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Cite this article: Wiens JJ. 2015 Explaining large-scale patterns of vertebrate diversity. *Biol. Lett.* **11**: 20150506. http://dx.doi.org/10.1098/rsbl.2015.0506

Received: 11 June 2015
Accepted: 1 July 2015

Subject Areas:
ecology, evolution

Keywords:
diversification, ecology, habitat, phylogeny, species richness, Vertebrata

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Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2015.0506 or via http://rsbl.royalsocietypublishing.org.

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Evolutionary biology

Explaining large-scale patterns of vertebrate diversity

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The major clades of vertebrates differ dramatically in their current species richness, from 2 to more than 32 000 species each, but the causes of this variation remain poorly understood. For example, a previous study noted that vertebrate clades differ in their diversification rates, but did not explain why they differ. Using a time-calibrated phylogeny and phylogenetic comparative methods, I show that most variation in diversification rates among 12 major vertebrate clades has a simple ecological explanation: predominantly terrestrial clades (i.e. birds, mammals, and lizards and snakes) have higher net diversification rates than predominantly aquatic clades (i.e. amphibians, crocodilians, turtles and all fish clades). These differences in diversification rates are then strongly related to patterns of species richness. Habitat may be more important than other potential explanations for richness patterns in vertebrates (such as climate and metabolic rates) and may also help explain patterns of species richness in many other groups of organisms.

1. Introduction

Vertebrates are the dominant group of animals on the Earth, given their abundance, large body sizes and presence at the top of both aquatic and terrestrial foodwebs [1]. They include humans and most animals they consume, and may be the most intensively studied organisms. Yet, we know little about what explains their patterns of species richness among clades. For example, some vertebrate clades contain only a handful of living species (e.g. coelacanth (Actinistia) with 2, lungfish (Dipnoi) with 6 and crocodilians with 25), whereas others contains thousands (for example, birds (Aves) with more than 10 000, ray-finned fish (Actinopterygia) with more than 32 000; electronic supplementary material, table S1). To clarify, numerous studies have tested the causes of richness patterns within major vertebrate clades, such as the latitudinal richnesss gradient within amphibians and mammals (e.g. [2,3]). However, few studies have addressed the dramatic variation in richness across these clades. For example, Alfaro *et al.* [4] described dramatic variation in diversification rates among vertebrate clades, but did not test whether any intrinsic traits or ecological correlates explained why these rates varied. Several authors have hypothesized that occurrence in terrestrial habitats might generally increase diversification and richness of clades (given that terrestrial habitats were colonized later but have higher richness today), but without explicit quantitative analyses [5–8]. Here, I show that much of the variation in diversification rates and richness among major vertebrate clades can be explained by a simple ecological variable (ignored in most vertebrate studies): whether the clade contains predominantly aquatic or terrestrial species.

2. Material and methods

Detailed methods are provided in the electronic supplementary material, appendix S1. The time-calibrated phylogeny of gnathostomes from Alfaro *et al.* [4] was used to obtain clade ages. These ages and relationships are very similar to those from

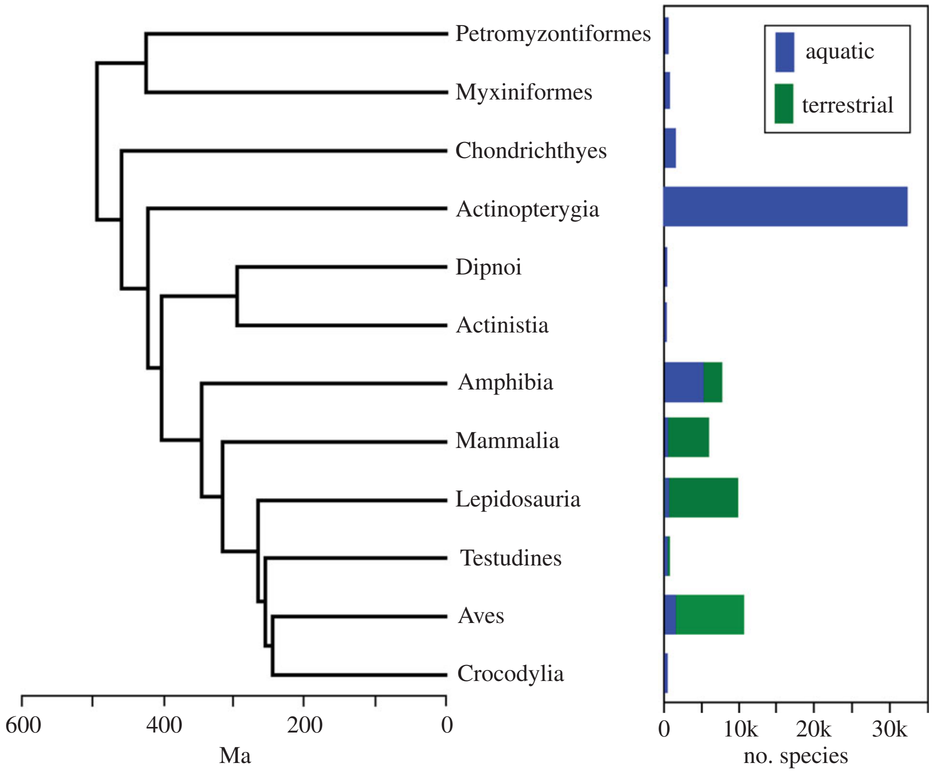

Figure 1. Phylogenetic tree of vertebrates used in the analyses, and species richness of the 12 major clades in aquatic and terrestrial habitats. The tree shown used ages for cyclostomes and the vertebrate root from Erwin *et al.* [12]; an alternative tree used dates from Blair & Hedges [13]. Myxiniformes, hagfish; Petromyzontiformes, lamprey; Actinopterygia, ray-finned fish; Chondrichthyes, sharks, rays, and relatives; Actinistia, coelacanth; Dipnoi, lungfish; Lepidosauria, lizards, snakes and tuatara; Testudines, turtles; Aves, birds; alligators, crocodiles, and relatives.

phylogenomic analyses using species-tree methods [9], but the tree [4] differs in including all major gnathostome clades. This phylogeny was expanded to include cyclostomes (lamprey, hagfish), using two sets of divergence times (trees, hereafter). Current numbers of described species in each habitat and clade were summarized from literature sources and online databases. Species were considered aquatic if they spend a significant portion of their lives in water, including fish, amphibians with aquatic larval stages, and tetrapods occuring primarily in aquatic habitats. The net diversification rate of each clade was estimated using the method-of-moments estimator for stem ages [10], using three assumed ratios of extinction to speciation (relative extinction fraction: $e = 0$, 0.5 and 0.9). Analyses were repeated for all three relative extinction fractions and both trees. The net diversification rate incorporates the impacts of both speciation and extinction, but does not require that speciation, extinction or diversification be constant over time [8]. The stem age incorporates the entire history of the clade, and not simply the age of the clade of surviving species (which could be substantially younger). The relationship between the diversification rate of each clade and its proportion of terrestrial species was tested using phylogenetic generalized least-squares (PGLS) regression, which accounts for phylogenetic non-independence of clades [11]. Data on stem ages, richness, diversification rates and proportions of terrestrial species for each major clade are summarized in the electronic supplementary material, table S1. The phylogeny and richness patterns are also summarized in figure 1.

3. Results

There is a significant, positive relationship between the proportion of terrestrial species in each clade and the clade's diversification rate (figure 2), explaining roughly two-thirds of the variation in diversification rates among clades (table 1). Moreover, there is a significant, positive relationship between

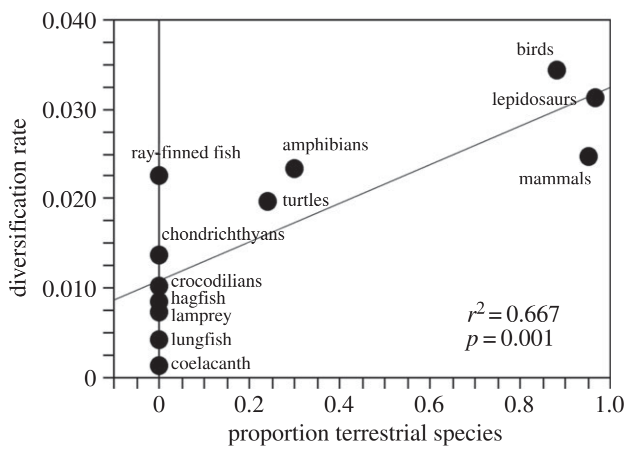

Figure 2. Relationship between habitat (proportion of terrestrial species) and net diversification rates among 12 major vertebrate clades. Results are based on ordinary least-squares regression (to illustrate the raw data), the root age of Erwin *et al.* [12], and an extinction fraction of 0.5 (full results in table 1).

diversification rates and richness among these clades (table 1). Although ray-finned fish (Actinopterygia) might appear to be a strong exception to the overall pattern (aquatic, with high richness; figure 1), they are relatively old, and therefore have lower diversification rates than predominantly terrestrial clades (birds, mammals and lepidosaurs; figure 2).

4. Discussion

Vertebrates are one of the most well-studied groups of organisms, but few studies have addressed why their major clades differ so dramatically in their current richness. The results here show that habitat explains most variation in large-scale

Table 1. Relationships between the proportion of terrestrial species in major vertebrate clades and their net diversification rates (estimated under three relative extinction fractions), and using two alternate ages for cyclostomes and the vertebrate root [12,13]. AIC, Akaike information criterion; div. rate, diversification rate; prop., proportion.

variables	r^2	*p*-value	AIC
Erwin *et al.* [12] tree			
div. rate ($e = 0$) ~ prop. terrestrial	0.6594	0.0008	75.4384
div. rate ($e = 0.5$) ~ prop. terrestrial	0.6615	0.0008	74.8602
[a]div. rate ($e = 0.9$) ~ prop. terrestrial	0.6685	0.0011	79.8808
ln-species ~ div. rate ($e = 0$)	0.8471	<0.0001	40.5479
ln-species ~ div. rate ($e = 0.5$)	0.8617	<0.0001	39.4395
ln-species ~ div. rate ($e = 0.9$)	0.8765	<0.0001	38.2015
Blair & Hedges [13] tree			
div. rate ($e = 0$) ~ prop. terrestrial	0.6503	0.0020	70.3817
div. rate ($e = 0.5$) ~ prop. terrestrial	0.6431	0.0022	69.7182
div. rate ($e = 0.9$) ~ prop. terrestrial	0.6308	0.0026	67.1607
ln-species ~ div. rate ($e = 0$)	0.7996	0.0002	39.3290
ln-species ~ div. rate ($e = 0.5$)	0.8164	0.0001	38.4524
ln-species ~ div. rate ($e = 0.9$)	0.8356	<0.0001	37.3477

[a]Optimization for PGLS analysis failed, and ordinary least-squares regression was used instead.

patterns of vertebrate diversification and richness. These results are surprising in showing that a relatively simple ecological variable explains variation in diversification rates over a timescale of more than 500 Myr (figure 1), and that variation in diversification rates in turn explains large-scale richness patterns among clades (table 1). Furthermore, this ecological variable is not often considered in explaining large-scale richness patterns among clades. Yet, these results suggest that habitat might be more important than other, more conventional explanations for vertebrate richness patterns.

For example, the results here show that climate may not always be the primary driver of large-scale richness patterns among clades. Many vertebrate clades do show a strong latitudinal diversity gradient (e.g. amphibians and mammals; [2,3]). However, the most species-poor of these 12 major vertebrate clades are aquatic clades that occur almost exclusively in tropical regions (e.g. actinistians, crocodilians and dipnoans; [1]). In these cases, the negative effects of habitat on diversification seem to overcome the potentially positive impacts associated with occurrence in tropical regions.

Similarly, some authors have suggested that higher metabolic rates drive higher rates of diversification (e.g. [14,15]). Birds and mammals are endothermic and thus have metabolic rates approximately 10 higher than those of most comparably sized ectothermic vertebrates [1]. However, treating endothermy as a binary variable shows no significant relationship with diversification rates (electronic supplementary material, table S2). Moreover, models including both habitat and endothermy explain negligible additional variation and have a higher Akaike information criterion (AIC), relative to models based on habitat alone (table 1 and electronic supplementary material, table S2).

Previous authors have suggested that clades occurring in marine habitats may have lower diversification rates than those on land, given higher species richness in terrestrial environments overall coupled with the more recent invasion of these habitats [5–8]. However, none has tested whether habitats explain large-scale patterns of diversification and species richness among clades. Further, the results here combine marine and freshwater habitats. Interestingly, marine habitats alone (i.e. proportion of primarily marine species in each clade) do not show a significant relationship with diversification rates (electronic supplementary material, table S3, appendix S1).

Several potential sources of error might change the detailed results of this study, but not the overall conclusions. For example, the tree used (figure 1) may be incorrect in showing Actinistia (coelacanth) and Dipnoi (lungfish) as sister taxa (instead of Dipnoi as sister to Tetrapoda; e.g. [16]). However, these alternative relationships would simply make these two clades older and would lower their diversification rates even further. The same reasoning applies to Mixiniformes (hagfish) and Petromyzontiformes (lamprey), whose relationships with each other and with other vertebrates have been controversial (see electronic supplementary material, appendix S1). Furthermore, there is a continuum in habitat usage between species that are fully aquatic and fully terrestrial. Here, species were considered aquatic if they were dependent on water, even if they spend considerable time on land. A different threshold might change the results somewhat. However, all fish clades, all crocodilians and most turtle species should be considered aquatic by most definitions. Categorizing some birds, lepidosaurs and mammals may be more challenging, but any changes would have little impact on the conclusions here, since these clades are mostly terrestrial anyways (electronic supplementary material, table S1). Considering most amphibians to be terrestrial rather than aquatic (70 versus 30%) yields similar results, with an even stronger relationship between terrestrial habitats and diversification (electronic supplementary material, table S4). There are also different possible ways of dividing vertebrates into clades, which might influence the results. However, the goal here was to explain patterns of richness among major vertebrate groups. Subdividing these clades further would presumably generate additional variation in diversification rates that would then require additional variables to explain. Finally, new species continue to be described in most clades. The analyses here focus on differences in diversification rates among clades, and should be robust to increasing species numbers (especially in larger clades).

Importantly, the results here are not inconsistent with very fast diversification rates in some aquatic subclades within these major groups (e.g. acanthomorphs and cichlids within actinopterygian fish [4]) nor with fluctuations in species richness within clades over time (for example, due to global mass extinction events). The rates estimated here are the outcome of both of these dynamics on net diversification rates and present-day richness of these major clades. The results show that habitat is an important predictor of these large-scale patterns of diversification and diversity, even if habitat alone does not explain every pattern in every subclade at every point in time.

A major topic for future research following from these results is to understand how occurrence in terrestrial habitats drives higher diversification rates, and how aquatic habitats lower diversification rates. Various hypotheses have been proposed to explain why marine habitats have lower diversification rates, such as more limited barriers to dispersal in marine habitats [5–7]. Interestingly, this explanation may not apply to freshwater habitats, which may instead promote geographical isolation. One possibility is that both marine and freshwater habitats lower diversification rates of aquatic clades by increasing their net extinction rates. Indeed, many of the species-poor, aquatic clades of vertebrates have extensive fossil records and appear to have had much higher diversity in the past (for example, crocodilians, coelacanth and lungfish; [1]). Addressing this topic quantitatively could be an intriguing area for further study.

In summary, the results here show that a simple ecological variable (habitat) explains much of the variation in diversification rates and species richness among major vertebrate clades. This variable has been largely ignored in explaining patterns of vertebrate diversity and may be relevant to many other major groups (e.g. plants, arthropods and molluscs). The results also raise the possibility that local-scale habitats may be more important than large-scale climates in explaining patterns of clade diversification and richness.

Data accessibility. All data are accessible in the electronic supplementary material.

Author contributions. J.J.W. designed the study, performed the analyses and wrote the paper.

Competing interests. The author declares no competing interests.

Funding. I received no specific funding for this study.

Acknowledgements. I thank E. Park for assistance compiling richness data and two reviewers for helpful comments.

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Appendix S1. Detailed methods.

The relationships and ages of most major clades were based on those estimated by Alfaro *et al.* [4]. These relationships and ages are extremely similar to those estimated using phylogenomic data and species-tree methods [9]. These trees differ primarily in that the tree of Alfaro *et al.* [4] includes several major clades not included by Chiari *et al.* [9], including Actinistia, Actinopterygia, and Chondrichthyes. The tree of Alfaro *et al.* [4] includes almost all major vertebrate clades, except for Mixiniformes and Petromyzontiformes (also excluded by Chiari *et al.* [9]). These were treated as sister taxa, following Blair & Hedges [16], Kuraku & Kuratani [17], Near (combined Bayesian analyses including all taxa and characters, his Fig. 6B [18]), and Heimberg *et al.* [19]. The placement of these taxa has been controversial in the prior literature, however [18, 19].

Cyclostomes were manually added to the tree added using two different sets of dates. First, the age of the cyclostome root (and the stem-group ages of Myxiniformes and Petromyzontiformes; 430 Ma) was taken from Kuraku & Kuratani [17] and the crown-group age of Vertebrata was taken from Erwin *et al.* ([15]; from their Fig. 1). Second, the vertebrate crown-group age and the stem-group ages for Mixiniformes and Petromyzontiformes were taken from Blair & Hedges [16]. The two trees used are shown in nexus format in electronic supplementary material, appendix S2 and S3.

The number of species in each clade and the proportion of aquatic species were estimated from literature sources and from reliable, updated internet databases. All clades of traditionally recognized fish were considered to be aquatic (Actinopterygia [ray-finned fish], Actinistia [coelacanths], Chondrichthyes [sharks and rays], Dipnoi [lungfish], Myxiniformes [hagfish], Petromyzontiformes [lampreys], following [1]), and their species richness was estimated based on Roskov et al. [20], which incorporates estimates from FishBase [21]. Approximately 70% of amphibian species were considered freshwater (minimally living in water as larvae) and 30% were considered fully terrestrial [22], with a total of 7,389 species [23]. Mammals include 139 marine species [24] and 124 freshwater species [25]. Subtracting these numbers from the 5,560 total mammal species [20], yields 5,297 terrestrial mammal species. The estimate of total mammalian richness (5,560 species; [20]) is similar to other recent estimates (5,513; [26]). There are 96 marine lepidosaurus, including 1 lizard and 95 snakes [24], along with 73 freshwater lizard species, and 153 freshwater snake species [27, 28]. The remaining lepidosaurs were considered to be terrestrial, from a total number of 9,672 [29]. There are 9 marine turtle species [20], and 250 freshwater species [30]. The remaining turtle species (from a total of 341 [29]) were considered to be terrestrial. There are 2 marine crocodilian species and 23 freshwater species [31], with a total of 25 [29]. There are estimated to be 645 marine bird species [24] and 560 freshwater species [32], with a total of 10,306 bird species [20]. Other bird species were considered terrestrial. This estimate of total bird richness is similar to other recent estimates (10,425; [26]). It should be noted that the number of freshwater species in some clades may be somewhat underestimated (given that most estimates of the number of freshwater species are from 2008). However, this should have minimal impact on the final results, since most of the relevant clades have very small proportions of aquatic species.

Rates of net diversification were estimated using the method-of-moments estimator for stem ages [10]. Stem ages were used to incorporate the entire history of the clade, and not merely the age of the clade of surviving species (e.g. a clade of 20 living species could have a stem-group age of 250 Ma but have a crown-group age of only 2 Ma; using the crown-group age would imply that the clade had diversified rapidly, whereas the stem-group age would correctly indicate a low net rate across the entire history of the group). Three values of the ratio of extinction to speciation were used for estimating diversification rates: a low value (e=0, no extinction), a very high value (e=0.9, following from Magallón & Sanderson [10]), and an intermediate value (e=0.5). Analyses were repeated using all three values, but results were similar across all three.

Estimates of net diversification rates have been criticized because diversification rates can vary over time within clades [33]. Nevertheless, these same estimators remain widely used, even by their critics [34]. Furthemore, the possibility that diversification rates are decoupled from richess patterns by variation in rates over time can be addressed by testing for a strong relationship between species richness and diversification rates among clades [8].

Several other approaches for estimating and comparing diversification rates are available [35]. However, most other approaches would require extensive, time-calibrated species-level phylogenies within each clade [35], which are entirely lacking for some of these 12 clades and highly variable in their completeness among the others. In addition, the approach used here is especially useful for estimating and comparing diversification rates among higher taxa [8] and for addressing how much variation in these rates can be explained by a given ecological variable.

The relationship between the proportion of aquatic species in each clade and the diversification rate of clades was tested using phylogenetic generalized least squares

(PGLS: [11]), using both phylogenies. PGLS was implemented in the R package caper [36], version 0.5.2. Branch lengths were transformed based on the maximum likelihood value of lambda [37] estimated for the data for each analysis. Values of kappa and delta were fixed at 1. Diversification rates were multiplied by 1,000 to ensure non-negative values of the AIC (Akaike Information Criterion): this otherwise has no impact on the results. In a few cases, the phylogenetic optimization of the PGLS failed. In these cases, the analysis was repeated using ordinary least-squares (OLS) regression in R. Results from OLS were very similar to those from PGLS.

As an ancillary analysis, the relationship between the proportion of marine species and diversification was also tested. The number of marine species in most clades was estimated from the WoRMS database [24], as described above. Among the aquatic clades not discussed above, Mixiniformes and Actinistia were all considered marine [21]. Dipnoans were all considered to occur in freshwater [1, 21]. Following Carrete-Vega & Wiens [38], species whose habitats included freshwater were considered to be freshwater. The number of freshwater chondrichthyans (including species that occur in both fresh and brackish waters) was estimated from Leveque *et al.* [39]. Thus, there were estimated to be 132 freshwater chondrichthyans (25 strictly freshwater), for a total of 11% freshwater species. Following Carrete-Vega and Wiens [38], 49% of actinopterygian fish were considered to be freshwater (or partially freshwater). By this criterion, all lampreys were also considered to be freshwater (based on habitat descriptions in FishBase [21]).

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Appendix S2. Tree with root age for vertebrates following Erwin *et al.* [15].

((Petromyzontiformes:430.000000,Myxiniformes:430.000000):71.189200,(Chondrichthyes:465.795764,(((Amphibia:350.668262,((Lepidosauria:270.295370,(Testudines:259.728688,(Aves:249.059465,Crocodylia:249.059465):10.669223):10.566682):50.039961,Mammalia:320.335331):30.332930):57.946272,(Dipnoi:299.831518,Actinistia:299.831518):108.783016):19.230139,Actinopterygia:427.844672):37.951091):35.393400):0;

Appendix S3. Tree with root age for vertebrates following Blair & Hedges [16].

((Petromyzontiformes:520.000000,Myxiniformes:520.000000):132.000000,(Chondrichthyes:465.795764,(((Amphibia:350.668262,((Lepidosauria:270.295370,(Testudines:259.728688,(Aves:249.059465,Crocodylia:249.059465):10.669223):10.566682):50.039961,Mammalia:320.335331):30.332930):57.946272,(Dipnoi:299.831518,Actinistia:299.831518):108.783016):19.230139,Actinopterygia:427.844672):37.951091):186.204200):0;

Table S1. Data for 12 major clades of vertebrates, including numbers of described, extant species, stem-group ages (in millions of years ago), proportions of terrestrial and marine species (note: remaining species are freshwater), and estimated diversification rates under three relative extinction fractions (e=0, 0.5, and 0.9). For Petromyzontiformes and Mixiniformes, two sets of dates were used (Erwin *et al.* [15]/Blair & Hedges [16]), and two sets of diversification rates were estimated.

Clade	Species richness	Stem-group age	Prop. terrestrial	Prop. marine
Petromyzontiformes	47	430/520	0.000	0.00
Mixiniformes	78	430/520	0.000	1.00
Chondrichthyes	1204	465.796	0.000	0.89
Amphibia	7389	350.668	0.300	0.00
Lepidosauria	9672	270.295	0.967	0.01
Testudines	341	259.729	0.240	0.03
Aves	10306	249.060	0.883	0.06
Crocodylia	25	249.060	0.000	0.08
Mammalia	5560	320.335	0.953	0.02
Dipnoi	6	299.832	0.000	0.00
Actinistia	2	299.832	0.000	1.00
Actinopterygia	31483	427.885	0.000	0.49

Clade	Div. rate (e=0)	Div. rate (e=0.5)	Div. rate (e=0.9)
Petromyzontiformes	0.00895383/ 0.00740413	0.00739082/ 0.00611164	0.00400643/ 0.00331301
Mixiniformes	0.01013188/ 0.00837829	0.00854954/ 0.00706981	0.00503098/ 0.00416024
Chondrichthyes	0.01522857	0.01374226	0.01030122
Amphibia	0.02540220	0.02342594	0.01883940
Lepidosauria	0.03395171	0.03138768	0.02543638
Testudines	0.02245375	0.01979629	0.01368870
Aves	0.03710150	0.03431883	0.02785989
Crocodylia	0.01292412	0.01029854	0.00491359
Mammalia	0.02691977	0.02475652	0.01973677
Dipnoi	0.00597589	0.00417822	0.00135231
Actinistia	0.00231179	0.00135231	0.00031788
Actinopterygia	0.02420559	0.02258573	0.01882494

Table S2. Relationships between endothermy and net diversification rates (estimated under three relative extinction fractions, e=0, 0.5, and 0.9) for two alternative root ages for vertebrates and cyclostomes [15, 16]. * = optimization for PGLS analysis failed, and OLS regression was used instead.

Variables	r^2	P	AIC
Erwin *et al.* tree			
Div. rate (e=0) ~ endothermy	0.2677	0.0846	83.7217
Div. rate (e=0.5) ~ endothermy	0.2707	0.0822	83.1027
*Div. rate (e=0.9) ~ endothermy	0.3049	0.0627	88.7671
Div. rate (e=0) ~ endo. + prop. terr.	0.6616	0.0092	77.3672
Div. rate (e=0.5) ~ endo. + prop. terr.	0.6637	0.0089	76.7894
*Div. rate (e=0.9) ~ endo. + prop. terr.	0.6729	0.006	81.7224

Blair & Hedges tree	r^2	P	AIC
Div. rate (e=0) ~ endothermy	0.2075	0.1856	77.0245
Div. rate (e=0.5) ~ endothermy	0.2080	0.1848	76.2816
Div. rate (e=0.9) ~ endothermy	0.2134	0.1766	73.7336
Div. rate (e=0) ~ endo. + prop. terr.	0.6559	0.0184	72.2206
Div. rate (e=0.5) ~ endo. + prop. terr.	0.6483	0.0200	71.5699
Div. rate (e=0.9) ~ endo. + prop. terr.	0.6351	0.0230	69.0448

Table S3. Relationships between net diversification rates (estimated under three relative extinction fractions, e=0, 0.5, and 0.9) and the proportion of marine species in each clade, for two alternative root ages for vertebrates and cyclostomes [15, 16]. * = optimization for PGLS analysis failed, and ordinary least squares regression was used instead.

Variables	r^2	*P*	AIC
Erwin *et al.* tree			
*Div. rate (e=0) ~ proportion marine	0.1744	0.2049	85.5219
Div. rate (e=0.5) ~ proportion marine	0.1554	0.2441	84.9817
Div. rate (e=0.9) ~ proportion marine	0.1109	0.3670	82.8391

Blair & Hedges tree	r^2	*P*	AIC
Div. rate (e=0) ~ proportion marine	0.1396	0.3250	77.8466
Div. rate (e=0.5) ~ proportion marine	0.1240	0.3689	77.2893
Div. rate (e=0.9) ~ proportion marine	0.0882	0.4927	75.2104

Table S4. Relationships between net diversification rates (estimated under three relative extinction fractions, e=0, 0.5, and 0.9, and using both trees) and the proportion of terrestrial species in each clade, after assigning 70% of amphibian species to be terrestrial rather than aquatic (initial analyses assumed that 70% of amphibian species are aquatic).

Variables	r^2	P	AIC
Erwin *et al.* tree			
Div. rate (e=0) ~ proportion terr.	0.6916	0.0005	74.3444
Div. rate (e=0.5) ~ proportion terr.	0.6968	0.0004	73.6473
Div. rate (e=0.9) ~ proportion terr.	0.7101	0.0003	71.2079

Blair & Hedges tree	r^2	P	AIC
Div. rate (e=0) ~ proportion terr.	0.6790	0.0013	69.5249
Div. rate (e=0.5) ~ proportion terr.	0.6744	0.0014	68.7977
Div. rate (e=0.9) ~ proportion terr.	0.6676	0.0016	66.1100