

Evolutionary time and species diversity in aquatic ecosystems worldwide

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ABSTRACT

The latitudinal diversity gradient (LDG) is frequently described as the most dramatic biodiversity pattern on Earth, yet ecologists and biogeographers have failed to reach consensus on its primary cause. A key problem in explaining the LDG involves collinearity between multiple factors that are predicted to affect species richness in the same direction. In terrestrial systems, energy input, geographic area, and evolutionary time for species accumulation tend to covary positively with species richness at the largest spatial scales, such that their individual contributions to the LDG are confounded in global analyses. I review three diversity patterns from marine and freshwater systems that break this collinearity and which may thus provide stronger tests of the influence of time on global richness gradients. Specifically, I contrast biodiversity patterns along oceanic depth gradients, in geologically young *versus* ancient lakes, and in the north *versus* south polar marine biomes. I focus primarily on fishes due to greater data availability but synthesize patterns for invertebrates where possible. I find that regional-to-global species richness generally declines with depth in the oceans, despite the great age and stability of the deep-sea biome. Geologically ancient lakes generally do not contain more species than young lakes, and the Antarctic marine biome is not appreciably more species rich than the much younger Arctic marine biome. However, endemism is consistently higher in older systems. Patterns for invertebrate groups are less clear than for fishes and reflect a critical need for primary biodiversity data. In summary, the available data suggest that species richness is either decoupled from or only weakly related to the amount of time for diversification. These results suggest that energy, productivity, or geographic area are the primary drivers of large-scale diversity gradients. To the extent that marine and terrestrial diversity gradients result from similar processes, these examples provide evidence against a primary role for evolutionary time as the cause of the LDG.

Key words: biodiversity, species richness, diversification, deep sea, polar, biome, lake, marine, ocean, latitudinal diversity gradient.

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I. INTRODUCTION

Few patterns in nature are more dramatic, inspiring, and maddening than the latitudinal diversity gradient (LDG). The LDG has been described as Earth's 'first-order biodiversity pattern' (Krug *et al.*, 2009) and has been the subject of numerous reviews and syntheses, many of which have catalogued a seemingly vast array of causal mechanisms (Pianka, 1966; Willig, Kaufman & Stevens, 2003; Fine, 2015; Mittelbach *et al.*, 2007; Rosenzweig, 1995). At least for terrestrial systems, the major challenge in explaining the LDG is the collinearity of key explanatory variables, all of which covary positively with species richness at the largest spatial scales. In comparison to biomes from higher latitudes, the tropics are old (Fischer, 1960; Fine & Ree, 2006; Wiens & Donoghue, 2004), they are large (Terborgh, 1973; Rosenzweig, 1995, 1992), they are productive (Kucharik *et al.*, 2000), and they are warm (Hawkins *et al.*, 2003).

Considered from first principles, all of these factors are predicted to have positive effects on species richness at regional to continental scales. All other things being equal, older biomes will have had more time for species to accumulate relative to geologically young biomes. Regions with increased energy input may have faster rates of speciation (Allen, Brown & Gillooly, 2002; Worm & Tittensor, 2016), lower extinction rates (Storch & Okie, 2019), and they may have greater ecological resource availability (Evans, Warren & Gaston, 2005). Similarly, geographic area is predicted to affect evolutionary rates of speciation and extinction (Rosenzweig, 1992; Losos & Schluter, 2000; Wagner, Harmon & Seehausen, 2014), leading to tropical diversity excess (Rosenzweig, 1995). These general factors – energy and area – can affect species richness through equilibrium or non-equilibrium mechanisms, depending on whether realized diversity is the outcome of a balanced, diversity-dependent speciation–extinction process (Storch & Okie, 2019; Rabosky & Hurlbert, 2015; Etienne *et al.*, 2019; Pontarp *et al.*, 2019). The key point is that, at the global scale, these three factors are generally aligned in the same direction and it is thus unsurprising that disagreements persist over their relative importance.

Large-scale patterns of biological diversity can generally be subdivided into three omnibus hypotheses, with more specific mechanisms for the LDG subsumed within and combining across these categories (Etienne *et al.*, 2019). Diversity is higher in some regions relative to others because (1) they have had more time for diversity to accumulate (time hypothesis), (2) diversity accumulates more rapidly (evolutionary rate and dispersal hypotheses), and/or (3) regions differ in their carrying capacity or ecological limits. Although several other explanations may not fit comfortably into these categories (Colwell, Rahbek & Gotelli, 2004) these categories (time, rate, carrying capacity) are the 'big three': they have garnered the most research attention, and the majority of specific hypotheses fall under their purview. The first two mechanisms are non-equilibrium and predict that the LDG will continue to evolve through time if environmental and other conditions remain constant. The latter hypothesis is

equilibrium, but requires no commitment to a specific mechanism for the equilibrium: the 'carrying capacity' can be viewed phenomenologically as the realized diversity from a balanced speciation–extinction process and encompasses a broad range of candidate mechanisms (Etienne *et al.*, 2019; Storch & Okie, 2019; Rabosky, 2013). Rejection of any one of these three hypotheses automatically rejects the set of sub-hypotheses within each category, and – prior to formulating tests of more specific causal mechanisms – we ought to determine whether we can reject any of the big three. Minimally, we should attempt to determine the relative importance of these generalized factors and to determine (1) what unique predictions follow from each, and (2) what systems are best suited to testing those unique predictions.

Herein, I argue that integrative thinking across the divide between aquatic/marine and terrestrial ecology can illuminate the causes of the terrestrial LDG. As pointed out by Valentine & Jablonski (2015), marine systems break several confounding correlations between potential drivers of terrestrial gradients. If we believe that general processes mediate diversity gradients at the largest scales, then their actions should be manifest both in terrestrial and marine systems (Worm & Tittensor, 2018).

In spite of the collinearity between key predictor variables (age, area, energy) in the terrestrial realm, marine and lacustrine environments provide replicate experiments that are especially well suited to disentangling the role of evolutionary time from other factors. Three natural sets of contrasts allow explicit study of the role of time in the generation of diversity gradients, and I illustrate the outcome of these contrasts for the diversity of extant fishes, which comprise roughly half of all vertebrate biodiversity. I focus primarily on fishes because their diversity patterns are well characterized, although I comment on spatial diversity patterns in other taxa where possible. A major point of this review, however, is that – despite the promise of these systems to illuminate the causes of the terrestrial LDG – there is an acute need for primary biodiversity data from each of these systems, such that we can determine whether patterns for fishes hold for the biota more generally.

The first contrast is the difference in species richness between shallow water marine environments and the deep sea. The deep sea experiences extreme energy limitation, yet probably represents the oldest and largest temporally continuous ecosystem on Earth. The second contrast involves differences in species richness among lake communities that differ in age. Many such lakes exist, with well-established geochronologies, in a variety of continental settings. A final contrast involves high-latitude marine fish communities from the Arctic and the Antarctic. Despite a number of similarities between these polar systems, they are dramatically different in age. If evolutionary time is the critical variable affecting diversity at the scale of biogeographical provinces, then we can make the following predictions: (1) the deep sea, characterized by greater age, stability, and geographic area than any comparable biome, should be correspondingly enriched in species diversity. (2) Geologically ancient lakes should

harbour more diverse fish assemblages than young lakes, once additional covarying factors are accounted for (e.g. depth, geographic area). (3) The number of fishes found in the Antarctic should greatly exceed that of the Arctic, because the coldwater Antarctic marine environment is approximately 10 times older than the corresponding Arctic marine system.

These patterns may appear to be smaller-scale features of the biosphere relative to the LDG and thus, potentially less representative of truly ‘global’ biodiversity patterns (Krug *et al.*, 2009). However, the deep sea comprises a vastly greater fraction of the Earth’s habitable volume (Dawson, 2012) and habitable area than any other biome: the contrast in species richness between the deep sea and all other biomes may thus represent an even more general biodiversity pattern than the LDG itself. One might also question whether the causal mechanisms that shape large-scale diversity patterns should differ fundamentally between aquatic and terrestrial systems, for reasons related to the physical properties of aquatic *versus* aerial media and other factors (Huston, 1994). There are, in addition, numerous differences between marine and terrestrial systems involving aggregate macroecological features, such as geographic range size (Tomasovych *et al.*, 2016; Pie *et al.*, 2021). My objective here is to explore these issues under the assumption that large-scale evolutionary and ecological processes are more likely to differ in degree (e.g. statistically) than in kind (e.g. fundamentally) between these types of systems (Dawson & Hamner, 2008; Webb, 2012). In Section VI, I comment on the potential for identifying equivalent terrestrial contrasts to address the collinearity problem that has challenged our understanding of the LDG.

II. STATISTICAL PRELUDE TO THE PATTERNS

Many prior studies on the causes of the LDG and other gradients in species richness have implied a role for evolutionary time based on (1) positive correlations between time and the number of endemic species within a region (Jetz & Fine, 2012), and (2) positive correlations between the ages of clades within regions and their species richness (Wiens *et al.*, 2007). My focus here is on total species richness within regions, not on the number or proportion of endemic species. There are good reasons to predict that endemic species richness should rise with ecosystem age: speciation takes time, and thus the number of taxa that are unique to a region will necessarily be lower in systems that have had less time for speciation. But a correlation of endemic richness with time is not informative with respect to the importance of time in species richness more generally, because endemic species might simply replace non-endemics without changing the total richness of the system (Rabosky & Hurlbert, 2015).

In the examples below, I avoid using clade age as a proxy for evolutionary time within regions, except as a minimum bound on the timing of biome colonization. The correlation between clade age and species richness is only weakly

informative with respect to the role of time in species richness patterns, particularly when biome age and species richness are positively correlated (Hurlbert & Stegen, 2014; Rabosky & Hurlbert, 2015). Older biomes will, in general, harbour older clades, if for no other reason than that biome age imposes a bound on the possible range of clade ages. Moreover, under equilibrium diversity models, species-rich clades are expected to be older than species-poor clades, despite no causal relationship between species richness and clade age. This latter result follows immediately from both population genetics (Wakeley, 2008) and ecological neutral theory (Hubbell, 2001), whereby the expected time to common ancestry of a sample of species (or alleles) is a strict function of the size of the sample. These first-principle predictions with respect to species richness and clade age are borne out by simulation studies under both neutral and non-neutral models of regional community assembly (Hurlbert & Stegen, 2014).

For several of the systems below – the contrast between ancient and young lakes, and between the Arctic and the Antarctic – the comparisons involve faunas that have been assembled over vastly different timescales. Such regions are expected to show substantial (multi-fold) differences in their proportional diversity if time is the dominant contributor to species richness at the regional scale and if faunal build-up follows an unregulated, non-equilibrium model of diversity (Wiens, 2011). Consider the simplest model for two regional biotas *A* and *B*, of ages t_A and t_B , where the initial number of species is exactly equal for each region, where species build-up proceeds with identical, time-constant net rates of species diversification (r), and where there is no subsequent immigration to the region after time $t = 0$. The proportional difference in species richness for the regions will be on the order of $\exp(r(t_A - t_B))$, where t_A is the age of the older region. Thus, for regions such as the Arctic and Antarctic – potentially differing fivefold or tenfold in age – we should expect vastly greater species diversity in the older region. Allowing immigration to continue into each region during faunal build-up will only exacerbate these differences, as each successful colonist may then contribute (exponentially) to further diversification. These and other informal calculations reveal the profound impact of time on species richness under unregulated, exponential models of diversity accumulation (Rabosky & Benson, 2021). A finding that an evolutionarily ‘young’ biota contains 70% of the species richness observed in an ‘old’ biota would reveal, at best, a weak imprint of time overall, if – given the observed age variation – the unregulated (non-equilibrium) models predict order-of-magnitude differences in species richness.

III. SPECIES RICHNESS IN THE DEEP SEA

The deep sea presents a key test of age and area-based explanations for global diversity gradients. The deep sea is the oldest, largest, and most stable ecosystem on Earth, and it is also the most energy limited. The areal extent of the deep sea, and

the abyssal plains (>4000 m in depth) in particular, are without parallel (Fig. 1): more than 50% of the Earth's surface is more than 3 km beneath the surface of the sea (Anderson & Anderson, 2010; Tanner, 1962). All metrics associated with energy input and productivity decrease with depth as one moves from the continental margins to the abyssal plains (Rex & Etter, 2010; McClain, Rex & Etter, 2009). Benthic standing stock declines by two to three orders of magnitude on the abyssal plain, relative to the continental shelves (McClain *et al.*, 2009).

The deep sea is also characterized by long-term stability: it has served as a refuge during mass extinction events and evidence from multiple groups suggests that the deep-sea biota has been more resilient than shallow water taxa, at least since the Late Jurassic (Thuy *et al.*, 2014). Moreover, oceanic fish community structure during the Cenozoic appears to be largely independent of climate change and other forcing variables (Sibert *et al.*, 2016). Major oceanic anoxic events (OAEs) during the Mesozoic and Cenozoic appear to have had little effect on deep-sea biodiversity (Thuy *et al.*, 2012, 2014). Extinction pulses have occurred in benthic foraminiferan assemblages at several times during the Cenozoic (Kennett & Stott, 1991; Thomas, 2007), including the Palaeocene–Eocene thermal maximum at 56 million years ago (Ma). However, these events appear to have had little impact beyond transient ecological disruption of the deep-sea system (Yamaguchi & Norris, 2012) and there is no evidence for global extinctions in any other groups (Speijer *et al.*, 2012), including fishes (Priede & Froese, 2013).

Congruence of crown ages across multiple groups of organisms can reveal parallel impacts of mass extinction and coordinated recovery (Alfaro *et al.*, 2018; Oliver & Hugall, 2017). To address the history of deep-sea occupancy, I extracted stem and crown clade ages for 19 major clades of predominantly deep-sea fishes (Priede & Froese, 2013; Priede, 2017) (Fig. 2) from a recent time-calibrated phylogeny for ray-finned fishes (Rabosky *et al.*, 2018). Many highly specialized deep-sea clades appear to have occupied the deep sea for more than 50 million years (e.g. Lophiiformes, Stomiiformes, Myctophiformes, Beryciformes). Several clades of perciform fishes radiated into deep-water habitats relatively recently (Zoarcidae, Liparidae), but diversification in these groups may have been driven by the expansion of cold-water biomes at high latitudes during the past 30 million years (Rabosky *et al.*, 2018). Most importantly, the variability in crown ages across clades implies that fish biodiversity in the deep sea is not structured by recovery from mass extinction associated with major oceanographic events during the Cenozoic, consistent with palaeontological evidence for more-or-less stable oceanic fish communities across these events (Sibert *et al.*, 2016). Debate persists regarding the impacts of Cretaceous and Palaeocene turnover events on the deep sea benthos more generally (Jacobs & Lindberg, 1998; Lins *et al.*, 2012; Priede, 2017), but the system appears to have been relatively stable over the timescales most relevant to the establishment of modern diversity gradients. If time, area, or time-integrated area (Fine & Ree, 2006) are the

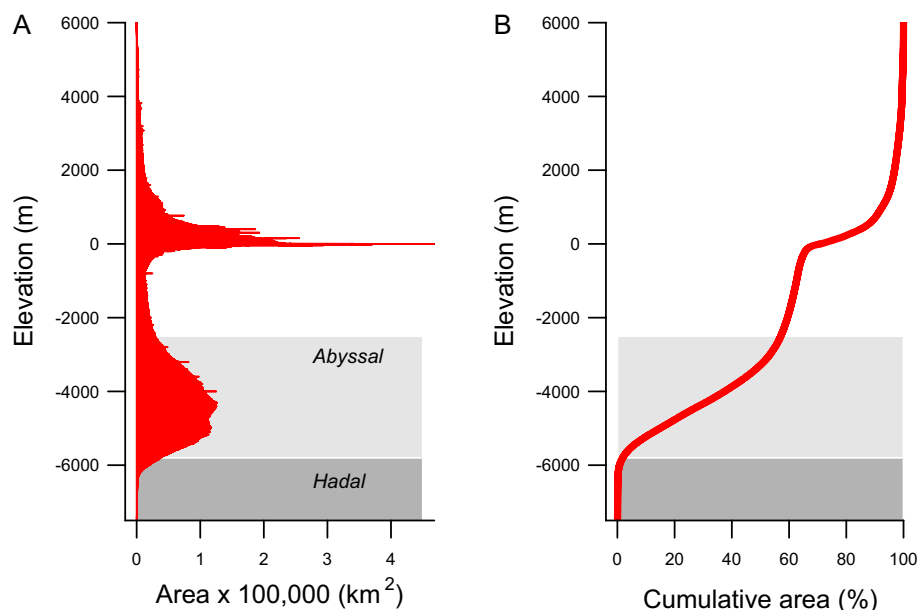


Fig. 1. (A) Hypsometric curve of the Earth, showing the amount of planetary surface area as a function of elevation. (B) Cumulative proportion of area equal to or less than a given elevation. The deep sea (grey shading; abyssal and hadal zones) accounts for nearly 60% of Earth's surface area, more than all other biomes combined. These areas pertain only to benthic or other surficial habitats. If we consider habitats in three dimensions, by including the vast bathypelagic and abyssopelagic zones, then the deep sea comprises an even greater proportion of 'habitable volume' (Dawson, 2012) relative to other biological zones. Data from Eakins & Sharman (2012).

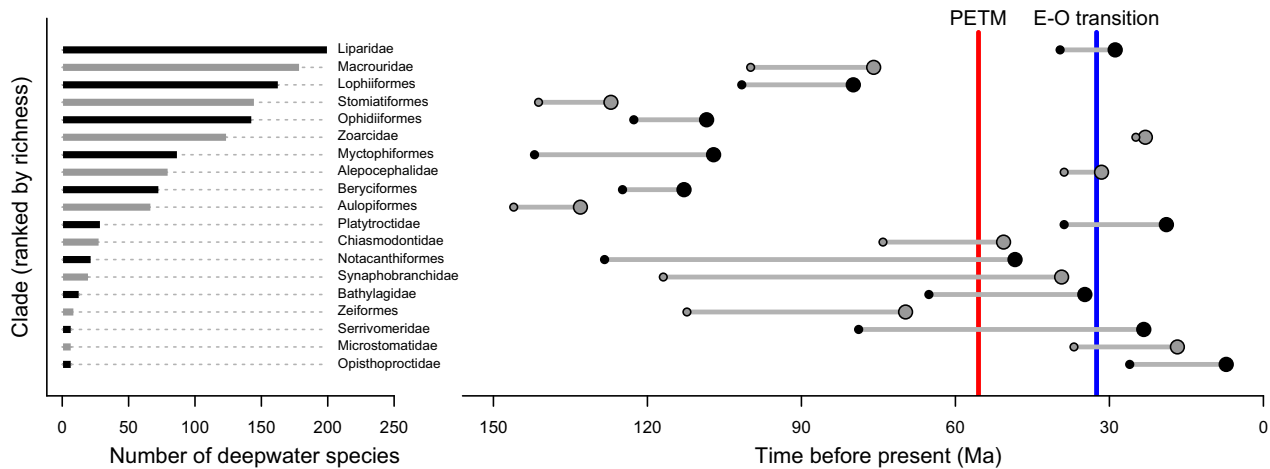


Fig. 2. Patterns of species richness (left) and clade ages (right) for 19 clades of fishes that account for the overwhelming majority of deep-sea species richness. Clades are family- and order-level taxa that are principally found in deep-sea habitats (see Table 2 in Priede & Froese, 2013). Numbers of deep-water species are taken from depth ranges for each taxon available through Fishbase (Froese & Pauly, 2017) and compiled by Rabosky *et al.* (2018); species were considered ‘deep-water’ if their maximum depth range exceeded 1000 m. Stem and crown ages for each clade were extracted from a recent time-calibrated phylogenetic tree for fishes (Rabosky *et al.*, 2018). Alternating grey and black colours for richness histograms and clade ages are provided solely to assist readers in matching clades in the left and right portions of the figure. Many deep-sea clades originated prior to major perturbations to the Earth’s oceans, including the Palaeocene–Eocene Thermal Maximum (PETM) and the greenhouse-to-icehouse transition at the Eocene–Oligocene boundary (E–O transition). That many of the most species-rich clades appear to have colonized the deep sea prior to the PETM implies long-term stability of Earth’s largest biome.

primary drivers of species richness, then we should observe extremely high species richness in the deep sea.

There has been considerable debate over whether biodiversity in the deep sea is ‘hyperdiverse or hype’ (McClain & Schlacher, 2015; Lambhead & Boucher, 2003; Rex & Etter, 2010). For fishes, the pattern is unequivocal: there are far more species in the shallow oceans than in the deep sea. To illustrate this pattern, I extracted data for 10,277 species of marine fishes (~66% of total marine species) from FishBase (Froese & Pauly, 2017) for which minimum and maximum depth estimates are available; the decline in global richness as a function of depth is shown in Fig. 3A. This pattern holds for local community richness (Lorance, Souissi & Uiblen, 2002; Kendall & Haedrich, 2006) and for global summaries based on depth ranges (Fig. 3B). The pattern of decreasing richness with depth even holds for pelagic communities (Smith & Brown, 2002), indicating that exceptional richness of reef-associated or shallow-demersal fishes alone do not drive the overall pattern (Fig. 3C). Deep-sea fishes are ecologically similar to fishes in other biomes, at least in terms of trophic ecology and body size distributions (Priede, 2017) and this comparability implies that they may provide especially useful insights into the terrestrial LDG. This ecological similarity does not hold for deposit-feeding invertebrates, which are typically much smaller than their terrestrial equivalents (Jumars *et al.*, 1990), potentially contributing to unusual patterns of alpha diversity in the deep sea (Rex & Etter, 2010).

Patterns of species richness in other taxa remain poorly known, at least at the regional-to-global scales that are relevant here. Many studies have documented exceptional

fine-scale diversity in benthic deep-sea communities (Hessler & Sanders, 1967; Etter & Mullineaux, 2001), leading some researchers to suggest that deep-sea diversity may rival that found in tropical forests (Grassle & Maciolek, 1992; Grassle, 1989). But at larger spatial scales there is little evidence for exceptional deep-sea diversity and increasing evidence that species richness declines with depth towards the abyssal zone (Costello & Chaudhary, 2017; O’Hara *et al.*, 2019). The evidence for high regional-to-global deep-sea diversity comes from extrapolation: patterns of species accumulation from local samples are used to derive an estimate of the rate at which new species are likely to be encountered, which – considered at the scale of ocean basins – yields extremely high estimates of global richness for some taxa (Grassle & Maciolek, 1992). This approach has been sharply criticized (Lambhead & Boucher, 2003; Gray, 2001), and extrapolation from local deep-sea samples appears to overestimate global richness by at least an order of magnitude (May, 1992; Koslow, Williams & Paxton, 1997). Furthermore, recent surveys have revealed that even local diversity for many groups does not increase systematically with depth (Wei, 2006; Wei *et al.*, 2010; Carvalho *et al.*, 2013; Rex & Etter, 2010). Depth–richness patterns for several groups are shown in Fig. 4.

While more data are needed, geographic ranges for many deep-sea taxa appear to be large (McClain & Hardy, 2010; Costello & Chaudhary, 2017) and evidence suggests that high richness at local scales in the deep ocean reflects, in part, a lack of dispersal constraints on individual organisms (Costello & Chaudhary, 2017; Rex & Etter, 2010). Local assemblages in the deep sea might therefore have high

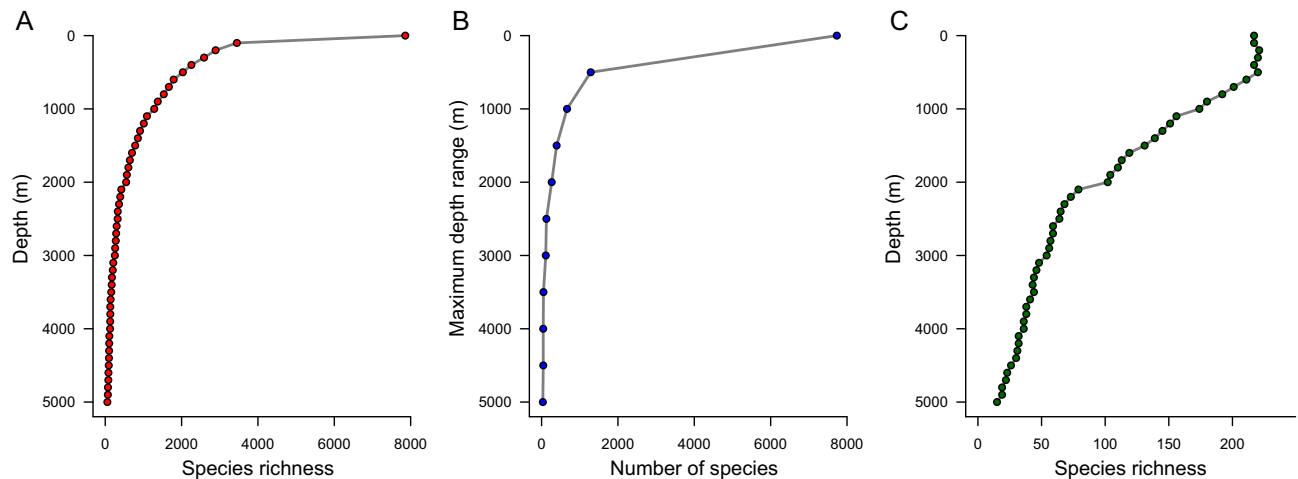


Fig. 3. Bathymetric distribution of species richness for marine fishes, showing monotonic declines in species richness with increasing depth. (A) Total number of species per depth interval at the global scale. Counts represent all species with a Fishbase depth range intersecting a given bathymetric interval (100 m bands). (B) Frequency distribution of maximum depth for marine fishes in Fishbase, binned by 500 m depth intervals. (C) Bathymetric distribution of richness for fishes in pelagic (open-ocean) grid cells only. This analysis indicates that the shallow-water peak in marine fish diversity is not driven by the extreme diversity of shallow-water tropical systems. Grid cells in C were from the Rabosky *et al.* (2018) spatial data set, with open-ocean cells defined as those with a mean depth of at least 3000 m. Data in A include all marine species for which depth ranges are available, or approximately 66% of total marine diversity.

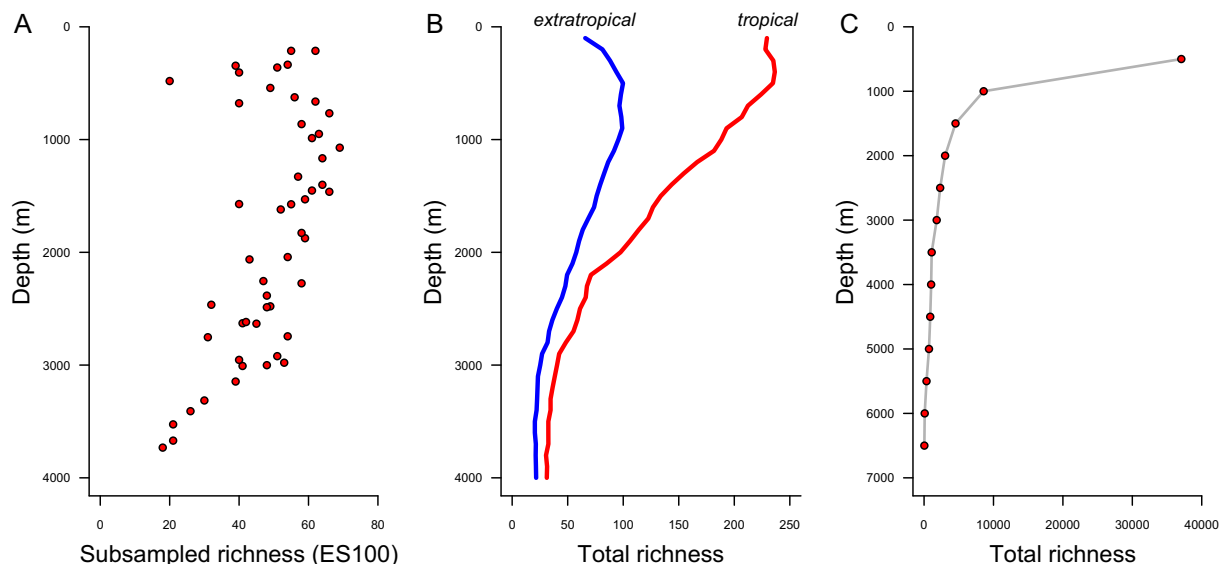


Fig. 4. Bathymetric distribution of species richness for marine macrofauna. (A) Local species richness as a function of depth for macroinvertebrates, using benthic core samples taken in the Gulf of Mexico. ES100 is the expected number of species present in a sample of 100 individual organisms and is necessary to account for heterogeneity in the density of individuals along depth gradients in the deep sea. (B) Regional diversity of brittle stars (Ophiuroidea) in the Southern Hemisphere as a function of depth for tropical and extratropical regions. (C) Global richness by depth class for 32,328 species of marine metazoan taxa (data from Costello & Chaudhary, 2017). Gulf of Mexico data set (A) is from Wei (2006) and Wei *et al.* (2010) and includes six major clades of macroinvertebrates: amphipods, bivalves, cumaceans, isopods, polychaetes, and aplousobranchs. Brittle star diversity (B) is estimated from bathymetric and latitudinal distributions of individual taxa provided by O'Hara *et al.* (2019). Data in C include fishes and are partially redundant with those in Fig. 3.

richness relative to the number of individuals sampled, but these patterns may be driven by exceptionally strong regional enrichment processes that have no analogue in terrestrial

systems. Some abyssal assemblages may even represent massive sink populations, maintained by recurrent immigration from shallower bathyal communities (Rex *et al.*, 2005).

The deep sea may be diverse at local scales, but increasing evidence suggests that it is not exceptionally diverse relative to its vast area (McClain & Schlacher, 2015) and that global-scale richness is not particularly high. Nonetheless, with the conspicuous exception of fishes, generalizations about the deep ocean are likely to remain controversial pending comprehensive surveys of invertebrate diversity across different depths, latitudes, and productivity regimes.

IV. BIODIVERSITY IN FRESHWATER LAKES

Freshwater lacustrine communities have been widely used in comparative analyses of the causes of evolutionary diversification (Hanly, Mittelbach & Schemske, 2017; Seehausen, 2006; Seehausen & Wagner, 2014; Wagner *et al.*, 2014). Many lakes have reasonably well-characterized geochronologies such that researchers can test the contribution of time to total species richness, although the environmental histories of some ancient lakes remain both complex and controversial (Lyons *et al.*, 2015; Ivory *et al.*, 2016; Cohen, 2003). Nonetheless, geologically determined ages for lakes provide an upper bound on the amount of time available for community assembly, whether through speciation or immigration. As such, lakes arguably provide more robust estimates of evolutionary time than most terrestrial systems, which frequently rely on clade age as a surrogate variable (Rabosky & Hurlbert, 2015). Even if environmental histories for terrestrial and lacustrine systems suffer from equivalent uncertainty, the large number of lakes for which comparative data exist (Barbour & Brown, 1974; Hanly *et al.*, 2017) facilitates replicated statistical comparisons and increased power to extract an evolutionary signal from noisy background data.

Most importantly, lakes break the collinearity between age, area, and energy that has thwarted consensus on the causes of the terrestrial LDG. Consider the contrast between Siberia's Lake Baikal and North America's Lake Superior, largest of the Laurentian Great Lakes. The lakes have many similarities: they are cold, oligotrophic, high-latitude lakes with similar littoral-zone areas (Vadeboncoeur, McIntyre & Vander Zanden, 2011). Yet their ages differ by many millions of years, with Baikal representing a geologically ancient lake – one of the oldest on Earth – and Superior an extremely young lake that formed after the last glacial maximum. In the case of Baikal, this great age has translated into high endemism: the lake supports numerous endemic fishes, invertebrates, and even an endemic seal that may have occupied the lake basin for several million years (Palo & Vainola, 2006). If evolutionary time is important, we should expect to see a strong effect in this and other lacustrine systems, given extreme disparities in the amount of time for evolutionary and ecological processes to assemble these regional biotas.

To assess the relationship between lake age and species richness, I combined data from two compilations (Vadeboncoeur *et al.*, 2011; Hanly *et al.*, 2017). For the

14 lakes considered in Vadeboncoeur *et al.* (2011), fish species richness totals were extracted from their Fig. 3. Ages of several lakes in the Hanly *et al.* (2017) data set were modified for accuracy as follows: the age of Lake Malawi was increased from 0.1 to 0.8 Ma, following Wagner *et al.* (2014) and Ivory *et al.* (2016); Lake Tanganyika's age was constrained to 7.4 Ma based on palaeogeographic reconstructions in Cohen *et al.* (1997); and Lake Tahoe was constrained to 0.94 Ma following Kortemeier *et al.* (2018). The merged data set contained 83 lakes with estimates of both species richness and lake age.

There is no relationship between geological estimates of lake age and total species richness (Spearman $r = 0$, $p = 0.99$, $N = 83$ lakes; Fig. 5A). Lake area, however, is highly correlated with richness (Fig. 5B; $r = 0.62$, $p < 0.001$, $N = 83$). When these factors are included in a multiple regression model, area alone predicts richness, and there is no evidence for an interaction between age and area (age effect: slope = 0, $t = -0.2$, $p = 0.85$). A model with area as the only covariate ($t = 7.0$, $p < 0.001$, $r^2 = 0.38$) outperforms a model with lake age only [Δ AIC (Akaike Information Criterion) = 37.9] as well as models that include both age and area (Δ AIC > 1.9). Similar results are obtained when analyses are limited to the 19 lakes in the data set that predate the last glacial cycle (age > 0.02 Ma), although lake area and age are positively correlated for this subset ($r = 0.58$, $p = 0.01$). A model with log-transformed lake area as the only covariate outperforms models with both age and area (Δ AIC = 1.95) and a model with lake age only (Δ AIC = 11.6). Similar results were reported in a number of previous studies: Seehausen (2006) and Wagner, Harmon & Seehausen (2012) found no effect of time on species richness of replicate lacustrine cichlid radiations, and Vadeboncoeur *et al.* (2011) found no effect of lake age on fish richness for the world's 14 largest lakes (Fig. 5C).

An obvious explanation for these results would be that geological age determinations are sufficiently inaccurate as to eliminate the expected effect of time on richness. Geological ages of lake formation might be decoupled from the subsequent history of environmental change (e.g. desiccation events) that determine the chronology of lake diversification (Cohen, 2012), leading to overestimation of the amount of time for species accumulation. Conversely, chronologies that assume complete extirpation of the lake biota during environmental catastrophes (e.g. desiccation of Lake Victoria at 15–25 kya) will underestimate effective evolutionary time if elements of the lake biota persisted in regional refugia (Elmer *et al.*, 2009). If community assembly occurred over timescales that are decoupled from geochronological lake age, then we would not necessarily expect to retain a signal of age on total richness. Fortunately, there is an important control experiment that can be performed. If lake ages used in the preceding analyses are reasonable estimates of the amount of time for community assembly, then we should expect older lakes to contain a greater proportion of endemic taxa, even if time does not control total richness. There is a positive correlation between the proportion of endemics and lake age (Spearman $r = 0.47$, $p < 0.001$, $N = 83$), and

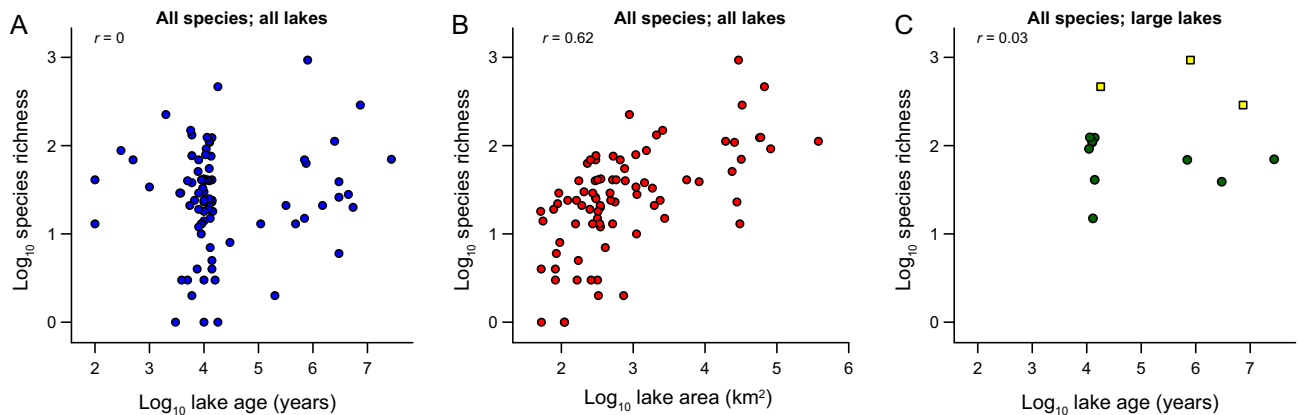


Fig. 5. Species richness of fishes in lakes as a function of age and area. (A) Richness as a function of the best estimate of lake age. (B) Richness as a function of lake surface area. (C) Richness as a function of lake age for 14 large lakes studied by Vadeboncoeur *et al.* (2011). Squares denote the three lakes that contain cichlids (Victoria, Malawi, Tanganyika). Data are from Hanly *et al.* (2017) and Vadeboncoeur *et al.* (2011).

between the number of endemics and lake age ($r = 0.48$, $p < 0.001$, $N = 83$), similar to results from Hanly *et al.* (2017), who compiled most of the data. Ancient Lake Baikal, for example, hosts an evolutionary radiation of ~40 endemic cottid sculpins and has a high proportion of endemic richness (53%). It should be noted that these endemicity proportions do not include totals from a number of extremely young (< 10,000 years) lakes known to harbour sympatric, ecomorphologically diverse assemblages of salmonid fishes that have not been formally recognized taxonomically (Doenz *et al.*, 2019; Skulason, Noakes & Snorrason, 1989). Despite the recent nature of these radiations, the number of ecomorphs appears to scale with lake size and depth, suggesting that at least some lineages undergo rapid evolutionary responses to ecological opportunity and are largely unconstrained by time (Doenz *et al.*, 2019).

In summary, freshwater lakes provide replicate examples whereby age, area, and energy are decoupled. For fishes, there is no evidence that time affects total richness, even though it predicts levels of endemism within lakes. Similar examples are known for island systems (Lim & Marshall, 2017; Gillespie, 2004), where the temporal dynamics of island physiography facilitate a decoupling between time and species richness (Whittaker, Triantis & Ladle, 2008). There are three caveats to these conclusions that must be acknowledged. First, the species richness totals given above include the outcome of both evolutionary diversification and immigration, and the regional pool of colonists is generally shaped by processes that pre-date the origins of lakes themselves. At least for some taxa, biotas assembled by *in situ* diversification appear to be more species rich than immigration-derived biotas (Rabosky & Glor, 2010; Wagner *et al.*, 2014; Lomolino, 2000). In an island biogeographic framework (MacArthur, 1969; MacArthur & Wilson, 1967), species richness can be viewed as a dynamic balance between processes that pump diversity into the system (immigration, speciation) and those that remove species (extinction).

Systems that can accumulate diversity *via* immigration and speciation should therefore contain more species than those that only support immigration, even if richness is largely equilibrium and independent of time. Greater species richness should be observed in lakes that have achieved a minimum age for the completion of the speciation process (Etienne & Rosindell, 2012; Dynesius & Jansson, 2014), or – equivalently – in lakes that are of sufficient age as to offset the ‘lag-time’ to taxonomic species recognition. We thus might observe proportionately higher species richness for lakes that are old enough or large enough (Kisel & Barraclough, 2010; Coyne & Price, 2000) to support speciation processes, even if there is no general influence of time on diversification beyond these time–area thresholds. This effect should be manifest as a proportional increase in richness for lakes that contain endemic species. Interestingly, there is no support for this phenomenon in the fish data set: controlling for lake area, there is no effect of the presence of endemic species (binary: present/absent) on total richness ($\Delta\text{AIC} = 1.1$) in the Hanly *et al.* (2017) data set.

A second caveat is that, at least for the largest African lakes, there is a massive effect of cichlids on total species richness. This effect is so strong (Fig. 6), and the number of ancient lakes sufficiently small, that overall correlations between age, richness, and other factors are likely to be influenced by the presence or absence of cichlids. Importantly, there is no correlation between the ages of lacustrine cichlid radiations and their species richness, after controlling for the effects of lake area (Wagner *et al.*, 2014; Seehausen, 2006). Even after dropping the three ancient lakes with cichlids from the Vadeboncoeur *et al.* (2011) data set, there is either no correlation or a weak negative correlation between lake age and the number of fish species present (Fig. 5C, green points; $r = -0.52$, $p = 0.09$).

Finally, and most importantly, patterns for fishes might not be representative of those in other taxa, and several of the world’s most ancient large lakes are home to major evolutionary radiations of one or more groups. Multiple endemic

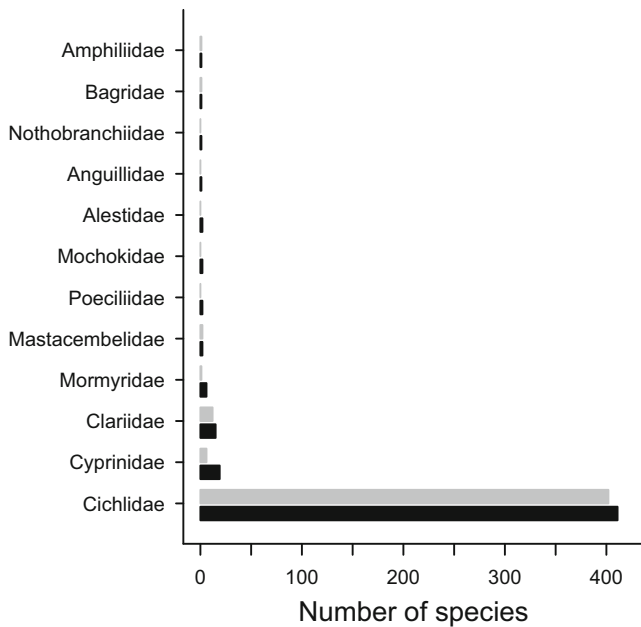


Fig. 6. Species richness for 12 families of fishes in Lake Malawi, partitioned into total (black) and endemic (grey) numbers of species. The lake is massively enriched in cichlid fishes relative to other taxonomic groups. Importantly, this ‘cichlid effect’ also causes the lake to have exceptional species diversity relative to its area (Fig. 5C). Across 14 of the world’s largest lakes (Fig. 5C), 75% of all fishes are cichlids, and this diversity is concentrated in just three African lakes in which cichlids have radiated. Figure based on comprehensive checklist for Lake Malawi fishes from Oliver (2019).

radiations of crustaceans and molluscs are known from Lake Baikal, including a massive clade of gammaroid amphipods [>275 species (Takhteev, 2000; Takhteev, Berezina & Sidorov, 2015)]. Lake Tanganyika is home to an exceptional radiation of ostracods (>200 species; Cohen, 2000) and hosts three or more radiations of gastropods [>80 species (Glaubrecht, 2008; Seddon *et al.*, 2011)]. Overall, there is a positive relationship between the number of gastropod taxa and lake age ($r = 0.80$, $p = 0.002$). However, young Lake Victoria has the same number of gastropod taxa as ancient Lake Malawi (Seddon *et al.*, 2011) and twice as many bivalve species (17 *versus* 8), despite the 10- to 100-fold difference in age between these systems. For the large-lakes data set from Vadeboncoeur *et al.* (2011), there is no effect of lake age on invertebrate species richness ($r = -0.31$, $p = 0.27$, $N = 14$; Fig. 7), although Vadeboncoeur *et al.* (2011) acknowledge great uncertainties in both calibrated estimates of lake age and in the invertebrate richness values.

It is possible that some invertebrate lacustrine radiations represent idiosyncrasies of clade-specific diversification processes. The gammaroid amphipods of Lake Baikal, for example, are far more species rich than amphipod clades from other ancient lakes (Adamowicz *et al.*, 2018; Wysocka *et al.*, 2014). They have diversified into a wide variety of ecological roles (Naumenko *et al.*, 2017), including many that parallel those found in marine settings (Takhteev, 2000). Perhaps Lake Baikal has accumulated several clades of ‘rule-breaking’ invertebrate taxa that defy conventional expectations based on species–area relationships and other ecological principles, much as cichlids appear to do in East African

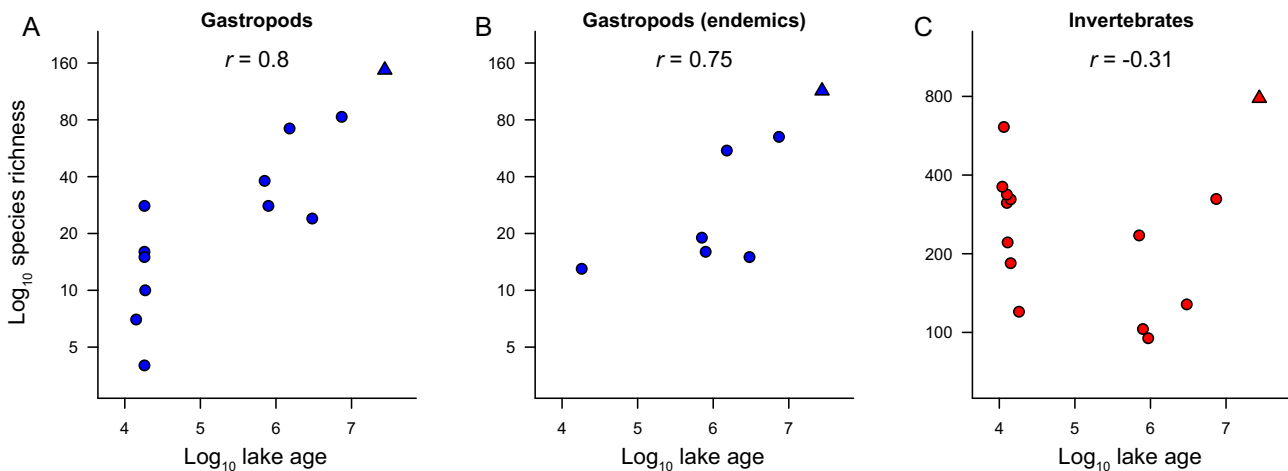


Fig. 7. Species richness as a function of lake age for invertebrates in 14 of the world’s largest lakes. (A) Lake age and species richness for gastropods, showing a positive relationship between estimated lake age and species richness. (B) Corresponding relationship for endemic gastropod taxa only; the number of endemic species increases as a function of lake age. (C) Total invertebrate richness is uncorrelated with lake age. Lake Baikal is the oldest lake in the data set and contains many species of amphipods, gastropods, and ostracods; it appears to be much more diverse than any other lake on Earth for invertebrates (Vadeboncoeur *et al.*, 2011). However, species richness for invertebrates in other ancient lakes is not especially great when compared to much younger lakes, even though several such ancient lakes are characterized by high proportions of endemics. Gastropod data from Seddon *et al.* (2011) and invertebrate data extracted manually from Fig. 5 of Vadeboncoeur *et al.* (2011). Invertebrate richness estimates are likely characterized by high uncertainty and the results in C should be interpreted with caution.

lakes (Fig. 6). Or perhaps there is something special about freshwater fishes, potentially reflecting fundamental differences in speciation processes relative to other taxa or systems (Seehausen & Wagner, 2014).

V. CONTRAST BETWEEN POLAR FAUNAS

Earth's two polar regions – the Arctic and the Antarctic – are characterized by low temperatures and minimal solar insolation. In the broadest sense, their geographic areas are similar: the Southern Ocean is approximately twice as large as the Arctic Ocean, but this difference is offset by proportionately greater continental shelf area in the Arctic (McBride *et al.*, 2014). This is not to imply that the systems are similar in most other respects: the Antarctic realm is essentially a continent surrounded by oceans, and the Arctic is an ocean surrounded by continents. These basic geographies have led to physical and biological differences relating to upwelling, nutrient availability, disturbance regimes, and other factors (McBride *et al.*, 2014; Ronowicz *et al.*, 2019), and there is little consensus on how these factors should influence broad-scale diversity patterns within the regions.

However, there is one profound difference between these systems that should have had a predictable and substantive effect on diversity: the discrepancy in the amount of time that has been available for the assembly of their respective biotas (Eastman, 1997; Clarke & Crame, 2010; Crame, 1997; Ekman, 1953). The formation of the Antarctic Circumpolar Current (ACC) resulted in a long history of isolation for the Southern Ocean, and biogeographers have described the region as harbouring ‘the world’s most distinctive marine biota’ (Briggs, 2003, p. 12). The Southern Ocean is thermally isolated from adjacent ocean regions through steep temperature gradients created by the ACC, which traps a massive body of very cold water (-1.8 – 2°C) around Antarctica. The Southern Ocean thus results from a significant oceanographic feature that has been present for 20–30 million years and which presents a major physiological barrier to dispersal by marine organisms. The biogeographic history of the Arctic is more complex, but marine communities generally appear to have been assembled during the past 2 million years, following the onset of major cooling events in the northern hemisphere approximately 2–3 Ma (Clarke & Crame, 2010; Josefson & Mokievsky, 2013).

Despite the great age differences between these systems, the Arctic and Antarctic harbour roughly the same number of marine fishes, with an estimated 275–350 species in the Antarctic (Eastman, 1997, 2005) and 242–375 species in the Arctic (Mecklenburg *et al.*, 2016; Eastman, 1997). Higher-level taxonomic diversity is broadly comparable for the systems, with perciform fishes heavily represented in both polar regions (see Extended Data Fig. 7 in Rabosky *et al.*, 2018). However, levels of endemism are very different: considering species restricted to the coldest water regions, Eastman (1997) reports that 88% of Antarctic fishes are

endemic *versus* 25% for Arctic fishes. The Antarctic fauna is dominated by a spectacular radiation of notothenioid icefishes, most of which are restricted to the Southern Ocean. Most high-latitude Arctic fishes are closely related to cool-water north-temperate lineages, but there is little evidence for evolutionary radiations within the north polar region (Rabosky *et al.*, 2018). Importantly, recent intraspecific genetic surveys of Antarctic icefishes suggest that taxonomic diversity in some genera might be overestimated (Parker *et al.*, 2022), potentially reducing the overall differences in total richness between these high-latitude faunas.

In summary, the Arctic and Antarctic represent largely independent biomes that differ approximately tenfold in age. One important caveat is that, as for the lacustrine systems discussed previously, the expected contribution of time to species richness under non-equilibrium models will depend on the extinction history of the biomes. There are important, yet complex, differences in the extinction histories of the Antarctic and Arctic faunas (Krug *et al.*, 2010). Regardless, the age differential between the systems has not translated into appreciably greater species diversity for the much older Southern Ocean. The comparisons above focus exclusively on species richness, and thus ignore many differences in the ecological structure of the Antarctic and Arctic marine biotas (McBride *et al.*, 2014; Ronowicz *et al.*, 2019). For example, Antarctic icefishes alone are characterized by much greater morphological and ecological diversity than comparable clades of fishes from the high Arctic (Eastman, 1997). Regardless of the effects of time on species richness *per se*, it is likely to be an important factor in explaining differences in phenotypic and ecological disparity in these systems.

The obvious question for polar comparisons is whether patterns in fishes are similar to those for other taxa. Traditional views on the diversity of the polar seas held that the Antarctic is more species rich than the Arctic for most groups of organisms (Ekman, 1953). For brittle stars and sea stars, for example, standardized sampling identified higher species richness in the Antarctic (Piepenburg, Voss & Gutt, 1997). However, some recent tabulations suggest that the overall richness of benthic faunas in the Antarctic and Arctic are broadly comparable (Piepenburg, 2005; Sirenko, 2009; Clarke & Crame, 2010), although benthic invertebrate biomass is much higher in the Antarctic (Sirenko, 2009). For both regions, the total number of marine invertebrate species is reportedly on the order of 4000–7000 (Bluhm *et al.*, 2011; Piepenburg, 2005). Piepenburg *et al.* (2011) suggest that the benthic invertebrate fauna of the Antarctic is higher than that of the Arctic, but nonetheless comparable in broad outline; they find little evidence for the traditional view of dramatically impoverished Arctic diversity. Ronowicz *et al.* (2019) reported broadly comparable diversity of hydrozoans for the Arctic and Antarctic (252 *versus* 233 species), while noting that the overall number of Arctic invertebrate species listed in global databases is approximately 60% of the totals for the Antarctic. Legenzynska, De Broyer & Weslawski (2020) summarized polar crustacean diversity, concluding that species richness for the Arctic and Antarctic are broadly

similar (Arctic: 1930 species; Antarctic: 2250 species), despite substantive differences in endemism and taxonomic structure. As Clarke & Crame (2010) note, it is difficult to interpret overall numbers from large-scale tabulations, as they typically mix taxonomic inventories from different habitats, depths, and sampling protocols. To address some issues of comparability, Sirenko (2009) compared the species richness of macrobenthic communities in the Laptev Sea (Arctic) to the Weddell Sea (Antarctic), reporting 1414 species in the Arctic *versus* 1528 in the Antarctic. Pairwise Arctic–Antarctic comparisons of species richness for major invertebrate groups from the Sirenko (2009) data set are shown in Fig. 8.

As for fishes, the Antarctic invertebrate fauna is characterized by high endemism: for many major invertebrate groups, the proportion of species restricted to the region exceeds 50% (Griffiths, 2010; Eastman, 2005; Legenzynska *et al.*, 2020). By contrast, there are relatively few true Arctic endemics (Josefson & Mokievsky, 2013). Overall, the pattern for invertebrates on the continental shelves is consistent with broadly similar diversities in the Antarctic and Arctic, but where the vastly greater evolutionary age and isolation of the Antarctic has resulted in a greater proportion of regionally endemic taxa. Recent deep-sea surveys in the Antarctic – particularly through the ANDEEP expeditions to the Weddell Sea – suggest that much remains to be known about the deep polar oceans (Brandt *et al.*, 2007). Results from these expeditions have not been fully integrated into a general comparative framework, but preliminary work suggests that

some taxonomic components of the deep Southern Ocean might be far more diverse than traditionally assumed (Ramirez-Llodra *et al.*, 2010). On the other hand, some of this work also suggests that the Antarctic deep sea might be more similar to deep-sea faunas elsewhere and composed principally of more geographically widespread taxa rather than Southern Ocean endemics (Schuller, Ebbe & Wagele, 2009). In summary, and in contrast to fishes, invertebrate diversity in the both the Antarctic and Arctic remain poorly known, and extensive taxonomic work and field inventories are clearly needed before we can make definitive comparisons of diversity in these regions (Griffiths, 2010; Josefson & Mokievsky, 2013).

VI. EQUIVALENT CONTRASTS IN TERRESTRIAL BIOMES

Although there is an apparent latitudinal gradient in ‘time for diversification’ in the northern hemisphere (Sandel *et al.*, 2011; Fine & Ree, 2006; Fischer, 1960), collinearity with other factors implies that the LDG itself is poorly suited for testing hypotheses about the drivers of global diversity gradients. However, comparisons can be made among geographic regions that are broadly similar in other climatic factors. Such inter-regional analyses have been performed for deserts (Pianka, 1986; Tejero-Cicuendez *et al.*, 2022), moist-

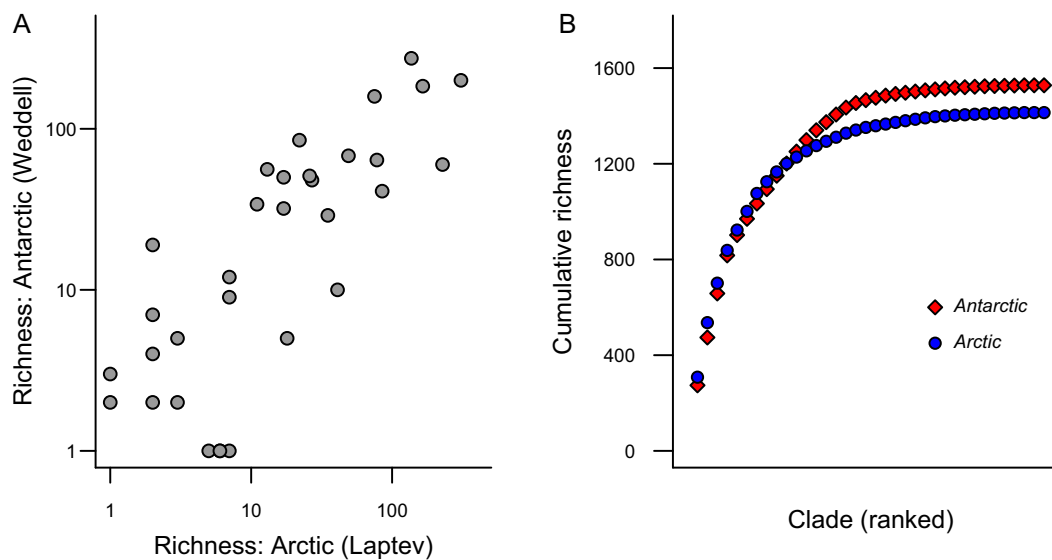


Fig. 8. Species richness patterns in benthic invertebrate communities from the Arctic (Laptev Sea) and Antarctic (Weddell Sea). (A) Pairwise comparison of richness for major invertebrate clades. The five most species-rich clades for both regions include the Amphipoda, Bryozoa, and Gastropoda. However, the Polychaeta are much more species-rich in the Arctic, and Porifera is much more species-rich in the Antarctic. (B) Cumulative contributions of individual invertebrate clades to total richness in the Arctic (Laptev Sea; circles) and Antarctic (Weddell Sea; diamonds). Totals for the Laptev Sea and Weddell Sea are 1414 and 1528 species, respectively. Despite the general similarity in richness for these regions, these data mask profound ecological differences, including a much greater biomass of the shelf macrobenthos in the Antarctic and greater diversity of infaunal animals in the Arctic (Sirenko, 2009). Data from Sirenko (2009).

temperate forests (Latham & Ricklefs, 1993), tropical rainforests (Couvreur, 2015), and mediterranean biomes (Rundel *et al.*, 2016).

Unfortunately, in these and other terrestrial systems, both age and area are typically less clear than for the marine and freshwater lacustrine systems discussed herein. Most terrestrial biomes are characterized by complex environmental histories. Ascribing an age and area to a particular biome requires strong assumptions about continuity of the biome through geological time, although lacustrine systems are certainly not free from similar assumptions (Cohen, 2012). Terrestrial biomes typically emerge from the interaction between temperature and precipitation, both of which have varied considerably at timescales on the order of 10,000–100,000 years. By contrast, the age contrasts for marine and lacustrine systems described here emerge from more-or-less discrete events (e.g. formation of the ACC) or from first-order properties of physical materials and physically bounded spaces (deep sea; freshwater lakes). The time-integrated-area framework (Fine & Ree, 2006) is an important conceptual tool that can potentially accommodate the complex environmental histories of terrestrial biomes, but applying this framework requires detailed information about palaeoenvironments that may not be available for most systems. Estimates of the amount of time for diversification in terrestrial regions frequently relies on inferences from the ages of clades within regions (Couvreur, 2015; Wiens *et al.*, 2007), but clade age need not reflect time for diversification in any meaningful sense (Rabosky & Hurlbert, 2015; Rabosky & Benson, 2021). Numerous factors (extinction and lineage turnover; diversity-dependence) can decouple the timescale of ‘phylogenetic’ diversification from the true amount of time for diversification within regions.

VII. OUTSTANDING QUESTIONS

The patterns described herein raise a number of questions for future research. In general, there is an acute need for primary biodiversity data from these systems, especially for invertebrate groups. Key questions for these systems include:

- (a) To what extent are patterns described for fishes representative of those in other groups? Invertebrate species richness in many systems remains poorly known (Ramirez-Llodra *et al.*, 2010; Vadeboncoeur *et al.*, 2011). This lack of information severely limits our ability to generalize about processes influencing community assembly. Understanding the relationships between local, regional and global diversity for marine invertebrates along oceanic depth gradients is a key frontier for future research. Our inventory of regional and global diversity in the deep sea is far less complete than for any comparable biotic province on Earth (Ramirez-Llodra *et al.*, 2010; McClain & Schlacher, 2015). Critical knowledge gaps remain for many invertebrate groups in freshwater lakes (Vadeboncoeur *et al.*, 2011), yet these systems ‘are among the most extensively and rapidly altered ecosystems on the planet’ (Carpenter, Stanley & Vander Zanden, 2011, p. 75). Increased open water in the Arctic has the potential to cause profound yet unpredictable ecological shifts that may reshape the structure of pelagic and benthic faunas alike (McBride *et al.*, 2014).
- (b) At least one of the patterns discussed herein is even more general than the marine or terrestrial LDG. One could argue that the true ‘first-order biodiversity pattern’ (Krug *et al.*, 2009) is not the LDG but rather the contrast in species richness between the vast abyssal plains of the deep sea and all other biomes. It is this pattern, not the LDG, that would stand out most prominently to an extra-terrestrial scientist charged with characterizing biodiversity across the entirety of Earth’s surface. The deep sea accounts for more of the biosphere than all other biomes combined, and explaining biodiversity patterns in that very large, old, and stable biome is a pressing challenge for macroecology and macroevolution.
- (c) Analyses of age–richness relationships for lakes typically rely on simplistic ‘point estimates’ of lake age. To what extent do simplified histories limit our ability to understand the dynamics of community assembly in these systems? Higher resolution data are needed to describe the environmental history of lake basins through time (Ivory *et al.*, 2016). Lake sediments provide depositional records that can be used to reconstruct climate and lake levels through time, but the potential of these data is largely unrealized for most ancient lakes (Cohen, 2012). Fossils preserved in sediment cores can even provide a direct window into the history of community assembly in ancient lakes. For example, a Lake Tanganyika or Lake Baikal drilling project could provide insights into the dynamics of ostracod species richness over timescales of hundreds of thousands to millions of years (Cohen & Salzburger, 2017).
- (d) What explains patterns of species richness in ‘rule-breaking’ clades, such as east African cichlids or Lake Baikal’s amphipod and ostracod species flocks? Species richness in these groups is massively elevated relative to expectations based on conventional species–area or species–energy relationships (Figs. 5 and 6). Patterns of richness in such clades appear inconsistent with a simple effect of time on the accumulation of species within lakes. Rather, some lakes – sometimes old (Baikal), sometimes not (Victoria) – contain clades that have undergone dramatic evolutionary radiations, in a manner that appears somewhat unpredictable from time, area, productivity, and other lake properties.
- (e) What is the relationship between energy, productivity, latitude, and species richness in the deep sea? Emerging evidence suggests that regions of high export productivity are associated with higher species richness in the abyss (Woolley *et al.*, 2016; Downey, Fuchs & Janussen, 2018), but data are too limited at present to enable further generalization.

(f) How do ecological relationships differ between systems with broad-scale similarities in richness, and what do these differences imply about the role of time and other factors in community assembly? In this review, for example, I described similarities between systems (e.g. Antarctic, Arctic) with respect to species richness only, but there are numerous differences in community organization and abundance between these systems. It is possible that a more nuanced assessment of ecological similarity and differences would alter our expectations about the relationships between time, energy, area, and species richness.

VIII. CONCLUSIONS

(1) The terrestrial LDG is typically viewed as an endpoint for investigation, rather than one example of a large-scale diversity pattern that is mediated by highly general evolutionary and ecological processes. With relatively few exceptions (Woolley *et al.*, 2016; Worm & Tittensor, 2018; Valentine & Jablonski, 2015), insights from aquatic systems have not been fully integrated into our explanatory paradigms for the terrestrial LDG.

(2) Marine and freshwater lacustrine systems provide a series of replicate experiments that partially isolate the effects of evolutionary time on species richness. Unlike terrestrial biomes, these aquatic systems break the collinearity between time and other factors that are predicted to have similar effects on species richness, such as temperature (Valentine & Jablonski, 2015).

(3) For fishes in all three biogeographic systems considered here – the deep sea, the Antarctic, and ancient lakes – greater time for diversification has failed to produce the expected increase in species richness relative to other systems. To the extent that these results can be generalized to the terrestrial LDG, they suggest that time is unlikely to be the primary cause of the variation in species richness between tropical and extratropical regions. Other lines of evidence support this conclusion, particularly from the fossil record. At time-scales relevant to the establishment of modern diversity gradients (e.g. 10–50 million years), there is little evidence that species richness increases appreciably with time (Benson *et al.*, 2016; Alroy, 2010; Knoll, 1986; Rabosky & Hurlbert, 2015), and much evidence for long-term equivalence of speciation and extinction rates (Marshall, 2017).

(4) Incorporating insights from the marine and lacustrine systems described here will help constrain the set of plausible mechanisms that generate and maintain the terrestrial LDG and other gradients (Dawson, 2012). However, progress in these systems will require a much greater commitment to documenting primary biodiversity patterns in non-vertebrate clades.

(5) Despite the promise that these systems offer for understanding global diversity patterns, we are racing against time: the impacts of climate change, invasive species,

eutrophication, and other factors are likely to intensify in the foreseeable future and will erode our ability to understand faunas that have been assembled over kiloyear to megayear (10^3 – 10^6) timescales. Whether we can document biodiversity patterns in these systems quickly enough to outpace the rate at which the data are lost forever remains to be seen.

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