammals
- Biota convergences occur between regions with similar climates
- Extreme biota convergences are found between Australia and other continents

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In Brief

Evolutionary convergences are common at the species scale. Using data on traits, phylogeny, and range maps of nearly all mammals of the world, Mazel et al. scale up convergence from species to assemblages and find region-wide biota convergence between regions with similar climates, particularly between Australia and other continents.



The Geography of Ecological Niche Evolution in Mammals

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SUMMARY

Convergent adaptive evolution of species' ecological niches—i.e., the appearance of similar niches in independent lineages—is the result of natural selection acting on niche-related species traits (“traits” hereafter) and contrasts with neutral evolution [1–4]. Although trait convergences are recognized as being of importance at the species scale, we still know little about the impact of species convergence on the overall trait and niche structure of entire biotas at large spatial scales [5]. Here, we map the convergent evolution of four traits (diet, body mass, activity cycle, and foraging strata) for mammal species and assemblages (defined at 200 × 200 km resolution) at a global scale. Using data on the geographic distributions, traits, and phylogenetic relationships of species and by comparing observed patterns of trait β -diversity to evolutionary neutral expectations, we show that trait convergence is not restricted to particular lineages but scales up to entire assemblages (i.e., whole species communities). We find region-wide biota convergence in traits between regions with similar climates, particularly between Australia and other continents. Pairs of assemblages that show trait divergence often involves Arctic regions where rapid evolutionary changes occurred in response to extreme climatic constraints. By integrating both macroecological and macroevolutionary approaches into a single framework, our study quantifies the crucial role of evolutionary processes such as natural selection in the spatial distribution and structure of large-scale species assemblages.

RESULTS AND DISCUSSION

Convergent evolution caused by natural selection occurs when independent lineages that experience the same environmental constraints evolve similar morphological, physiological, and/or behavioral traits [1, 4], ultimately leading them to occupy similar

ecological niches. Parallelism, where similar trait changes occur in closely related ancestors, is sometimes distinguished from convergence because it usually occurs at a smaller phylogenetic scale. However, parallelism and convergence are part of a continuum, hampering any attempt to draw a clear distinction between them [1, 4]; thus, we use the term “convergence” for all phylogenetic scales. (As proposed in [4], “parallelism” should be restricted to characterizing the degree of molecular similarities underlying phenotypic convergences.) Convergent evolution leads to higher ecological niche and trait similarity between unrelated species than expected under neutral evolution, where niches or traits shift along a continuous axis or between discrete states in a random way through evolutionary time [2, 3, 6, 7]. Although these neutral-like evolutions can be generated by randomly fluctuating natural selection [8], typical random walk models still represent the most realistic macroevolutionary models of neutral evolution so far. There is empirical evidence of convergent trait and niche evolution in all major kingdoms [3, 9–12], but this has not yet been quantified at the species scale for large clades, or at the scale of entire species assemblages at broad spatial scales (e.g., grid-based assemblages).

Here, we report the first global analysis of species-level evolutionary convergence and divergence of ecological niches for 4,736 terrestrial mammals. Species ecological niches were defined using a set of four traits (diet, body mass, activity cycle, and foraging strata) that produce a coarse representation of animal Eltonian niches [13–16]. Whereas diet and body mass directly refer to species resource requirements, activity cycle and foraging strata represent behavioral traits reflecting how species acquire food from their environment. We developed a phylogenetically standardized trait distance metric that contrasts observed trait distances between species pairs (i.e., all possible pairs of species in the dataset, not just sister-species pairs) to trait distances expected under a neutral (Brownian or Markov) model of trait evolution with a single rate [3, 6, 17] [metric = (observed distance – mean expected distances) / standard deviation of expected distances; see [Supplemental Experimental Procedures](#) and [Tables S1](#) and [S2](#)]. Observed and neutral distances were computed using the Gower distance metric, which allows mixing categorical and continuous traits. Negative (positive) standardized trait distances mean that observed distances are lower (higher) than neutral expectations, suggesting trait convergences (divergences) between species.

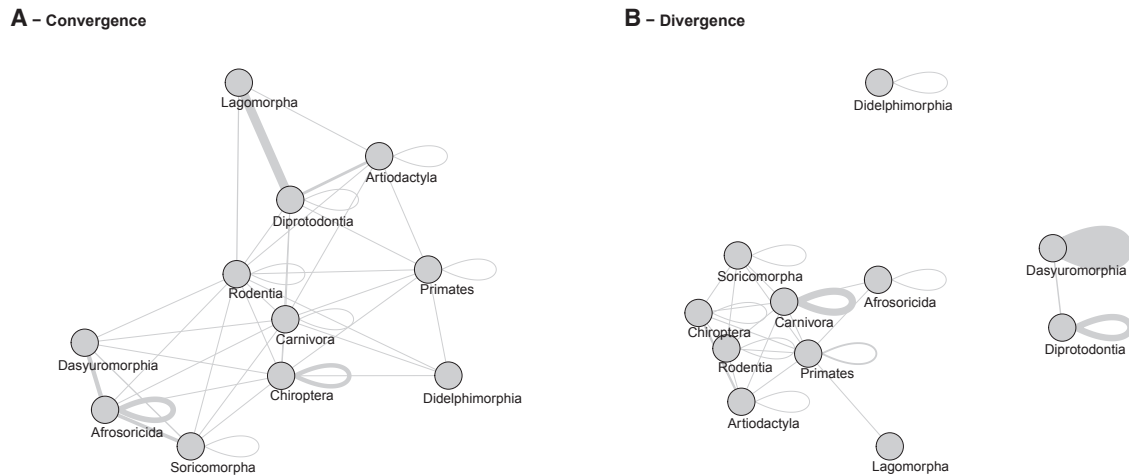


Figure 1. Patterns of Species Convergence and Divergence across and within the Main Orders of Mammals

The figure shows a network representation of convergence (A) and divergence (B) patterns at the species scale. Nodes represent the main mammalian orders involved in either the top 0.1% of convergent (A) or top 0.1% of divergent (B) pairs of species. Lines between nodes depict convergence/divergence events between (or within, when a node is linked to itself) orders. Line width indicates the relative number of pairs of species involved in convergence/divergence events, standardized by the relative richness of each order (line length is arbitrary). See also [Figure S1](#).

Overall, extreme niche convergence and divergence between species pairs, as assessed by the four traits, were widespread across the mammalian tree of life ([Figures 1 and S1](#)). Pairs of species harboring higher trait similarities than expected under neutral evolution included the classical examples of marsupial-placental convergence. For example, Artiodactyla (e.g., deer) and Diprotodontia (e.g., kangaroos) as well as Soricomorpha (e.g., shrews) and some Dasyuromorphia species (shrew-like marsupials) show low phylogenetically standardized functional trait distances, because they both involve clades that evolved toward large herbivore phenotypes and small insectivore phenotypes, respectively. Within the placentals, shrew-like species from different orders like Afrosoricida (e.g., shrew tenrecs) and Soricomorpha also showed higher functional trait convergence than expected under a neutral model of evolution. In these cases, convergence has been so strong that even former morphology-based systematics mistakenly grouped these species into the same paraphyletic order [18] (Insectivora). These convergences probably result from strong energetic constraints related to a strictly insectivorous diet in specific climatic conditions: insectivores preying on small insects are generally very small (at the lower body size limit for mammalian physiology) and have very similar teeth morphology [19]. Variations in morphological traits, especially body mass, have also commonly been related to climatic gradient (referred to as Bergmann's rule), thereby generating similar body mass patterns in independent species assemblages occupying equivalent climatic space. Bats also showed low levels of functional trait distance within their own order ([Figure 1](#)), because a large number of bats share the same diet and therefore harbor trait conservatism (i.e., the tendency for lineages to retain ancestral traits [20, 21]). Closely related species can have very divergent traits, especially within Dasyuromorphia (marsupial carnivores) or Carnivora ([Figure 1](#)). Divergent pairs of species (i.e., species harboring divergent traits) within Carnivora generally inhabit very distinct environments, for instance with one living in a temperate or tropical re-

gion and another inhabiting Arctic regions (e.g., polar bear versus other bears [22]), which suggests an interplay between high dispersal capabilities and strong natural selection, especially for top predators in the Arctic.

While trait convergence and divergence patterns at the species scale seem to be present in mammals, it remains unknown whether and how these species-scale patterns contribute to the trait structure of entire species assemblages, and in particular to trait similarity between different biotas [5]. We define here species assemblages as the sets of species whose range maps intersect with grid cells defined at 200 × 200 km resolution. We investigated how much the similarity of niche-related species traits between assemblages (i.e., trait β -diversity) differs from expected similarities assuming a neutral model of evolution. Theory predicts that trait convergence (or divergence) events at the species level scale up to entire assemblages if multiple pairs of convergent (or divergent) species show the same geographical distribution [5, 23, 24]. For example, if two independent adaptive radiations occurred in two different regions, so that the same ecological/functional guilds independently evolved in the two clades of the two regions, we would expect to find high trait similarity between these regions (low trait β -diversity) despite the differing evolutionary backgrounds (i.e., assemblage convergence) [24]. In this case, multiple species-level convergence events do scale up to trait convergence between entire assemblages. Although there are a few published examples for small clades [25–27], evidence of evolutionary trait convergence at the scale of entire biotas is mostly qualitative [5].

We scaled up our species-scale analysis to the assemblage scale using global species distribution data. We tested for assemblage convergence and divergence by extending our species-scale trait distance metric to an assemblage-scale trait β -diversity metric [(observed trait β – mean expected trait β) / standard deviation of expected trait β]. Expected trait β -diversity was computed using the simulated trait data previously used for the species-scale analysis. This phylogenetically standardized

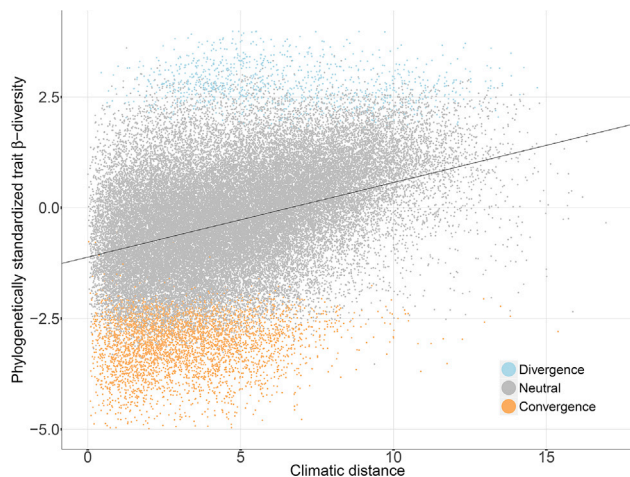


Figure 2. Relationship between Phylogenetically Standardized Trait β -Diversity and Climatic Distances between Assemblages

Deviations of observed trait β -diversity from a neutral model of evolution (i.e., phylogenetically standardized trait β -diversity) are plotted against climatic distances between assemblages worldwide (for the purposes of clarity, only 50,000 assemblage pairs are represented). Climatic distances are Euclidian distances between assemblages in the climatic space of the two first axes of a principal-component analysis of 19 bioclimatic variables. The solid diagonal line shows the mixed model fit (slope estimate 0.17; 95% confidence interval: 0.16–0.17, fitted on 200 stratified grid cells; see [Supplemental Experimental Procedures](#) and [Figure S4](#)). If the observed trait β -diversity between two assemblages is significantly lower or higher than neutral expectations, points are shown in orange or blue, respectively. See also [Figures S2–S4](#).

trait β -diversity measures the extent to which observed trait β -diversity was lower (convergence) or higher (divergence) than expected under neutral evolution (see [Supplemental Experimental Procedures](#) for details). We found that most pairs of assemblages (83%) show trait similarity that does not differ from expectations based on neutral evolution. However, many pairs of assemblages showed strong signatures of trait convergence: 13% (12%–16% when using alternative evolutionary model parameters of the Markov model; see [Supplemental Experimental Procedures](#)) of all pairs of assemblages showed lower functional trait distances than expected under Brownian motion (BM) (orange dots in [Figure 2](#)). In contrast, the signature of assemblage divergence was less pronounced, with only 4% (4% when using alternative parameters; see [Supplemental Experimental Procedures](#)) of all pairs of assemblages showing significant divergence (blue dots in [Figure 2](#)).

If convergent evolution at the global scale is driven by natural selection, we expect evolutionarily convergent assemblages to occur in similar climatic conditions. This hypothesis predicts that phylogenetically standardized trait β -diversity is lower between assemblages that experience similar climatic conditions, and that it increases when the climatic distances between assemblages increase. Globally, we found a positive and significant relationship between phylogenetically standardized trait β -diversity and climatic distance (slope mean estimate 0.17; 95% confidence interval: 0.16–0.17; [Figure 2](#)), indicating that the convergence of assemblages increased significantly with climate similarity. To make sure our results were driven by a general tendency across clades and traits, we re-estimated

this relationship while (1) removing some important mammalian clades (i.e., Rodentia, Chiroptera, Soricomorpha, Primates, Carnivora, Diprotodontia, and Artiodactyla; see [Figures S2A–S2H](#)), (2) keeping all possible combinations of three out of four broad trait categories ([Figures S3A–S3D](#)), and (3) bootstrapping trait items within broad categories ([Figure S3E](#), [Table S3](#), and [Supplemental Experimental Procedures](#)). We further assessed the sensitivity of our results to the neutral models used by re-estimating the climate-convergence relationship with other parameterizations and choice of models ([Figures S3F–S3H](#)). In addition, we used ordination techniques to produce a composite trait axis that was subsequently used to test for a potential bias related to the fact that the correlation between observed traits was not taken into account in our initial neutral model (see [Supplemental Experimental Procedures](#), [Table S2](#), and [Figures S3I and S3J](#)). All of these sensitivity analyses demonstrate that our results are (1) robust to the manner in which neutral models of evolution are calibrated and defined and (2) generalizable across clades and traits. Therefore, our results represent an emergent property of mammalian distribution and evolution and support the hypothesis that natural selection was important in shaping the evolutionary and geographical patterns of mammalian trait diversity.

Finally, to identify which regions contribute most to the convergent and divergent patterns, we spatially mapped the extreme convergent and divergent pairs of assemblages. In order to visualize the degree of assemblage convergence for each assemblage, we averaged, for each grid cell in the world, its standardized trait distance value to all other cells of the world. Australia harbored assemblages that exhibit the highest levels of assemblage trait convergence ([Figure 3](#)). Extremes of assemblage convergence are evident between, for example, Australia and northern temperate regions or Africa ([Figure 4](#); [Movie S1](#)). Importantly, this result is recovered across all of our sensitivity analysis ([Figures S2 and S3](#)), demonstrating that Australia shows a strong and recurrent pattern of convergence. This is due to the fact that Australia has experienced multiple adaptive radiations during its long geological isolation [28–30]. In particular, Australia’s mammalian fauna is dominated by marsupials, a clade for which we found strong similarities with placental species in the species-level analyses ([Figures 1 and S1](#)) and that contributes significantly to the extreme Australian assemblage convergence ([Figure S2K](#)). Our results thereby provide quantitative evidence for the long-standing hypothesis of assemblage-scale trait convergence between the Australian marsupial and the northern temperate placental biota [5]. However, the extreme convergence found in Australia is not restricted to marsupials alone but is also driven by other clades (e.g., native rodents; [Figures S2I and S2J](#)). This result reflects the fact that Australia harbors a unique fauna within which convergence with other faunas of the world has occurred repeatedly through evolutionary time, and is not restricted to one particular clade [29, 30]. Interestingly, we did not recover extreme cases of assemblage convergence in Madagascar, even though it is known that this occurred in some groups endemic to the island (e.g., tenrecs). This is likely because these groups do not represent the majority of species within the assemblages, so that the species-level convergences do not scale up to entire assemblages.

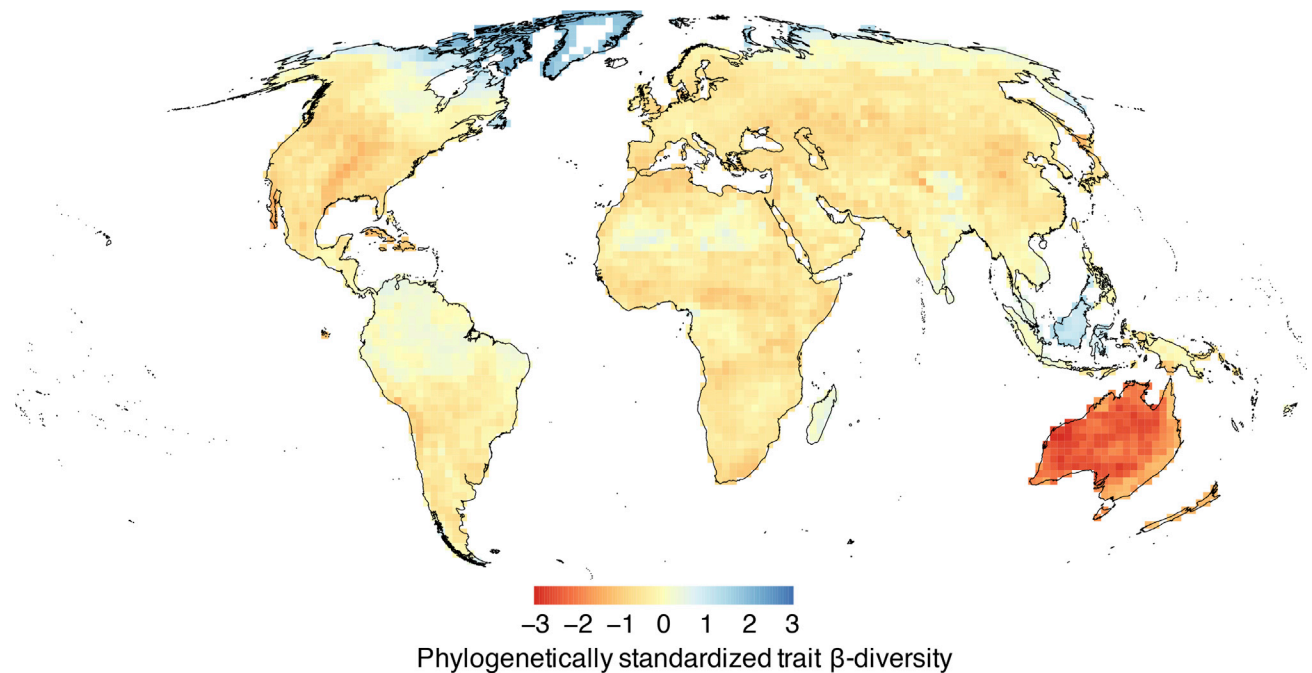


Figure 3. Spatial Patterns of Global Assemblage Scale Convergence and Divergence

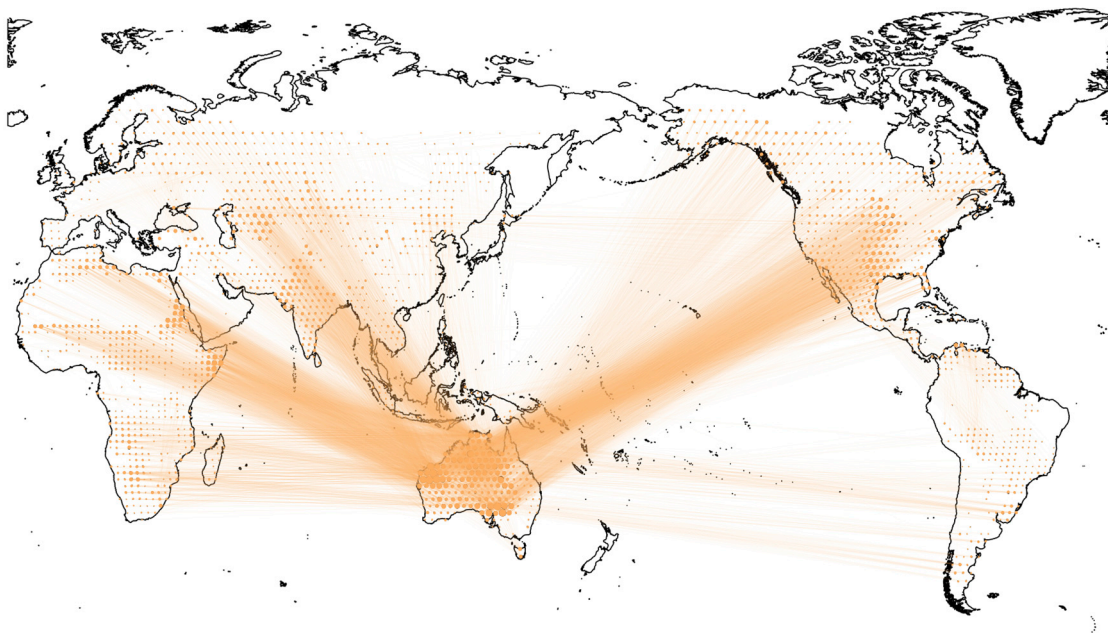
The map represents the global distribution of phylogenetically standardized trait β -diversity averaged by grid cell (i.e., for a given grid cell, pairwise trait β -diversity values are averaged across all other grid cells in the world). Red and blue colors indicate assemblage convergence and divergence, respectively.

The spatial pattern of the most divergent assemblages involved the Arctic region (northern North America and Greenland) and tropical or temperate zones in different continents (e.g., southern Eurasia or Southeast Asia; see Figure 4) and is generated by species that inhabit the Arctic and have close relatives in temperate or tropical regions with divergent trait characteristics. Significantly divergent pairs of assemblages were much less common than convergent ones (4% versus 13%) and mostly concerned species-poor assemblages adapted to climatically extreme or narrow environmental conditions (e.g., Arctic regions).

In this study, we showed that natural selection of mammalian traits influences the trait structure of entire assemblages at the global scale, and in particular the assemblage-scale convergence between the Australian and Eurasian, North American, and African faunas. Although these convergences are measured here in terms of coarse-scale niche-related traits, it is likely that they emerge from multiple finer-scale morphological, behavioral, and physiological convergent traits. For example, the independent emergence of large herbivores in Marsupialia and Placentalia (e.g., kangaroos and deer) is also associated with convergent physiological and anatomical traits not measured in this study, even in the absence of strong morphological convergences. Throughout our analysis, we argued that the assemblage-scale trait convergences detected resulted from repeated species-level evolutionary convergence events, i.e., in situ adaptive evolution (ISE) in distinct regions [27, 31]. However, deviations from evolutionarily neutral expectations may also arise in other evolutionary and biogeographical scenarios, for example an ecologically conservative dispersal process [27, 31] (ECD). In this scenario, (1) some lineages harbor less trait distance than expected under a neutral model of evolution because of trait

conservatism [20] and (2) dispersal events allow these lineages to colonize different assemblages (e.g., when the two sister species are allopatric). Trait conservatism occurs when, for example, the traits of two sister species have evolved very slowly (or not at all) since their last common ancestor. Clades that evolved more slowly than the rate average over the entire mammal phylogeny will harbor lower trait distances than predicted under our single-rate BM model. If some assemblages are composed mainly of species that belong to those clades with relatively low rates of trait evolution and also have high dispersal abilities, we would find trait similarity between these assemblages to be much lower than expected under BM, and they would be detected as “convergent” by our approach. For example, bats, which show high trait conservatism (Figure 1), are widespread across the globe and contribute to the high convergence in Australia (Figure S2L). The scope of our analysis and our methods used are not designed to disentangle the relative contributions of ISE and ECD to the globally observed assemblage convergence. Future research needs to explicitly relate the timing of trait evolution to colonization and diversification in distinct geographic regions [27, 31] to be able to measure the relative contribution of the two processes or, alternatively, to explicitly take into account rate variations across the mammalian tree of life. Nevertheless, our results strongly support that, at the global scale, niche-based processes play an important role in structuring the trait composition of mammal assemblages, by directly triggering convergent trait evolution (the ISE hypothesis), by environmental filtering of lineages experiencing niche conservatism (the ECD hypothesis), or by both processes. We acknowledge that our estimates of convergent and divergent assemblage pair proportions are the result of the two processes and that it remains

A – Convergence



B – Divergence

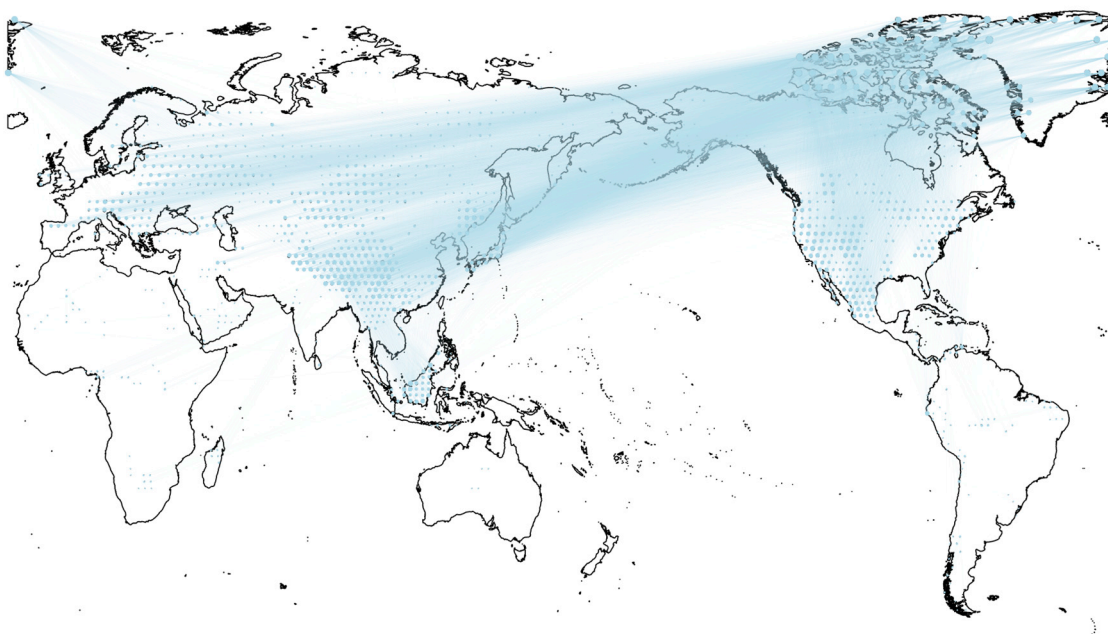


Figure 4. Spatial Patterns of Extremely Convergent and Divergent Pairs of Assemblages

The maps represent the global distributions of pairs of assemblages with the top 0.25% of the highest negative phylogenetically standardized trait β -diversity (i.e. assemblages that converge much more than expected under neutral evolution, A) and pairs of assemblages with the top 0.25% of the highest positive phylogenetically standardized trait β -diversity (i.e. assemblages that diverge much more than expected under neutral evolution, B). Filled circles represent assemblages, and circle diameter relates to the number of times a given assemblage is found in the top 0.25% of convergent (A) or divergent (B) pairs. See also [Figure S2–S4](#).

complicated to tease apart their relative importance. Additionally, our approach does not take into account trade-off between traits, which might bias our result toward an overestimation of convergence. Nevertheless, sensitivity analysis shows that the most

extreme cases of convergent assemblages detected in this study involved Australian versus Eurasian and/or North American assemblages ([Figures 3, 4, S2, and S3](#)). In these particular cases, historical dispersal between assemblages was low, suggesting

that the ISE hypothesis is more likely. Therefore, our work supports the long-standing hypothesis of convergence between the Australian and northern temperate faunas, both at the species level and at the assemblage level.

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures, three tables, Supplemental Experimental Procedures, and one movie and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.03.046>.

AUTHOR CONTRIBUTIONS

J.R. formatted the distribution data. F.M. conceived the study, with advice from S.L., R.O.W., and W.T. F.M. performed all analyses, with the assistance of R.O.W. and M.G. F.M. interpreted the results with the assistance of R.O.W., G.F.F., S.L., and W.T. F.M. and W.T. wrote the first version of the manuscript, and all authors contributed to revisions.

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