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Speciation rate and the diversity of fishes in freshwaters and the oceans

Short title: Speciation rate in freshwater fishes

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DATA AVAILABILITY STATEMENT

All files necessary to repeat the work described here are available through the Dryad digital data repository (DOI: doi:10.5061/dryad.7h44j0zr2), including salinity classifications, evolutionary rate information, analysis code, and Appendix S1. The time-calibrated phylogeny for ray-finned fishes is also available as the 'Timetree (Newick format)' at https://fishtreeoflife.org/downloads/.

ABSTRACT

Aim: The number of fish taxa that occur exclusively in marine biomes is approximately equal to the number that occur in freshwater biomes. Both the geographic area and habitable volume of the marine realm are vastly greater than for Earth's freshwater ecosystems, suggesting that the density of marine species is proportionately much lower in the oceans. Because freshwater lineages are relatively recently derived from older marine lineages, this difference in species density suggests that speciation rates might be elevated in freshwater systems. I tested whether speciation rates differ systematically between freshwater and marine habitats.

Location: Aquatic ecosystems worldwide

Taxon: Ray-finned fishes (Actinopterygii)

Methods: Marine-freshwater transitions were tabulated from literature survey and from ancestral state reconstruction. I tested for repeated effects of salinity transitions on speciation rate using formal state-dependent diversification methods (STRAPP, FiSSE). Using maximum likelihood, I then tested for absolute (unreplicated) differences in speciation rate between marine and freshwater lineages.

Results: Ray-finned fishes have undergone numerous transitions from marine to freshwater systems, but the vast majority of freshwater species richness has resulted from a handful of freshwater colonization events. Speciation rates in freshwater lineages are substantially faster on average than those of marine lineages, but transitions to freshwaters do not lead to elevated rates of speciation in general. This paradox of state-dependent diversification arises because of the disproportionate effect of several freshwater clades with high species richness and fast rates of speciation.

Main Conclusions: Transitions to freshwater do not cause faster rates of speciation, but freshwater ecosystems worldwide are dominated by several clades with relatively fast rates of speciation. There is no evidence that invasion of a novel habitat (freshwater) is generally sufficient to trigger a burst of speciation in colonizing lineages. These results raise an important conceptual problem for the interpretation of state-dependent diversification analyses.

Keywords: Freshwater, biodiversity, fishes, Actinopterygii, speciation, diversification, biogeography, diversity gradient

INTRODUCTION

The differences in species richness among Earth's major habitable zones (e.g., terrestrial; freshwater; marine) is of great interest to ecologists and evolutionary biologists and provides an important test for the generality of mechanisms that influence the dynamics of biological diversity in space and time (Webb, 2012; Worm & Tittensor, 2018). The contrast in species richness between marine and terrestrial environments has generated considerable interest, because terrestrial ecosystems are typically much more species-rich than marine systems. As May (1994) notes, this disparity in richness is unexpected from first-principle mechanisms in ecology (e.g., species-area relationship), given that oceans comprise a much larger fraction of

Earth's area than terrestrial habitats. For the contrast between marine and freshwater habitats, the disparity in geographic areas is even greater. The ratio of total surface area for marine systems relative to freshwater systems is approximately 100:1; for habitable volume (km^3), the ratio is on the order of 10,000:1 (Dawson, 2012). Even if we consider only continental shelf habitats, where the majority of marine species are located, the ratio of marine to freshwater areas is still biased towards the marine realm by a factor of 10 (Dawson, 2012). Under any simple relationship between geographic area, diversification, and species richness (Losos & Schluter, 2000; Rosenzweig, 1995; Wagner et al, 2014), we would expect greater species richness in marine environments relative to freshwaters.

Given this variation in geographic scale, the relative diversity of ray-finned fishes (Actinopterygii; hereafter, "fishes") in marine and freshwater habitats poses an intriguing evolutionary conundrum (Tedesco, Paradis, Leveque, & Hugueny, 2017). To a first approximation, the number of marine fishes is equal to the number of freshwater fishes, with roughly 15,000 species occurring in each of these habitats (Seehausen & Wagner, 2014). Vega and Wiens (2012) framed this observation with a provocative question: why are there so few fishes in the sea? Betancur-R et al (2015) observed that, while the ancestral state for major freshwater fish clades is clearly marine, many extant marine clades are relatively young, pointing to a possible role for extinction in eliminating many early-diverging fish lineages. Alfaro et al (2018) found that today's dominant marine clades generally diversified after the K-Pg extinction event; faster diversification rates for young marine lineages may have thus enabled them to "catch up" in species richness with older but more slowly-diversifying freshwater clades (Betancur-R et al., 2015).

There are several reasons to hypothesize that speciation rates might be elevated in lineages that have colonized freshwaters (Bloom, Weir, Piller, & Lovejoy, 2013). For example, freshwater systems are characterized by greater provincialism and afford greater opportunities for isolation and geographic speciation. Continental / freshwater systems are also more likely to be impacted by tectonic dynamism and other earth-system processes that can reshape drainage basins and facilitate allopatric speciation (Albert & Reis, 2011; Seehausen & Wagner, 2014). Differences in population structure between marine and freshwater systems (Palumbi, 1994; Schiebelhut &

Dawson, 2018) might translate into variation in diversification rates over macroevolutionary timescales (Bloom et al., 2013). Likewise, clades of fishes that have colonized freshwaters might represent lineages that have undergone shifts to novel adaptive zones, potentially leading to bursts of speciation (Betancur-R, Orti, Stein, Marceniuk, & Pyron, 2012).

However, contrasting predictions can also be made for each of the above proposals: speciation rates in lineages that have shifted to freshwaters might be dampened by interactions with incumbent clades that already occupy most available ecological space (Betancur-R et al., 2012; Bloom & Lovejoy, 2017). Likewise, the greater population structure of freshwater taxa might also reflect lower per-capita population sizes, smaller geographic range sizes, and greater likelihood of extinction of incipient species or population isolates (Bloom et al., 2013). At the macroevolutionary scale, elevated extinction rates of incipient species might translate into lower speciation rates overall, because population persistence is a critical component of the speciation process (Dynesius & Jansson, 2014; Harvey, Singhal, & Rabosky, 2019; Mayr, 1963; Rosenblum et al., 2012).

Previous studies of the marine-freshwater divide in ray-finned fishes have reached alternative conclusions regarding the effect of salinity transitions on diversification (Betancur-R et al., 2012; Bloom et al., 2013; Miller, Hayashi, Song, & Wiens, 2018; Tedesco et al., 2017; Vega & Wiens, 2012). In this article, I test whether freshwater and marine fishes differ systematically in the rate of speciation, using a comprehensive phylogeny for ray-finned fishes that includes approximately 40% of described species-level taxa (Rabosky et al., 2018). I focus on speciation and not net diversification rates, given that speciation rates are much more robustly estimated from molecular phylogenies (Nee, May, & Harvey, 1994; Title & Rabosky, 2019). I use several methods for inferring state-dependent speciation rates. Finally, I describe an important conceptual problem for the interpretation of causality in state-dependent diversification analysis.

METHODS

Data

Data on salinity environment (freshwater, brackish, marine) of 30,140 extant fishes were downloaded from Fishbase (Froese & Pauly, 2017). As a phylogenetic framework, I used the phylogeny of Actinopterygian fishes from Rabosky et al (2018), which was used to assess the relationship between latitude and speciation rate. This phylogeny is available through the R package 'fishtree' (Chang, Rabosky, Smith, & Alfaro, 2019) and is based on 11,638 species whose position was estimated from genetic data; the remaining 19,888 species were placed in the tree using stochastic polytomy resolution. The phylogeny was dated using 130 fossil calibration points. Rabosky et al (2018) estimated speciation rates for all fishes, and these data are available on Dryad (see Data Availability). Briefly, speciation rate estimates were inferred using the DR statistic ((Jetz, Thomas, Joy, Hartmann, & Mooers, 2012); hereafter, λ_{DR}) and BAMM (λ_{BAMM}). All speciation rates are per capita (per lineage) rates in units of new lineages per million years (my), or lineages my^{-1}.

λ_{DR} is a non-model-based estimator of speciation rate that is computed for a given species as a weighted average of the inverse branch lengths connecting the focal species to the root of the phylogeny (e.g., the root-to-tip set of branches). For a given tip, λ_{DR} is similar to the node-density estimator (Freckleton, Phillimore, & Pagel, 2008), but upweights the contribution of recent branch lengths and downweights those branches closer to the root. Speciation rate estimates from BAMM (Rabosky, 2014; Rabosky, Mitchell, & Chang, 2017) allowed rates of speciation to vary through time within rate regimes. Details of evolutionary rate estimation are described in Rabosky et al (2018). Importantly, our estimates of λ_{DR} were computed across a distribution of phylogenetic trees that included the full set of 31,526 ray-finned fishes, thus accounting for potential underestimation of rates due to incomplete taxon sampling. Speciation rate estimates from BAMM accounted for incomplete sampling at the family level using clade-specific sampling fractions. As in Rabosky et al (2018), formal analyses of the relationship between speciation rate and environment included only the set of species whose position was estimated from genetic data.

History of freshwater colonization

I inferred the history of freshwater colonization across fishes by reconstructing ancestral character states across the phylogeny and by literature survey. Ancestral state estimation was performed using maximum likelihood. There are numerous caveats that apply to ancestral state estimates at such large phylogenetic scales, including the confounding effects of character state-dependent diversification (Maddison, 2006; Maddison, Midford, & Otto, 2007) and heterotachy (King & Lee, 2015). However, addressing these issues within in a single phylogenetic framework is computationally intractable at present, given the size of the phylogenetic dataset. Hence, I use ancestral state estimation as a purely heuristic tool for visualization purposes and to validate and build upon literature-based inferences of marine-freshwater transitions. I repeated ancestral state estimation using maximum parsimony, which can accommodate extreme heterotachy in character change (King & Lee, 2015; Tuffley & Steel, 1997). The set of inferred freshwater colonization events is an extreme minimum estimate and is intended only to guide comparisons of speciation rates between freshwater and marine systems; further details on qualitative patterns observed are provided in the Results section. Formal analyses of the relationship between states and diversification are described in the following section and do not require the estimation of ancestral character states.

For ancestral state reconstruction, I coded each taxon into one of the following five character states: marine (MA), brackish-marine (BR-MA), freshwater (FW), brackish-freshwater (BR-FW), and brackish-freshwater-marine (BR-FW-MA). I did not distinguish between diadromous and non-diadromous fishes. To perform maximum likelihood estimation of ancestral states, I defined a transition matrix for shifts between these character states that assumed stepwise gain or loss of individual components (BR, FW, MA), and further assumed that all transitions between marine and freshwater environments moved through a brackish intermediate stage. For example, a transition from an exclusively marine to exclusively freshwater environment necessarily involved gain of a brackish state, gain of freshwater state, and the subsequent loss of both the marine and brackish states. The logic underlying stepwise gain and loss model is similar to the DEC biogeographic model developed by Ree and Smith (2008). Models for character transitions were implemented in the 'diversitree' package for R (FitzJohn, 2012).

Environment-dependent speciation rates

I focused on tip (recent) rates of speciation (λ_{DR}, λ_{BAMM}) and did not make inferences about historical bursts of speciation that might have occurred in particular lineages. These rates can be viewed as approximations of the rate of lineage splitting during the past 10 million years or so (Rabosky et al., 2018: Extended Data Figure 6). Questions about variation in speciation rates through time remain interesting, but are more challenging to address, given the vast (> 100 million year) differences in age among clades that have shifted from marine to freshwater environments. Likewise, I ignore rates of extinction and net diversification: λ_{DR} is an estimate of speciation and not net diversification (Title & Rabosky, 2019), and parametric estimates of speciation rates (λ_{BAMM}) are far more reliable than the corresponding extinction estimates (Davis, Midford, & Maddison, 2013; Mitchell, Etienne, & Rabosky, 2019).

I used two non-model-based methods to formally assess the relationship between salinity environment and speciation rate: STRAPP (Rabosky & Huang, 2015), and FiSSE (Rabosky & Goldberg, 2017). STRAPP is phylogenetically-structured permutation test for λ_{BAMM} that is expected to perform well at large phylogenetic scales where many rate regimes have been inferred; the fish phylogeny is well-suited for this method, as the posterior mean number of rate regimes across the fish phylogeny inferred with BAMM ranged from 120 - 145 (Rabosky et al., 2018). FiSSE tests whether the distribution of λ_{DR} differs between two character states and generates a corresponding null distribution through simulation. I performed tests for state-dependent speciation for exclusively marine (MA) and freshwater (FW) taxa, and I also tested the contrast in rates for a second grouping of taxa where marine and freshwater states included taxa with brackish affinities (e.g., "marine" = MA + BR-MA; "freshwater" = FW + BR-FW). In addition, I repeated these analyses after excluding a large and rapidly-speciating clade of freshwater fishes that was found to have a strong leveraging effect on the overall results (Cichlidae).

I performed a more informal test for the effects of salinity state change on speciation by defining a set of speciation contrasts for each predominantly freshwater clade of fishes across the phylogeny. For example, a radiation of approximately 27 freshwater halfbeaks (Beloniformes: *Hemirhamphodon*, *Nomorhamphus*, and *Dermogenys*) occurred in southeast Asian freshwaters

(Anderson & Collette, 1991), and I defined a corresponding marine "reference clade" for these taxa as the set of marine Beloniform lineages. I computed the mean tip rate across the freshwater clade and the corresponding rate across the marine reference clade. For some clades, the marine reference clade was necessarily quite large: for the Otophysi (9,400 species), for example, I defined the reference clade as the set of all marine teleosts. These analyses represent quasi-independent contrasts, because the marine reference groups may be shared across more than one freshwater origin.

I focused on clades that underwent radiations in freshwaters and thus limited those analyses to monophyletic sets of freshwater taxa, and I excluded those with complex patterns of transitions and reversals (e.g., Gobiiformes, Clupeiformes). I also excluded clades with fewer than 10 freshwater taxa, or representatives of freshwater radiations with very poor (< 5 tips) sampling in the tree (e.g., *Glossamia* cardinalfishes from New Guinea). Several clades of fishes are characterized by a complex history of transitions between freshwater, brackish, and marine environments (e.g., Gobiiformes, Clupeiformes; (Bloom & Lovejoy, 2014)) and due to limitations in the reference phylogeny, I did not attempt to explicitly infer each independent invasion of freshwater. I performed a two-sample t-test to assess whether the distribution of contrasts was significantly different from zero. A total of 15 freshwater clades were included in the contrast test (Appendix S1).

Finally, I tested whether speciation rates across families of freshwater fishes were significantly different from those of marine families. There is an important but subtle distinction between this analysis and the formal tests for state-dependent diversification. With state-dependent tests (e.g., FiSSE, STRAPP), we are concerned with identifying causality: does a shift to a particular character state have consequences for diversification? However, one can simply test whether rates themselves are significantly different between two groups (e.g., a single clade of freshwater fishes versus a clade of marine fishes), without requiring repeated effects of the trait on diversification.

I restricted my analysis to the set of families represented by at least 10 taxa in the phylogenetic tree of Rabosky et al (2018), and for which 90% of total species richness was restricted to either

freshwater or marine habitats. I made the simplifying assumption that all species from a common environment (e.g., FW + BR-FW) shared identical rates of speciation and extinction. I fit a constant-rate birth-death model to the set of freshwater clades and to the set of marine clades separately, accounting for incomplete sampling using family-specific sampling fractions. The full model has separate speciation and extinction rates for marine and freshwater habitats, for a total of four parameters. I compared this model to one where all clades share identical speciation and extinction rates, regardless of salinity environment (two parameters), and to an additional model where speciation rates but not extinction rates vary by salinity environment (three parameters). I repeated this exercise after excluding two major clades of freshwater fishes that were found to have a strong leveraging effect on the overall results (Cichlidae and Otophysi). Model-fitting used the 'diversitree' package for R (FitzJohn, 2012).

RESULTS

Tabulation of Fishbase data suggests that 13804 and 13531 species of ray-finned fishes inhabit exclusively freshwater or marine environments, respectively. An additional 725 and 1291 species inhabit freshwater-brackish and marine-brackish habitats. The Rabosky et al (2018) phylogeny includes 5096 freshwater and 4469 marine taxa that are represented by genetic data in the underlying supermatrix that was used to construct the tree.

A tabulation of ray-finned fish lineages that have transitioned from marine to freshwater environments is given in Appendix S1, and a phylogenetic perspective illustrating major lineages of freshwater fishes is shown in Figure 1. The contributions of each group to global freshwater fish diversity is illustrated in Figure 2. My tabulation of marine-freshwater transitions (Appendix S1) is highly incomplete and should not be considered an exhaustive list; I do not distinguish multiple freshwater invasions (and potentially, reverse transitions) in a number of groups with complex histories of trait evolution. These groups include gobiiform, mugiliform, atheriniform, and clupeiform fishes; several have already been the topic of dedicated analyses (Betancur-R et al., 2012; Bloom & Egan, 2018; Bloom et al., 2013). Appendix S1 also indicates whether a given origin is associated with a freshwater "radiation", which is defined here as diversification of a presumed freshwater ancestor into four or more species that exclusively

inhabit freshwater and for which multiple independent freshwater colonizations from marine
308 ancestors are unlikely. A clade may still constitute a radiation even if one or more lineages have secondarily reverted to marine environments, as in the case of the Otophysi (e.g., brackish-
310 marine reversals in ariid catfishes). For the purposes of this article, I treated several low-diversity non-teleost clades (Polypteriformes, Acipenseriformes, Amiiformes, Lepisteiformes) as distinct
312 units and did not collapse them into single freshwater group, given the vast evolutionary distances between these taxa (but see Betancur-R et al., 2015).

314

Overall, recent speciation rates in freshwater taxa are substantially faster than those in marine
316 taxa. For freshwater lineages (n = 5096), mean speciation rates are $\lambda_{BAMM} = 0.216$ and $\lambda_{DR} = 0.257$, versus $\lambda_{BAMM} = 0.121$ and $\lambda_{DR} = 0.155$ for marine fishes (n = 4469). For both λ_{BAMM} and
318 λ_{DR}, mean speciation rates for freshwater lineages are thus faster by approximately 0.1 lineages / my. A comparison of quantiles of the rate distributions for freshwater and marine lineages is
320 shown in Figure 3. Most of the effect is driven by pronounced differences at the high-end of the rate spectrum. Although median rates are not appreciably different for marine and freshwater
322 taxa (e.g., λ_{BAMM}: 0.06 vs 0.09), the rate distributions rapidly diverge for higher quantiles.

324 After accounting for phylogenetic pseudoreplication, there is no significant effect of state change on speciation rate (Table 1; STRAPP: p = 0.21, two-tailed; FiSSE: p = 0.1, two-tailed). These
326 results do not change when freshwater and marine states are expanded to include lineages that also inhabit brackish waters (e.g., FW = FW + BR-FW). For λ_{BAMM}, mean rates are 0.12 and
328 0.21 for marine and freshwater lineages (STRAPP p = 0.18), versus 0.15 and 0.25 for λ_{DR} (p = 0.09). The apparent weak effect of environment on speciation for FiSSE is largely due to the
330 presence of cichlids, an exclusively freshwater clade with both high species richness and high speciation rate. When cichlids are excluded from the analysis, the difference in speciation rates
332 for marine and freshwater taxa is much smaller; mean speciation rates for freshwater lineages drop to $\lambda_{BAMM} = 0.158$ and $\lambda_{DR} = 0.194$ (Table 1).

334

Inspection of the contrast in rates between freshwater taxa and their corresponding marine
336 reference group (Appendix S1) illustrates that shifts in salinity environment are not associated with a predictable effect on speciation rate (Figure 4). Paired-sample t-tests reveal no effect of

environment change on speciation rate for λ_{DR} ($t = 0.70$, $df = 15$, $p = 0.50$) or λ_{BAMM} ($t = 0.76$, $df = 15$, $p = 0.46$). Although these results are dependent on somewhat informally-defined marine reference clades (Appendix S1, Figure 4), they indicate that evolutionary transitions to freshwaters do not typically result in accelerated speciation, relative to rates observed for marine "outgroup" lineages.

In the maximum likelihood analysis across families, freshwater fishes are also found to speciate more rapidly than marine fishes. The overall speciation rate for marine families is $\lambda = 0.12$, versus $\lambda = 0.16$ for freshwater families (Table 2); note that these rates were estimated under a constant-rate birth-death process and thus differ from the tip rates (λ_{DR}, λ_{BAMM}) discussed previously. A model with separate rates for marine and freshwater lineages performed much better than a model where marine and freshwater families share rate parameters (Table 2). These results hold even after cichlids are dropped from the analysis, although speciation rate differences are substantially lower than when they are included (marine: $\lambda = 0.115$, versus $\lambda = 0.135$ for freshwater). However, after also removing the Otophysi – by far the most species-rich clade of freshwater fishes – we no longer recover an effect of salinity environment on speciation rate (Table 2).

DISCUSSION

There are reasons to predict both faster and lower rates of speciation for freshwater fishes, relative to lineages that inhabit marine environments (Betancur-R et al., 2012; Bloom et al., 2013). To a first-order approximation, the number of fishes that inhabit freshwater environments is equal to the number that inhabit marine environments, despite vast differences in the habitable area of these major habitats. Under a simple evolutionary species-area model (Rosenzweig, 1995; Wagner, Harmon, & Seehausen, 2014), we would thus expect greater richness in marine systems; faster diversification rates in freshwater environments is one potential solution to this apparent paradox of diversity and habitable area.

I found support for two seemingly contradictory results. First, there is no significant effect of salinity (freshwater, marine) on speciation rates as assessed using formal tests for state-

dependent speciation (Table 1). Second, speciation rates for freshwater fishes are significantly faster, on average, than those for marine fishes (Table 2). These results indicate that transitions to freshwater do not, in general, result in faster rates of speciation. At the same time, the "average" freshwater fish does indeed have speciation rates that are elevated relative to an "average" fish from a marine environment. These differences are especially pronounced for higher quantiles of the rate distribution for marine and freshwater fishes (Figure 3d, f). These results are generally consistent with those reported by Miller et al. (2018), who found weak to non-significant effects of salinity state on net diversification rates as inferred using formal state-dependent models.

In my analyses, the faster-speciation effect arises because of two clades that collectively account for more than 80% of all freshwater fish diversity: the Otophysi and the Cichlidae (two most species-rich clades in Figure 2a). When these clades are removed from the by-clade maximum likelihood analyses (Table 2), there is no significant difference in speciation rate between predominantly marine and freshwater clades. Interestingly, these clades impact the overall results for different reasons. Considering only tip speciation rates, cichlids have greatly elevated speciation rates (λ_{BAMM} = 0.59; λ_{DR} = 0.67) relative to marine taxa (λ_{BAMM} = 0.12, λ_{DR} = 0.16). Mean otophysan rates (λ_{BAMM} = 0.15; λ_{DR} = 0.20), in contrast, are weakly elevated relative to marine rates, but freshwater fish diversity is dominated by otophysans and the clade thus has a disproportionate leveraging effect on the overall results (Figure 2a; Table 2). It is thus possible that proportionally high freshwater fish diversity, relative to habitable area and volume, can be explained in part by faster rates of speciation in freshwater environments. Freshwater transitions do not appear to have a predictable effect on speciation rates (Table 1; Miller et al, 2018), but freshwaters are nonetheless dominated by representatives from several clades that have modest to substantially elevated rates of speciation. Put another way, faster speciation might contribute to the proportionately high diversity of freshwater fishes, despite no causal relationship (e.g., no repeatable effect) between the character state "freshwater" and speciation rate.

These results have implications for how we interpret causality in the context of formal tests for state-dependent diversification. As a purely hypothetical example, I will illustrate how the analysis of formal state-dependent models can provide a misleading view of the causes of large-scale diversity gradients. Consider the latitudinal diversity gradient (LDG), whereby Earth's

tropical regions contain far more species than temperate or polar regions. Many recent studies have addressed the causes of the LDG using phylogenetic tests for state-dependent diversification (Cardillo, Orme, & Owens, 2005; Rabosky et al., 2018; Rabosky, Title, & Huang, 2015; Rolland, Condamine, Jiguet, & Morlon, 2014). The logic underlying formal tests presented in these and other studies is that, if speciation (or diversification) is a primary cause of the latitudinal diversity gradient, then we should observe repeated effects of the character state (latitude) on speciation or diversification. This approach has the potential to greatly mislead with respect to the causes of the LDG and other major richness gradients, because diversity is often distributed unevenly across constituent clades within regions. We might find that latitude has no repeatable effect on diversification rates using formal phylogenetic analysis (sister-clade contrasts, state-dependent models, or other approaches). Yet the cause of the LDG might nonetheless involve faster speciation of just one or several component clades, provided that those clades contribute disproportionately to the total diversity of a given region. Figure 5 illustrates a hypothetical scenario whereby a single clade with fast diversification drives an overall diversity gradient across two biomes (biome XX and biome YY). In this example, clades from the more species-rich biome actually have slower rates of diversification than clades from the species-poor biome (Figure 5c). Note that the results in Fig. 5 are purely for illustration of the concept; the data are simulated and the logic underlying the figure potentially applies to any diversity gradient (e.g., LDG; marine versus freshwater; deep-sea versus shallow-sea; land versus ocean).

In the context of the present analysis, to explain global patterns of fish diversity, we cannot ignore clade-specific (unreplicated) factors, due to the extreme skew in richness among freshwater clades (Figure 2a). To a first approximation, freshwater fish diversity is best explained by whatever explains otophysan diversity. With the exception of African Rift lakes, tropical fish communities – lotic systems in particular – are dominated by otophysan fishes. It may be difficult or impossible to determine causality in the case of unreplicated, clade-specific factors. Is faster speciation a property of the otophysan clade more generally or is it the result of a clade-specific interaction with the environment (freshwater)? Regardless, the net result is the same: a single clade with elevated rates dominates a particular environmental setting, with profound consequences for overall species richness (Figure 5d). The HiSSE model has potential to uncover clade-specific "hidden" interactions between specific environments and

diversification (Beaulieu & O'Meara, 2016), although it should be noted that all clades shown in Figure 5 differ in their rate of diversification (Figure 5c) and thus, all clades effectively have unique clade-specific hidden states. How HiSSE would fare in the scenario illustrated in Figure 5, and how researchers would then interpret the outcome with respect to causality, remains an open question.

At least among vertebrates, this pattern of clade dominance may be more the rule than the exception. For example, the extreme diversity of neotropical birds is explained in large part by a spectacular radiation of suboscine passerines (Price, 2008; Rabosky et al., 2015; Winkler, Billerman, & Lovette, 2015), with secondary contributions from a large radiation of tropical tanagers (377 sp). Despite numerous evolutionary transitions between "tropical" and "non-tropical" states, exclusion of just these two clades is sufficient to eliminate the LDG for New World birds (Rabosky et al, 2015: Fig. 1). Likewise, the Amazonian peak in global snake diversity (Roll et al., 2017) is in large part the result of a dramatic radiation of dipsadine snakes (~700 sp; (Grazziotin et al., 2012)). This largely-tropical clade accounts for 50-65% of the local species richness in many of the most species-rich rainforest and savannah communities in South America (Duellman, 2005; Lima Pantoja, 2013).

Interestingly, and somewhat discouragingly, these results raise the possibility that explanations for freshwater fish diversity will face similar problems of collinearity that hinder analyses of terrestrial environments. Our ability to understand the terrestrial LDG is confounded by the fact that the tropics are simultaneously old, productive, and large. These factors are all predicted to affect species richness in the same direction, and it is thus difficult to disentangle the influence of any particular factor (Rabosky & Hurlbert, 2015). In the case of freshwater fishes, it appears that the dominant clade (Otophysi) is simultaneously much older than many other clades (Figure 1) with potentially elevated rates of speciation. Whether the relative influence of time, rate, and equilibrium processes can be disentangled for this group of fishes is an open question, although Betancur-R et al (2012) provide an interesting example for a smaller subclade (ariid catfishes). Although it may be challenging to derive a simple explanation for Otophysan richness, some insights may be gained by examining the factors that have affected diversification of replicate radiations within the group, perhaps within particular biogeographic theatres. Such a strategy

was used by Wagner et al (2012) to dissect the contributions of clade-specific and environmental factors to species richness in East African cichlids.

In conclusion, I found no evidence that shifts to freshwater environments are typically associated with elevated rates of speciation. Most freshwater clades are characterized by speciation rates that are not appreciably different from the rates of their closest marine relatives (Figure 4). However, rates are nonetheless elevated in general for freshwater fishes, due to the fact that several species rich clades (Otophysi, Cichlidae) are characterized by faster rates of speciation. These results draw attention to the fact that clade-specific patterns of diversification can have massive impacts on the overall species richness of a character state or geographic region, and highlight one manner in which formal analyses of state-dependent diversification can be positively misleading.

I recommend that researchers distinguish between (1) repeated effects of a character state on diversification rate, and (2) whether lineages that differ in phenotypic or geographic state are characterized by differential rates of diversification. It is this latter question that is most relevant to large-scale biodiversity patterns. For researchers who wish to understand the causes of geographic variation in species richness, the focus should be on determining whether evolutionary rates differ systematically across regions. Addressing this question does not necessarily require that traits (or geographic states) have repeated and predictable effects on diversification. Conversely, determining whether geographic region (e.g., "tropical" versus "temperate") is a potential cause of differential diversification does require that we observe repeated, phylogenetically-independent associations between rates and states. Is the goal of a given study to explain variation in species richness among regions (or character states), or is it to explain variation in evolutionary rates among clades? Understanding global diversity gradients requires a more nuanced view of causality than we typically allow and one that carefully discriminates between these two objectives.

Table 1. Tests for the effects of salinity environment (freshwater, FW; marine) on speciation rate in ray-finned fishes. λ_{FW} and λ_{MA} refer to mean (tip) speciation rates for freshwater and marine lineages, respectively. p-value is the two-tailed probability of the data under the null hypothesis of no relationship between salinity environment and speciation rate, using either STRAPP or FiSSE.

Test	λ_{FW}	λ_{MA}	*p*
STRAPP: Exclusively FW versus marine	0.216	0.121	0.21
STRAPP: FW versus marine, including brackish	0.211	0.116	0.18
STRAPP: Exclusively FW versus marine; no cichlidae	0.158	0.121	0.35
FiSSE: Exclusively FW versus marine	0.257	0.155	0.1
FiSSE: FW versus marine, including brackish	0.251	0.149	0.08
FiSSE: Exclusively FW versus marine; no cichlidae	0.194	0.155	0.48

Table 2. Maximum likelihood analysis of speciation rates for predominantly marine and freshwater clades. λ_{FW} and λ_{MA} denote freshwater and marine speciation rates; μ_{FW} and μ_{MA} denote freshwater and marine extinction rates. Equality of parameters indicates model where rates for freshwater and marine lineages are constrained to be equal. *np* = number of parameters in model.

Model	*np*	λ_{FW}	λ_{MA}	μ_{FW}	μ_{MA}	*logL*	*AIC*	*ΔAIC*
$\lambda_{FW} = \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	2	0.14	0.14	0.08	0.08	1724	-3444	140
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	3	0.15	0.13	0.07	0.07	1785	-3564	20
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} \neq \mu_{MA}$	4	0.16	0.12	0.09	0.06	1796	-3584	0
No Cichlidae								
$\lambda_{FW} = \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	2	0.13	0.13	0.06	0.06	214.8	-425.6	77.6
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	3	0.13	0.12	0.06	0.06	254.6	-503.2	0

$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} \neq \mu_{MA}$	4	0.14	0.12	0.06	0.06	254.9	-501.8	1.4
No Otophysi								
$\lambda_{FW} = \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	2	0.14	0.14	0.08	0.08	-715	1434	99
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	3	0.15	0.13	0.08	0.08	-697.8	1401.6	66.6
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} \neq \mu_{MA}$	4	0.2	0.12	0.15	0.06	-663.5	1335	0
No Cichlidae or Otophysi								
$\lambda_{FW} = \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	2	0.12	0.12	0.06	0.06	-2201.9	4407.8	0
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} = \mu_{MA}$	3	0.12	0.12	0.06	0.06	-2201.9	4409.8	2
$\lambda_{FW} \neq \lambda_{MA}$, $\mu_{FW} \neq \mu_{MA}$	4	0.12	0.12	0.06	0.06	-2201.7	4411.4	3.6

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510 FIGURES

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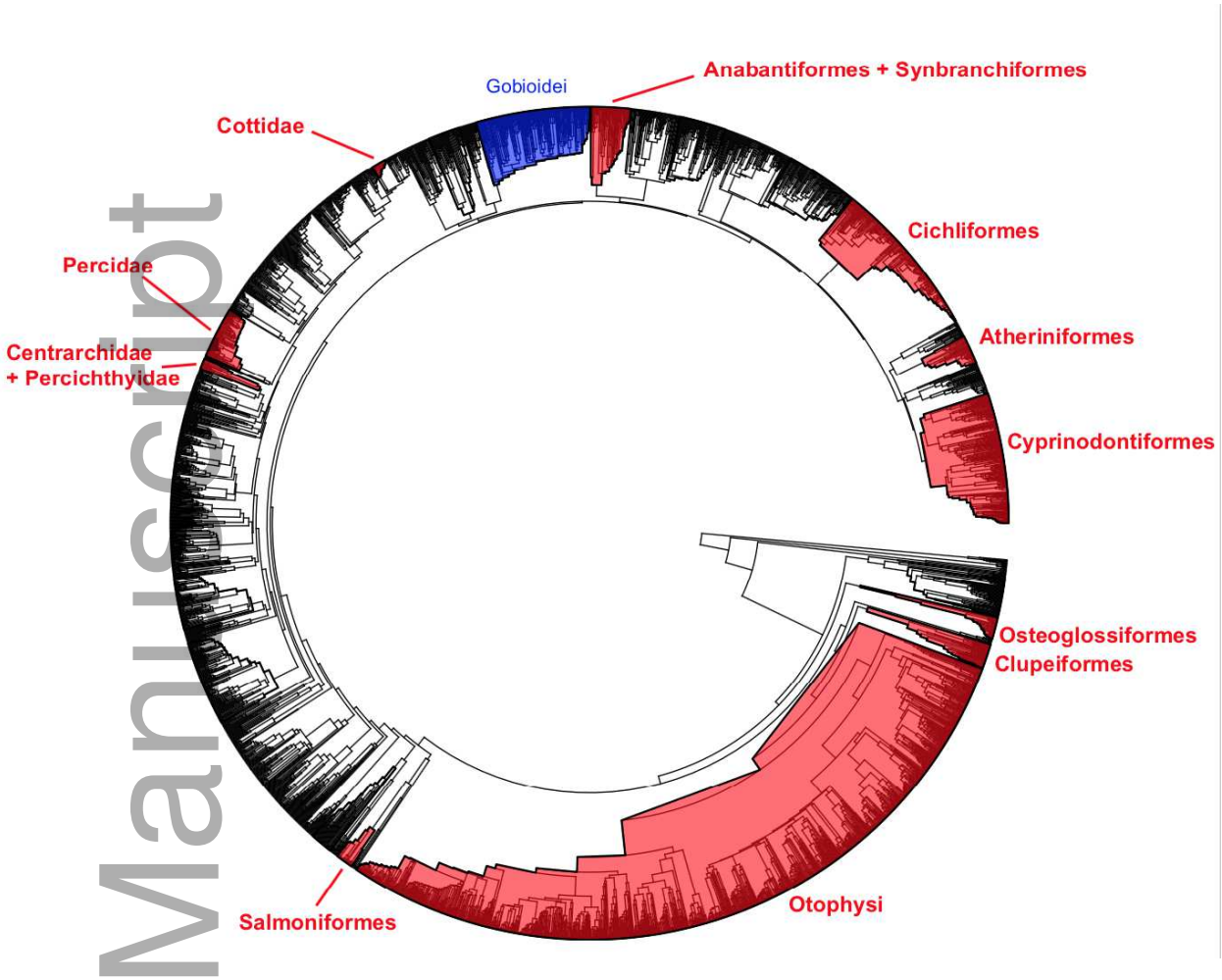

Figure 1. Phylogenetic distribution of major clades of freshwater fishes. The 12 labeled clades account for approximately 97% of the global diversity of freshwater fishes. Gobioidei (blue) has a much more complex pattern of transitions between marine and freshwater environments relative to other clades but nonetheless includes a number of freshwater species. Otophysi is by far the largest clade of freshwater fishes and includes more than 9000 freshwater-only species (of 9400 total). At least 39 additional origins of freshwater tolerance have occurred in other lineages of ray-finned fishes, accounting for approximately 400 additional freshwater taxa (Appendix S1). Reference phylogeny is taken from Rabosky et al (2018).

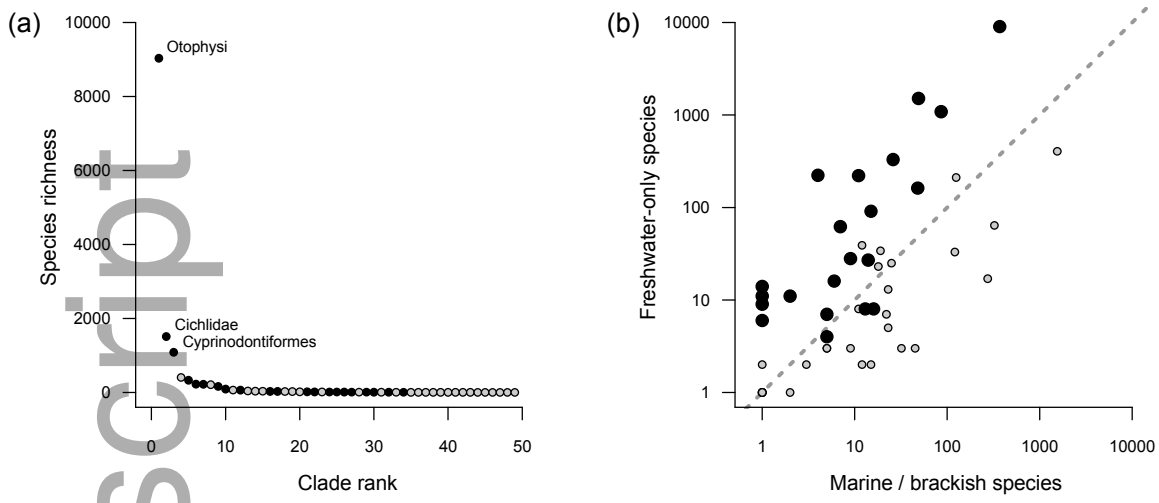

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Figure 2. (a) Variation in species richness across major clades of freshwater fishes (Appendix
530 S1); species richness indicates the number of exclusively-freshwater species and omits marine and brackish taxa from each clade. Clearly discernible freshwater radiations are shown in black;
532 gray points denote clades that may or may not constitute radiations and where the history of freshwater colonization is complex or ambiguous. The three labeled clades (Otophysi, Cichlidae,
534 Cyprinodontiformes) account for approximately 85% of global freshwater fish diversity. (b) The number of exclusively freshwater species versus the number of marine and brackish taxa, for the
536 49 clades illustrated in Appendix S1. Very few of the freshwater clades listed in Appendix S1 are restricted to freshwater; most contain at least a few taxa that inhabit marine or brackish
538 environments. Note that in (b), data are plotted on logarithmic scale.

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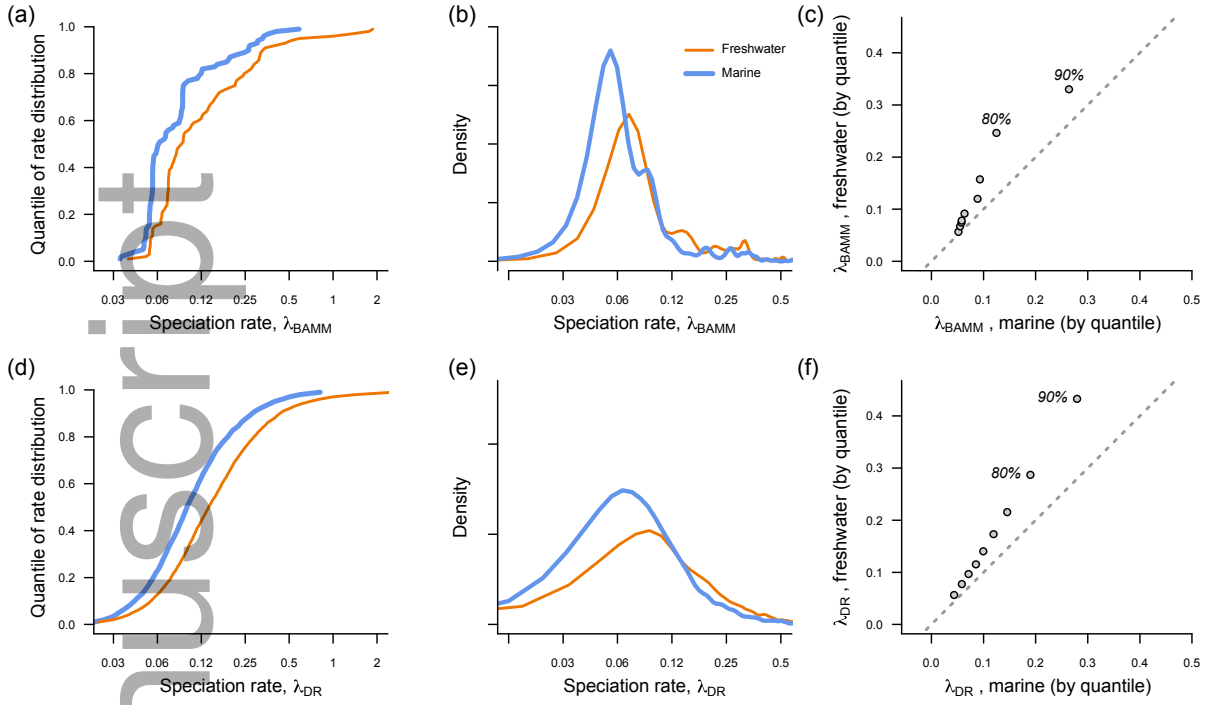

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544 Figure 3. Speciation rate distributions for freshwater (n = 5502) and marine (n = 5208) ray-finned fishes. (a) Distributional quantiles of λ_{BAMM} for marine (thick line) and freshwater taxa. 546 (b) Kernel density estimates of the distribution of λ_{BAMM} for marine and freshwater fishes. (c) Distributional quantiles of λ_{BAMM} (0.1, 0.2 ... 0.8, 0.9) for freshwater rate distribution as a 548 function of the corresponding quantile for the marine rate distribution. Identity line shown for reference (dotted). Although lower quantiles of the marine and freshwater rate distributions are 550 similar, they depart markedly for higher percentiles (> 0.70). This high-rate inflation yields mean rates for freshwater taxa that are much higher than for marine taxa (0.21 versus 0.12), even as the 552 medians are relatively similar (0.09 versus 0.06). Corresponding results for λ_{DR} are given in panels (d), (e), and (f). Speciation is given in units of lineages my^{-1}. Rates were computed only 554 from the set of taxa in the Rabosky et al (2018) phylogeny for which genetic data were available, thus ignoring taxa with positions estimated from stochastic polytomy resolution alone.

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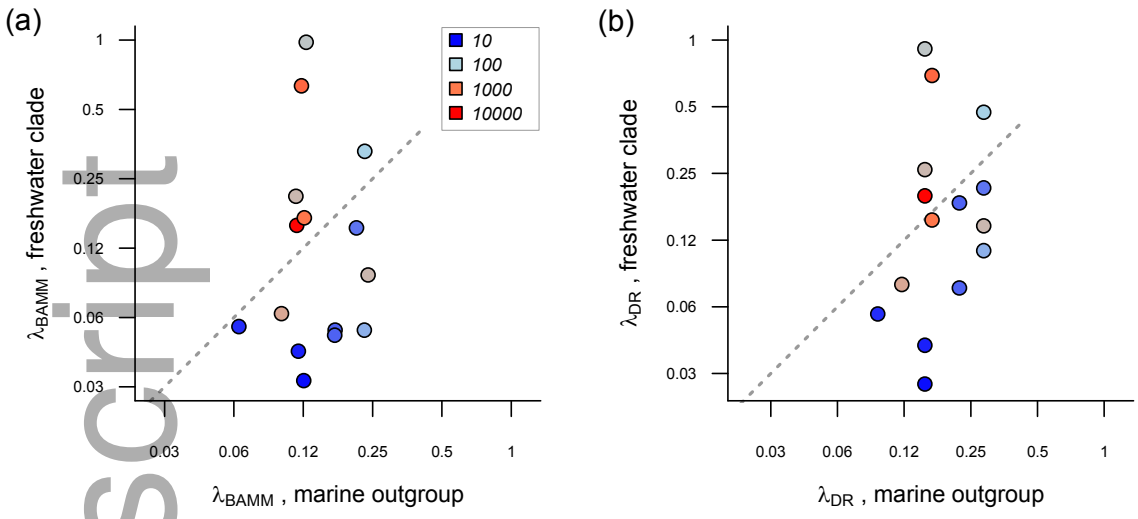
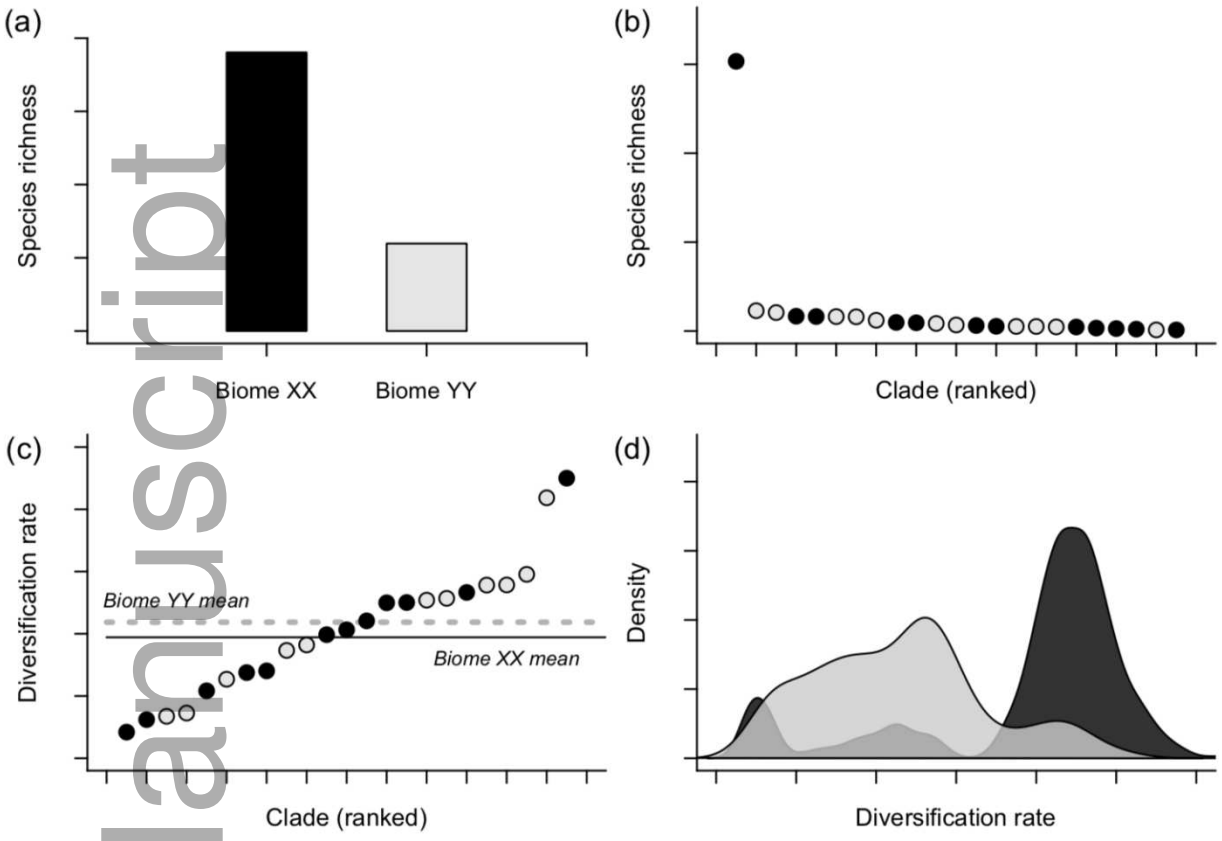


Figure 4. Quasi-independent contrasts for the effects of freshwater colonization on speciation rate. Speciation rates for freshwater radiations are shown as a function of the speciation rate for marine lineages from the corresponding "outgroup" (marine reference clade). If colonization and radiation in freshwaters is associated with elevated speciation rates, then freshwater clades should have faster rates relative to their corresponding marine outgroup. No significant effect of freshwater colonization is observed for λ_{BAMM} (a) or for λ_{DR} (b). Colors indicate the number of exclusively-freshwater species within each clade; see Appendix S1 for clade details.



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574 Figure 5. Tests for trait-dependent diversification can be positively misleading in the analysis of species richness gradients. The figure uses simulated data to show how geographic variation in
576 species richness can arise from differences in diversification rate, even when there is no repeatable effect of geographic region on diversification more generally. (a) Hypothetical
578 diversity gradient for a particular group of organisms, showing a species rich biome (XX) and a species-poor biome (YY). (b) Rank-order plot of species richness for individual clades that
580 comprise the diversity gradient illustrated in panel (a). Clades are found exclusively in biome XX (black) or biome YY (gray). (c) Clades vary in their diversification rate, and the mean rate
582 across all XX clades (solid line) is slightly less than the mean rate across all YY (dashed line) clades. (d) Frequency distribution of diversification rates across all species from biome XX
584 (black) and biome YY (gray), indicating that most species from the species-rich biome (XX) have fast rates of diversification relative to those from the species-poor (YY) biome. Biome XX
586 clades do not generally have fast rates of diversification (c), but a single exceptionally species-rich clade is characterized by fast rates, and this clade thus contributes disproportionately to the

overall diversity gradient. For this example, most trait-dependent analyses would find no effect of biome on diversification rate, and researchers might incorrectly conclude that diversification rate does not cause the diversity gradient. In fact, the gradient in this example is caused by faster diversification, but the effect is driven by a single clade with high species richness (b). The correct interpretation is that diversification rates vary systematically with respect to biome on a per-species basis, but the lack of repeated associations between biome and rate means that causality cannot be assigned to an effect of biome *per se*.

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BIOSKETCH

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