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THE ROYAL SOCIETY
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Common latitudinal gradients in functional richness and functional evenness across marine and terrestrial systems

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Functional diversity is an important aspect of biodiversity, but its relationship to species diversity in time and space is poorly understood. Here we compare spatial patterns of functional and taxonomic diversity across marine and terrestrial systems to identify commonalities in their respective ecological and evolutionary drivers. We placed species-level ecological traits into comparable multi-dimensional frameworks for two model systems, marine bivalves and terrestrial birds, and used global species-occurrence data to examine the distribution of functional diversity with latitude and longitude. In both systems, tropical faunas show high total functional richness (FR) but low functional evenness (FE) (i.e. the tropics contain a highly skewed distribution of species among functional groups). Functional groups that persist toward the poles become more uniform in species richness, such that FR declines and FE rises with latitude in both systems. Temperate assemblages are more functionally even than tropical assemblages subsampled to temperate levels of species richness, suggesting that high species richness in the tropics reflects a high degree of ecological specialization within a few functional groups and/or factors that favour high recent speciation or reduced extinction rates in those groups.

1. Introduction

Stark differences in the number of species between tropical and higher latitudes have long been apparent, and latitudinal gradients of biodiversity are a central focus of macroecological and biogeographic research in both terrestrial and marine systems [1–3]. Taxonomic trends have received the most attention, but spatial patterns occur in many aspects of global biodiversity, including phylogenetic, morphological and functional diversity [4–6]. Functional diversity, i.e. the variety of roles that species play in ecological communities, is now recognized as an important aspect of biodiversity, linking species and clades to the ecosystems they influence and evolve within. However, the relation of this extra-taxonomic component of biodiversity to latitude and its environmental correlates remains poorly understood [6,7].

Previous studies of functional diversity along latitudinal gradients have reported greater functional richness (FR) in the tropics, where FR is the number of functional groups *sensu* [8,9] (see also 'functional entities' of [10]).

Species richness saturates within these tropical functional groups, so that beyond a certain threshold, an increase in species richness is not accompanied by a rise in FR (e.g. [11–13]). This saturating pattern of FR does not in itself specify how species richness is distributed across functional groups, i.e. functional evenness (FE), which can give additional insights into mechanisms that generate and maintain higher species and functional diversity in the tropics. Disproportionate accumulation of species in certain functional groups towards the equator implies that aspects of those functional groups promote higher speciation or lower extinction rates in non-equilibrium cases, and/or enable greater coexistence (i.e. more species can be accommodated in those groups). For example, bird species in more open canopy habitat with a greater propensity to long-distance dispersal have lower rates of allopatric speciation and diversification than species in understory-foraging niches, which are less adapted morphologically for dispersal [14]. In accommodation arguments, functional groups that rely on resources that are more abundant or can be more finely partitioned in the tropics might be expected to maintain more species [5]. Alternatives such as these need to be assessed against a suitable null model because randomly drawing a few species from an uneven distribution yields increased evenness—the rarest functional groups will often go unsampled [9]. Hence, the random loss of species as one moves from the tropics to the temperate may not only drive a loss of functional groups, but also an increase in the evenness of those remaining.

Marine bivalves and terrestrial birds have each served as model systems for large-scale macroevolutionary and macroecological analyses. Both systems are taxonomically and ecologically diverse and geographically widespread, with strong and well-studied latitudinal gradients in species numbers [9,15–19]. Hence, comparative analyses allow us to test the generality of diversity patterns between marine and terrestrial environments [9]. Here, we apply a single set of analytical methods to the two systems to ask: (1) how do spatial patterns of FR and FE vary globally and regionally, (2) do functional groups show strongly nested spatial patterns or do they frequently turn over and (3) are the potential drivers of these patterns similar in marine and terrestrial environments? We address these questions both latitudinally and longitudinally, because both systems vary in species richness in both dimensions (e.g. [16,18]), suggesting that functional diversity might also vary longitudinally and these differences may inform our understanding of the latitudinal patterns. Finally, we show that the latitudinal pattern of FE cannot be explained entirely by attenuation of species numbers out of the tropics. We discuss how properties of the tropical environment, such as low seasonality in temperature, lack of freezing temperatures and unique habitat diversity, might lower FE by supporting higher trophic and habitat specialization relative to higher latitudes in some functional groups [3,20].

2. Material and methods

(a) Functional diversity of bivalves and birds in a common framework

Although functional diversity as an ecological concept has been in use for decades [21], it is variably defined and used [7,22,23]. We use a scheme of discrete functional categories that allow us to make comparable analyses of the global species-level datasets of these very different systems. Some types of continuous morphological data are available for both birds and bivalves, e.g. body size in both systems, and bill or tarsus length in studies of bird species' ecology and functional diversity (e.g. [24–26]), but these morphometric data are generally not easily related to ecological function in either system. Considerable scatter in morphological–ecological correlates results from multiple morphological solutions to the same ecological problem, e.g. in birds, both doves and finches consume small seeds [26–28], and in bivalves, solemyoids, mytiloids and lucinoids are all chemosymbiotic at different sizes and shapes [29]. Thus, for comparative purposes, we placed bird and bivalve species (n = 8005 and 5877, respectively) into discrete functional groups based on life habits and ecology.

We assigned each marine bivalve species a broad functional category of feeding, attachment to substratum, position in the substratum and mobility, following a standard scheme of ecological function after [9,30] (electronic supplementary material, table S1). This scheme generates 567 potential combinations, of which 49 are realized in the extant biota. For birds, we split the proportionate functional assignments of Wilman et al. [31] across nine diet categories and seven foraging stratum categories into discrete groups. We classified a diet generalist species as one in which no diet category exceeds 70%, resulting in five generalist categories: invertebrate prey (mostly insects for terrestrial species) + other plant components (excluding nectar), invertebrates + nectar, generalist carnivory, generalist omnivory and generalist herbivory (see electronic supplementary material for further details). We split species into foraging substratum categories using the same proportionate cut-offs. This resulted in a scheme with 126 potential combinations, of which 105 are biologically plausible (e.g. a piscivore cannot be an upper-branch forager) and 58 are realized in the extant biota (electronic supplementary material, table S2). We evaluated alternative proportionate cut-offs (e.g. 60% occupancy of a functional category as the cut-off for generalists) and obtained similar results to those presented here. Trait axes and categories of traits used for sorting species into groups were chosen so that no species were data deficient. This functional scheme has enough groups to detect functional differences across assemblages, but not too many to obscure the accumulation of species with similar ecological roles. Increasing the number of functional categories and associated traits will necessarily increase the number of functional groups, but both coarser and finer-scale functional schemes are known to capture similar functional diversity dynamics [32].

(b) Measuring functional richness and evenness

For any given locality, we define *functional richness* (FR) as the number of functional groups present, and *functional evenness* (FE) as the relative skew of the frequency distribution of species among the functional groups. We quantified FE as the ratio of the inverse Simpson's diversity index to the number of functional groups [33]:

$$\text{FE} = \frac{1}{\sum \left(n_i [n_i - 1] / N[N - 1] \right)} \times \frac{1}{N}.$$

Here n_i is the number of species in functional group i and N is the total number of functional groups. Simpson's index normalized by the number of functional groups provides an 'intuitive gradient in evenness' ([33], p. 121) that increases monotonically from 0 to 1 with skew in the number of species across functional groups. We adopt these metrics of functional diversity rather than the continuous distance-based metrics, 'FEve' and 'FRic' of Villéger et al. [34] because FE and FR do not require the transformation of the data from discrete to continuous form, which eases the interpretation of the functional diversity patterns for the questions addressed here. Bivalve functional diversity at regional

scales measured by FEve and FRic are qualitatively consistent with the results found here [9].

(c) Measuring spatial patterns in bird and bivalve functional diversity

We used georeferenced global bivalve species-occurrence data from the primary literature and museum collections ($n = 67\,435$ point occurrences across 6151 localities; electronic supplementary material, figure S1) and constructed species ranges as convex hulls of their point occurrences—a dataset that is robust to regional-scale sampling biases [19]. We included occurrences from the intertidal zone to the 200 m isobath, which is generally taken to mark the edge of the continental shelf; beyond this depth, the deep-sea is considered to comprise a separate ecological and evolutionary system (e.g. [35]). Bird occurrence data are assembled from bird species extent-of-occurrence maps provided by BirdLife International's Data Zone (accessed on 30 June 2017). Geographical ranges for species in these data are range-through reconstructions based on species-occurrence records; bird breeding ranges were used in all spatial analyses, following [36]. BirdLife maps are coarse-grained, but they are widely used and are currently the best source for broad-scale patterns of bird species diversity (as exemplified by [37], where data including those of BirdLife enable work on species distribution patterns at grains finer than the 1° used in this study).

We intersected bivalve and bird geographical range hulls with an equal-area grid (111 km × 111 km; approximately 1° latitude–longitude at the equator in a Lambert cylindrical equal-area projection). We summarized species-level patterns within these grid cells, across global latitudinal and longitudinal bands, and further summarized these spatial patterns within transects of continents, coastlines and climate zones as defined in electronic supplementary material, figure S2. We examined latitudinal and longitudinal assembly of functional groups at the global and coastline/continental scale using the R package 'betapart' [38] to calculate the relative contributions of 'nestedness' to functional dissimilarity across latitude, i.e. where latitudinal assemblages differ such that one is a subset of the other, in contrast to 'turnover' that summarizes gain and loss of functional groups between assemblages (see electronic supplementary material for further details).

To evaluate the effects of the latitudinal species richness gradient on latitudinal patterns in FE, we compared relatively lower species richness bivalve and bird assemblages from temperate grid cells to tropical grid-cell assemblages subsampled to the same species richness. If the increase in FE from tropics to poles arises primarily from the random drawing of smaller sets of species from a larger tropical distribution, i.e. the out-of-the-tropics expectation [9], we expect subsampled tropical assemblages to have evenness values equal to their richness-equivalents at high latitudes. If tropical assemblages subsampled to temperate-zone species richness levels show significantly lower evenness than richness-equivalents at higher latitudes, then species richness differences alone cannot fully explain the low tropical evenness, suggesting a role for tropical climates and attendant habitats.

3. Results

(a) Global and regional patterns of functional richness and evenness

(i) Functional richness

Across global latitudinal bands, both bird and bivalve FR are highest in the tropics and decrease toward the poles, roughly correlating with species richness but with peak FR extending well beyond the regions of maximum taxonomic richness (figure 1). Both bivalves and birds show a similar saturation of FR with species richness, with few functional groups added per grid cell above approximately 250 species in both systems (figure 2). For bivalves, species richness and FR are both highest in the tropical West Pacific, and in birds, they are both highest in the Northern Andes and east Himalaya, but in neither system do maximum species richness and FR coincide at the scale of a single grid cell, and no single grid cell contains all 49 bivalve functional groups or all 58 bird functional groups (figure 2).

(ii) Functional evenness

Both systems show a highly skewed distribution of species among functional groups, with a few groups of functionally similar species being hyperdiverse (e.g. shallow-infaunal siphonate suspension-feeding bivalves and upper-branch insectivorous birds), an assortment of groups having intermediate species richness, and many groups being species-poor (e.g. photosymbiotic bivalves like *Tridacna*, and semi-aquatic ectotherm-predators like *Corythornis madagascariensis*; electronic supplementary material, figure S3). FE is lowest in the tropics and increases towards the poles (figure 1). This hollow curve is seen globally and in each separate coastline and continental transect; it is not driven by a single region or transect (electronic supplementary material, figure S4, which presents FE at the equal-area grid-cell resolution to show longitudinal heterogeneity).

(b) Beta diversity of functional groups

Birds and bivalves also show parallels in the beta diversity of their ecological roles across latitude. Both systems show strong latitudinal nestedness rather than turnover, with bivalves the stronger of the two. Poleward assemblages are subsets of equatorward ones instead of distinct sets of functional groups (figure 4; electronic supplementary material, figure S5), and no functional groups occur exclusively outside of tropical latitudes (electronic supplementary material, figure S5). The failure of any tropical grid cell to contain all functional groups, noted above, results from the greater turnover of functional groups with longitude than with latitude. Birds show levels of longitudinal nestedness similar to their latitudinal patterns, whereas bivalves show more longitudinal turnover, largely between the major ocean basins (figure 4; electronic supplementary material, figure S5).

(c) Effects of species richness on functional richness and evenness with latitude

The increase in bird FE with latitude is broadly consistent with an out-of-the-tropics attenuation of species diversity, largely between 30° and 50° N (electronic supplementary material, figure S6). However, temperate assemblages of both birds and bivalves tend to have higher FE than tropical assemblages subsampled to the same species richness (70% and 79%, respectively, of 10 000 resampled tropical-temperate comparisons; figure 3). Thus, tropical assemblages show lower FE than expected if the latitudinal decline in species richness was the sole driver of latitudinal patterns in FE. In line with these effects, environmental filters appear to contribute to latitudinal trends in FE and FR: polar latitudes are more functionally even, likely owing to the loss of habitats and
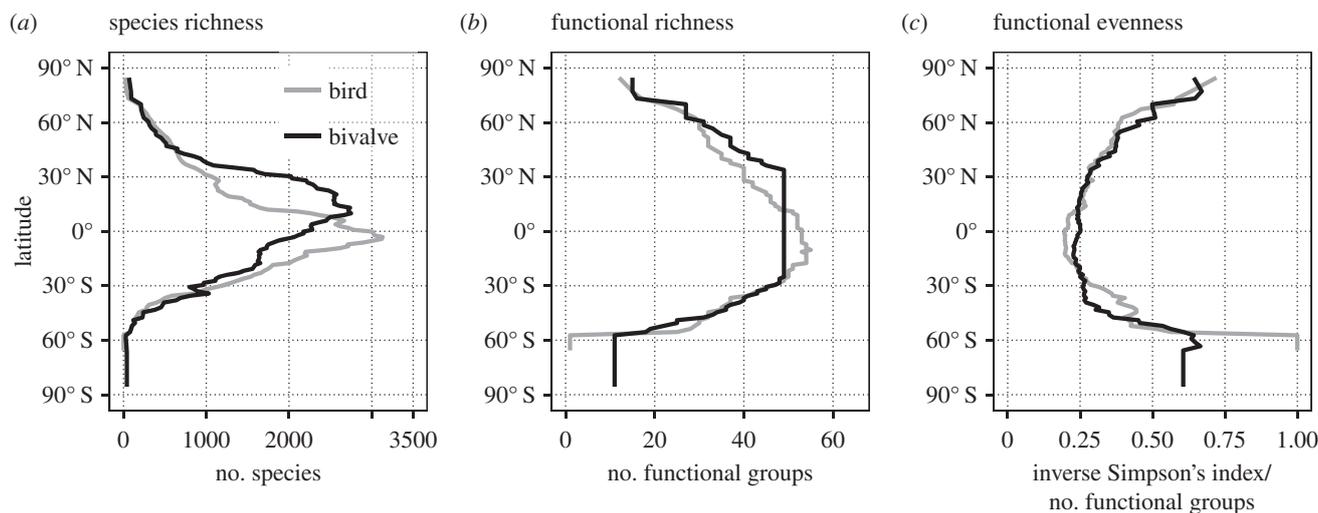
Figure 1. Latitudinal gradients in bird and bivalve species richness (*a*) peak in the tropics and decline monotonically toward each pole. Similarly, bivalve and bird functional richness (*b*) peaks in tropical latitudes and declines towards both poles. Functional evenness (*c*) for both systems is lowest (i.e. most uneven) in the tropics and increases towards the poles.

resources that support certain species-rich functional groups such as arboreal groups in birds and suspension-feeding groups in bivalves.

4. Discussion

Marine bivalves and terrestrial birds show similar latitudinal trends in FR and FE, with highest FR and lowest FE in the tropics, suggesting that macroecological differences between marine and terrestrial systems may not be as fundamental as sometimes argued (see also [39]). This is a striking result given the profound differences between marine and terrestrial environments [40], and the very different ecologies and evolutionary histories of our two study systems including differences in their mobility and dispersal ability, basic modes of nutrition, spatial heterogeneity of their habitats [41] and the extent to which populations are thought to be limited by predation and competition [42,43]. Further, the diversification of the Bivalvia has far deeper roots than birds, with many functional groups originating in the Palaeozoic and many more lineages and functional groups surviving the end-Cretaceous mass extinction than in modern birds [6,44]. Despite these inherent differences, the similarities in spatial patterning of FR and FE suggest common controls on functional diversity patterns in the two systems, at the scales analysed here.

In both systems, FR begins to plateau in the warm-temperate before reaching the tropical species richness peak (figure 1*b*), indicating that the accumulation of species in the richest functional groups is more important than the addition of functional groups for the attainment of high species numbers in the tropics. This latitudinal pattern in the distribution of species within functional groups is likely to remain similar for both birds and bivalves through the discovery of new species and further sampling. Birds and bivalves are most thoroughly described and sampled in temperate regions (particularly the north temperate) relative to tropical regions [19,45], suggesting the temperate values of FE are likely stable. The discovery and splitting of taxa in birds and bivalves will likely increase the species richness of tropical locales (e.g. [19,46,47]), and new tropical species of birds are mostly forest insectivores [46,47] that already

dominate and drive the observed low tropical evenness. Hundreds of new species would have to be disproportionately added to the low-richness functional groups (e.g. freshwater carnivores in birds, or photosymbiotic species for bivalves) for tropical evenness to approach temperate values.

Other geographically widespread clades or groups show a similar saturating pattern of FR with taxonomic richness at low latitudes, including New World bats [11], plants [12,48], mammals [5] and stream fish [13]. Thus, general drivers of a skewed pattern in FE across these disparate systems are likely to include a combination of differential diversification (origination and/or extinction of taxa within functional groups [9]), associated biogeographic dynamics and/or differential capacities among functional groups for finer subdivision or packing into ecological niche space [4], each of which we consider in the following sections.

(a) Origination and functional diversity

Associations between speciation rates and ecological function have been demonstrated in birds [14] and in bivalves [9]. Fossil data suggest that low tropical FE in bivalves derives from differential origination rates among taxa within functional categories, i.e. a 'supply-side' effect [9]. The evidence for a similar effect in birds is less direct. Bird speciation is often 'non-ecological', primarily driven by geographical separation of functionally similar species [49], and some bird functional groups may have greater possibilities for speciation because they occupy habitats that are more patchy and less easily dispersed across [14], or have adaptations that limit inherent dispersal ability [50,51], though not because of inherent relative success of different feeding or foraging modes. Thus, supply-side drivers of species diversity may well contribute to lower tropical FE in birds as well as bivalves, generating disproportionately high species richness in certain functional groups. However, insectivores, the group with the highest species numbers in the tropics (and therefore the largest contributions to low tropical FE), do not show heightened speciation overall [52], although some largely tropical insectivorous bird clades do have relatively high diversification rates [53].

Similar histories of regional environmental effects may also influence the similar latitudinal gradient in FE across the marine and terrestrial realms. The saturation of FR
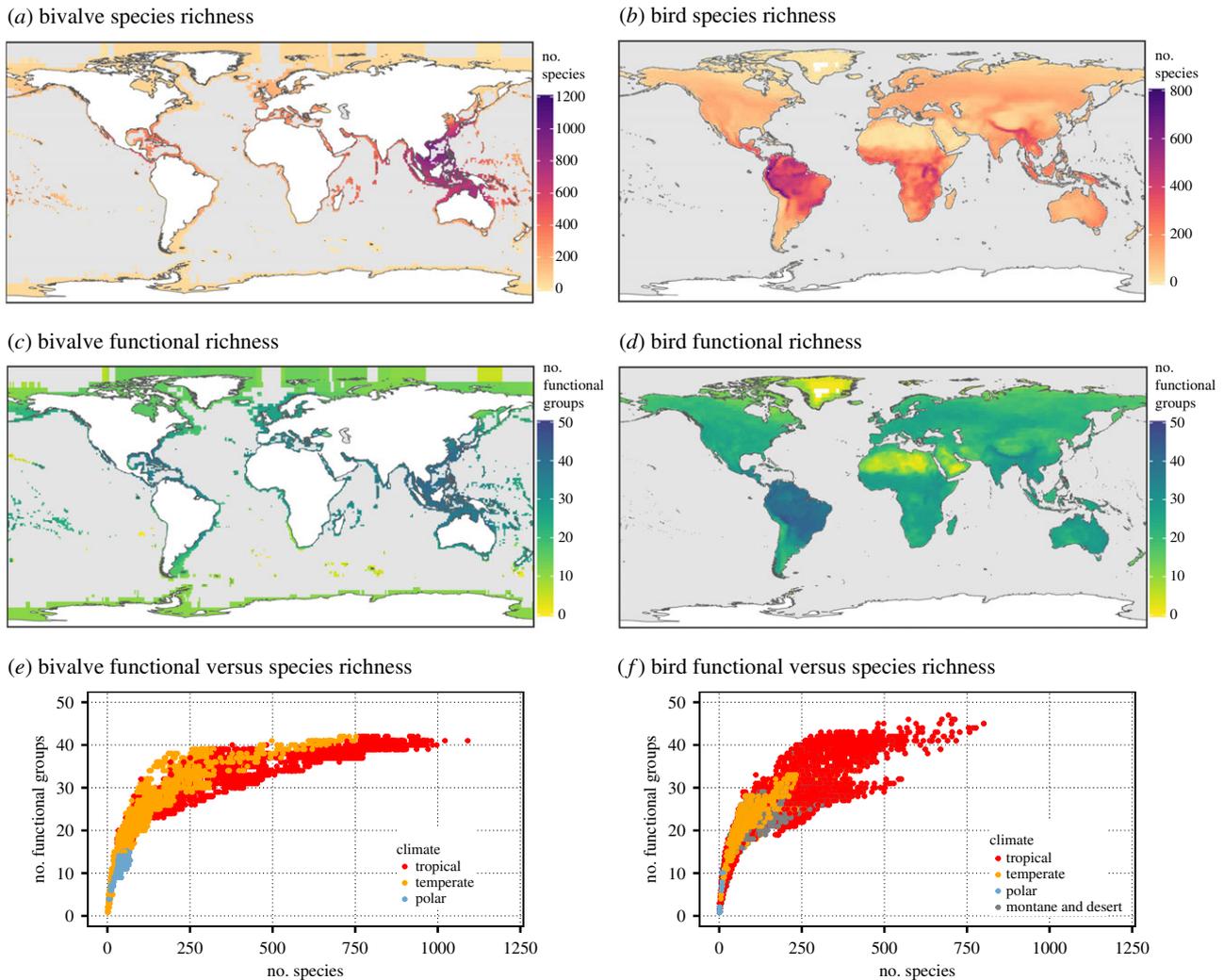
Figure 2. Global distribution of bivalve and bird species and functional richness. (*a*) Bivalve species richness peaks in the tropical West Pacific with a secondary hotspot of taxonomic diversity in the Caribbean. (*b*) Bird species richness peaks along the Andes, Amazon, Himalaya and tropical East Africa. (*c*) Bivalve functional richness peaks throughout the tropical latitudes along each coastline. (*d*) Bird functional richness is highest within the Amazon and Andes, and the Himalaya. (*e,f*) Bivalves pack more species per functional group in a given equal-area cell (approx. 1° latitude–longitude at the equator) than birds across major climate zones. (Online version in colour.)

relative to species richness indicates that global hotspots in taxonomic diversity involve the packing of species into functional groups, at least at the regional scale (figure 2). In both birds and bivalves, the most species-rich regions correspond to areas where factors such as late Cenozoic sea-level fluctuations and spatial heterogeneity, in combination with largely stable temperatures and resources, created many opportunities for allopatric splits into functionally equivalent species (the Andes and Indonesia in birds, the 'Coral Triangle' from the Philippines to Indonesia in bivalves). These historical factors can thus provide a biogeographic and evolutionary means of accommodating increased numbers of taxa without increasing regional FR (e.g. [6,54–56]).

In addition to each system's intrinsic diversification rates and regional environmental effects, the evolutionary age of assemblages may contribute to low FE in the tropics. In mammals, Oliveira *et al.* [5] argued that long periods of evolutionary time in a stable environment were necessary for the generation of novel roles, and notwithstanding tropical regions with high variation in precipitation, the tropics have widely been viewed as more stable than higher latitudes [57,58]. This claim may be most relevant for birds, in which a few species-poor tropical functional groups have deeper-

branching species from the Cenozoic radiation (e.g. the strictly aquatic, non-marine, generalist carnivore *Balaeniceps rex* [44]), but for bivalves, 30 of the present-day functional groups have been present continuously since the Mesozoic and include both species-rich and species-poor groups [6].

(b) Extinction and functional diversity

Extinction is associated with latitudinal patterns of FR, at least in bivalves. Cenozoic cooling of the Earth's poles has contributed to high-latitude extinction of functional groups, particularly following the onset of Southern Hemisphere glaciation before the end-Eocene [59,60]. Few data exist on the functional groups lost by birds either regionally or globally during the late Cenozoic (but see the extinction of the Phorusrhacidae, a group of large flightless carnivores, in the late Pleistocene [61]). Many of the bird and bivalve functional groups present in the tropics and absent at high latitudes are currently non-viable life modes for these high-latitude environments (photosymbiosis in bivalves and frugivory in birds), but determining the relative roles of extinction and environmental filtering in shaping these patterns will require additional, spatially explicit fossil data. The longitudinal
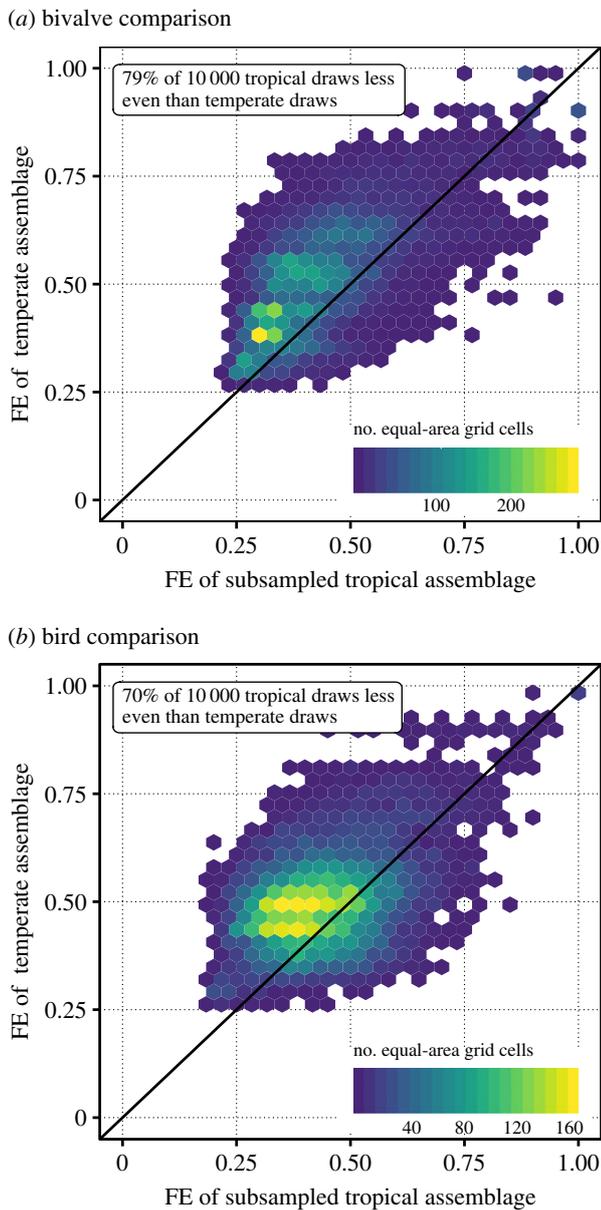
(a) bivalve comparison

(b) bird comparison

Figure 3. Comparison of temperate assemblage functional evenness to that of tropical assemblages subsampled to temperate species richness (method details in electronic supplementary material). (*a*) Nearly 80% of bivalve subsampled tropical assemblages have lower functional evenness than temperate assemblages. (*b*) Approximately 70% of bird subsampled tropical assemblages have lower functional evenness than temperate assemblages. (Online version in colour.)

turnover of functional groups is also related to extinction in some cases, e.g. the extinction of photosymbiotic bivalves in the W. Atlantic at the Eocene–Oligocene boundary [62].

The increase in FE with latitude also results in part from the disproportionate loss of taxa from high-diversity functional groups relative to low-diversity functional groups. Increased seasonality and/or reduced abundance of resources at high latitudes with Neogene cooling may have increased extinction rates of ecologically and physiologically specialized species within the richest extratropical functional groups (e.g. [20,63,64]). The pattern of Plio-Pleistocene extinction in north-temperate bivalves suggests the winnowing of species numbers even as the functional groups persisted, therefore increasing high-latitude FE [18]. A similar pattern is observed during mass extinctions, which increased FE through the preferential loss of taxa from hyperdiverse functional groups [6,65].

(c) Biogeographic and ecological accommodation of functional diversity

Variation in species richness among functional groups may be related not only to speciation and extinction rates but also to the ease with which species can come into sympatry and coexist [49]. The high species redundancy in large functional groups of reef fish apparently reflects multiple axes for niche subdivision (e.g. in prey location and in defense) [4]; similar effects may apply in our two systems where species redundancy may also reflect more available resources for some functional groups, enabling species to coexist because more individuals and populations can be supported [5,64]. The largest functional groups in bivalves and birds—shallow-burrowing suspension-feeding in bivalves (1182 species) and upper-branches insectivory in birds (1774 species)—are likely more finely subdividing niche space and exploiting more stable and/or abundant tropical resources [63,66]. These functional groups also show the strongest trends in species richness with latitude, and consequently, the strongest ties to key environmental correlates that can be related to their resource bases such as annual and seasonal dynamics in temperature for bivalves [67] and variation in both temperature and precipitation for birds [16,36]. Total resource abundance rather than niche subdivision is likely more important in accommodating bivalve functional redundancy because bivalve populations appear to be limited by predation more so than competition outside of space-limited rocky substrata [43]. By contrast, stronger interspecies competition among birds suggests that finer niche subdivision may be more important. In any case, regions where resource abundance is notably lower than in most tropical and temperate regions, e.g. deserts, islands and near the poles, FE is higher in both birds and bivalves (electronic supplementary material, figure S4).

The failure of all functional groups to occur in any one region of maximal taxonomic richness, also observed in mammals [5], results from the restricted geographical distributions of certain low-richness functional groups (e.g. in birds, the semi-aquatic ectotherm-feeders group no. 21 restricted to Madagascar). This pattern is much weaker in bivalves, where all functional groups occur in the high-richness Indo-Pacific, though not at the grid-cell level (figure 2). Longitudinal turnover is still evident in bivalves owing to their lower FR in the tropical Atlantic and east Pacific relative to the west Pacific. Thus, the two systems differ more in the details of their longitudinal patterns than in their latitudinal ones.

The relatively high FE of low-richness regions has been attributed to the latitudinal and longitudinal attenuation of uneven species-rich tropical assemblages [9], as sub-sampling of a fauna necessarily increases evenness, but our finer spatial resolution tropical–temperate resampling implies that the gradient in FE is steeper than expected (figure 3). In birds, a simple model for random loss of functional diversity with latitude is also not supported because multiple clades have colonized the tropics from the temperate zones [68,69]. Further, in bivalves and birds, the absence of some functional groups in high-latitude, low-richness regions can be directly attributed to climatic filtering. For example, in bivalves, 17/26 (65%) of missing tropical functional groups in polar regions suspension feed on phytoplankton, a resource that plummets in the dark winter months [6,60], and geographical variation in bird body mass [70], broad dietary guilds [36]
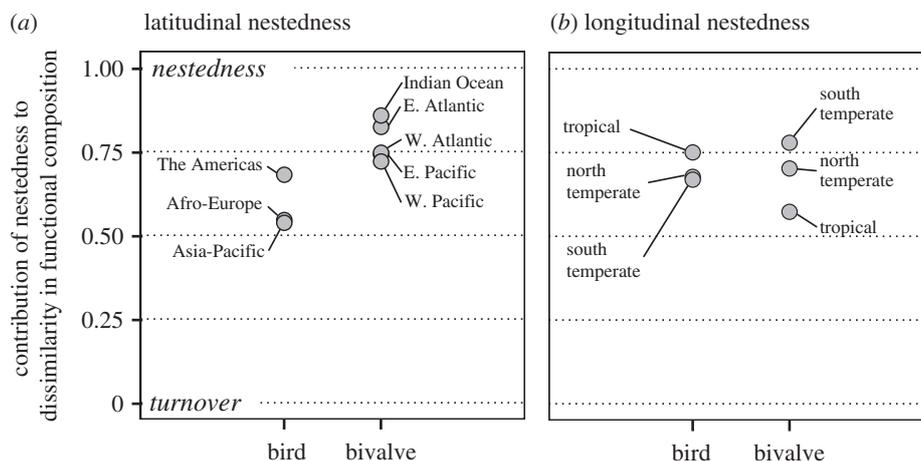
Figure 4. Contribution of nestedness to the latitudinal and longitudinal dissimilarities in the composition of functional assemblages. (*a*) Bivalves show greater nestedness of functional groups with latitude along coastlines than birds do within major continents. (*b*) Longitudinally, both systems have similar levels of nestedness.

and proportion of generalists [71], has been attributed to latitudinal availability of certain food resources and habitats (e.g. [72]).

While the evenness of functional assemblages is not entirely a product of species richness, suggesting that features of the tropical environment further influence the patterns reported here, more work is needed to determine when and how tropical communities reach low FE without the accumulation of very high species numbers in the most species-rich functional groups. Low-latitude terrestrial map cells that are resource-poor (deserts) or relatively isolated (islands) have higher FE than most low-latitude sites (electronic supplementary material, figure S4), probably because they lack the opportunity to gain large numbers of species such as the insectivorous birds that lower FE elsewhere in the tropics. Islands often have endemic 'super-generalist' bird species [73] that may preclude further establishment of similar bird species; such exclusion may not occur in bivalves, as bivalve tropical islands appear to have similarly low evenness to mainland coastal sites.

5. Conclusion

Marine bivalves and terrestrial birds face very different environmental challenges and differ in their behavioural, morphological and ecological capabilities, with contrasting biogeographic histories of diversification. When placed in a common analytical framework, the two systems exhibit similar global patterns in the two key components of functional diversity—richness and evenness. Comparing the geographical distribution of ecological roles in marine bivalves and terrestrial birds offers an opportunity to discover generalities about how these systems evolve within a broader macroecological context, and how ecological communities at varying latitudes are structured on land and in the sea, and provides a novel framework for analyses of species packing within regions and functional groups. The positive, asymptotic relationship of FR to species richness, the increase of FE at higher latitudes, and the importance of the tropical environment in promoting disparities in the accumulation of species richness among functional groups appear to be basic features structuring patterns of biodiversity.

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