LETTER

Extinction and time help drive the marine-terrestrial biodiversity gradient: is the ocean a deathtrap?

Elizabeth C. Miller* and
John J. Wiens

*Department of Ecology and
Evolutionary Biology, University of
Arizona, Tucson, AZ 85721–0088,
USA*

*Correspondence: E-mail:
ecmiller@email.arizona.edu*

Abstract

The marine-terrestrial richness gradient is among Earth's most dramatic biodiversity patterns, but its causes remain poorly understood. Here, we analyse detailed phylogenies of amniote clades, paleontological data and simulations to reveal the mechanisms underlying low marine richness, emphasising speciation, extinction and colonisation. We show that differences in diversification rates (speciation minus extinction) between habitats are often weak and inconsistent with observed richness patterns. Instead, the richness gradient is explained by limited time for speciation in marine habitats, since all extant marine clades are relatively young. Paleontological data show that older marine invasions have consistently ended in extinction. Simulations show that marine extinctions help drive the pattern of young, depauperate marine clades. This role for extinction is not discernible from molecular phylogenies alone, and not predicted by most previously hypothesised explanations for this gradient. Our results have important implications for the marine-terrestrial biodiversity gradient, and studies of biodiversity gradients in general.

INTRODUCTION

The greater richness on land relative to the ocean is among the most dramatic global species richness patterns (~ 85% vs. ~ 15% of macroscopic species; May 1994; Grosberg *et al.* 2012). This pattern is surprising because life originated in the ocean (Kenrick *et al.* 2012). The ocean also covers ~ 70% of Earth's surface (May 1994). Thus, the ocean should have higher richness based on both greater time and area. Several hypotheses have been proposed to explain higher richness on land, including greater primary productivity, habitat heterogeneity and opportunities for genetic isolation (e.g. Vermeij & Dudley 2000; Benton 2001; Grosberg *et al.* 2012). All factors must ultimately influence speciation, extinction, or the timing or frequency of dispersal between habitats, as these are the only mechanisms that directly change species richness of habitats (Ricklefs 1987).

The hypothesis that diversification rates (speciation minus extinction rates) differ between marine and terrestrial taxa was previously discussed in the paleontological literature (Benton 2001) but is rarely tested in a phylogenetic context. Recently, Wiens (2015) found support for higher net diversification rates in animal phyla with lower proportions of marine taxa. However, no study has attempted to disentangle the roles of speciation, extinction and colonisation patterns in producing greater species richness in terrestrial relative to marine environments. Most existing hypotheses imply reduced speciation in the ocean rather than greater extinction.

Amniote vertebrates (including mammals, birds, crocodilians, turtles and lepidosaurs [lizards and snakes]) are an excellent system for testing the mechanisms underlying the marine-terrestrial diversity gradient. First, the gradient occurs within each of these five major groups (1–4% marine; Boxshall *et al.* 2016). Second, amniotes have re-invaded the ocean many times since their origin 300–350 million years ago (Vermeij & Dudley 2000; Kelley & Pyenson 2015), and therefore have potential for high marine richness based on colonisation times alone (all else being equal). Third, relatively complete time-calibrated molecular phylogenies are available for all groups, facilitating analyses of diversification and colonisation. Fourth, amniotes have a well-documented fossil record in both marine and terrestrial environments (Benton 2001).

Here, we integrate molecular phylogenies, palaeontology and simulations to examine the mechanisms underlying the marine-terrestrial richness gradient in amniotes. We first test if extant marine lineages have lower diversification rates than non-marine lineages, and if differences are explained by speciation and/or extinction rates. We then use ancestral reconstructions to test if limited time in marine habitats can explain low marine richness. Finally, we integrate paleontological data and simulations to reveal the effects of extinction and time on marine richness. Our results have important implications for the marine-terrestrial richness gradient, and for biodiversity gradients in general.

MATERIALS AND METHODS

Phylogenies and habitat data

We obtained time-calibrated molecular phylogenies for mammals (5020 species sampled, including 94% of described species; Rolland *et al.* 2014), birds (6670, 67%; Jetz *et al.* 2012), lepidosaurs (4162, 42%; Zheng & Wiens 2016) and turtles (215, 61%; Jaffe *et al.* 2011; Table S1). To facilitate analyses,

we treated habitat as a binary character throughout the text. Species were coded as 'marine' if they were obligately dependent on marine environments. Species in other habitats (including terrestrial, freshwater and brackish environments) were coded as non-marine (Boxshall *et al.* 2016; see Appendix S1).

Net diversification rates

We first tested if clades with higher proportions of marine species have lower net diversification rates. We used the method-of-moments estimator for net diversification rates (Magallón & Sanderson 2001), following Wiens (2015). Simulations show this estimator can be relatively accurate, and does not require a positive relationship between clade age and richness (Kozak & Wiens 2016). Furthermore, net diversification rates can strongly predict richness among habitats even under diversity dependence (Pontarp & Wiens 2017).

We estimated net diversification rates of monophyletic families of mammals, birds and turtles. For lepidosaurs, we used genera of Elapidae, which contains 97% of marine lepidosaur species. The method-of-moments estimator requires clade ages, extant richness and an assumed relative extinction fraction ($\varepsilon = \mu/\lambda$, where λ = speciation rate and μ = extinction rate). We used standard alternative ε values of 0, 0.5 and 0.9. We used crown and stem ages from the phylogenies above. Extant species richness was obtained from Uetz & Hosek (2015; lepidosaurs, turtles), Wilson & Reeder (2005; mammals) and Jetz *et al.* (2012; birds).

We tested relationships between the net diversification rate of each clade and its proportion of marine species using phylogenetic generalised least squares regression (PGLS; Martins & Hansen 1997). We conducted separate analyses for turtles, mammals, birds and elapid snakes. For each clade, marine richness was estimated using the WoRMS database (Boxshall *et al.* 2016). Phylogenies were trimmed to one species per clade. PGLS analyses were conducted in the R package *caper*

version 0.5.2 (Orme 2013), with lambda estimated and kappa and delta set to one.

State-dependent speciation and extinction

To test the impact of habitat on speciation and extinction rates in the four amniote groups, we used the HiSSE approach in the package *hisse* version 1.8 (Hidden State Speciation and Extinction; Beaulieu & O'Meara 2016). HiSSE allows for the possibility that there are unmeasured states that impact diversification, partially overlapping with the observed states (here, marine and non-marine habitat).

HiSSE optimises species turnover ($\tau = \lambda + \mu$) and the extinction fraction ($\varepsilon = \mu/\lambda$) for states 1A, 1B, 0A and 0B, where 1 and 0 represent habitat and A and B, the hidden states. We tested three null models: (1) 'Null-Two' and (2) 'Null-Four', which assume all diversification rate differences among taxa are associated with the hidden states (not habitat), and (3) BiSSE-equivalent (Maddison *et al.* 2007), in which all differences are due to habitat, without measuring hidden states (see Appendix S2). We then fit four alternative HiSSE models: (4) a full HiSSE model, with ε and τ freely varying among the four states, (5) full model with τ constrained to be equal between habitats, (6) ε constrained, and (7) equal transition rates between habitats. We corrected for incomplete phylogenetic sampling using described richness for marine and non-marine habitats (references above; Table S1). The model with the lowest AIC was preferred and considered strongly supported given ΔAIC $\geq$ 4 from the next value (Burnham & Anderson 2002). We transformed τ and ε estimates to speciation and extinction rates (Table 1).

Simulations show that BiSSE-related methods can give problematic results when one state occurs in <10% of sampled species (Davis *et al.* 2013). Since marine species are rare in amniotes (1–4%), we also fit HiSSE models on clades chosen such that the proportion of marine species was >10% while maximising the total included species (maximising power).

Table 1 Results showing phylogenetic signal in habitat (D statistic) and HiSSE analyses of diversification rate differences between marine and non-marine lineages

Clade	D	HiSSE Best Model	AIC	Akaike weight	$r_{\text{marine-A}}$	$r_{\text{marine-B}}$	$r_{\text{nonmarine-A}}$	$r_{\text{nonmarine-B}}$
Mammals								
Trimmed	−0.48	*$\varepsilon_{\text{marine}} = \varepsilon_{\text{nonmarine}}$	4109.21	0.59	0.867	0.048	0.344	0.052
Whole	−0.51	$\varepsilon_{\text{marine}} = \varepsilon_{\text{nonmarine}}$	30 847.58	0.48	0.107	0.011	0.316	0.061
Birds								
Trimmed 1	−0.70	Full HiSSE	4932.21	0.93	0.035	0.070	0.039	0.147
Trimmed 2	0.24	*$\tau_{\text{marine}} = \tau_{\text{nonmarine}}$	2087.50	0.53	1.147	0.067	−0.486	0.057
Whole	−0.41	$\varepsilon_{\text{marine}} = \varepsilon_{\text{nonmarine}}$	42 785.86	1.00	0.606	0.080	0.274	0.050
Lepidosaurs								
Trimmed	−1.27	$\varepsilon_{\text{marine}} = \varepsilon_{\text{nonmarine}}$	2109.98	0.88	0.580	0.086	0.022	0.130
Whole	−0.94	*$\varepsilon_{\text{marine}} = \varepsilon_{\text{nonmarine}}$	32 927.49	0.70	0.100	0.658	0.151	0.031
Turtles	−1.41	Null-Four	1798.53	0.97	0.135 (A)	0.021 (B)	0.056 (C)	−0.0003 (D)

*=ΔAIC between best model and null model ≤ 4.
Values of D < 1 indicate high phylogenetic signal due to few observed sister-clade differences (Methods). We compared the fit of HiSSE models with asymmetrical parameters between habitats to alternative models that constrained these parameters to be equal. HiSSE optimises turnover ($\tau = \lambda + \mu$) and the extinction fraction ($\varepsilon = \mu/\lambda$), with results transformed to speciation (λ) and extinction (μ) here. Net diversification rate (r) is equal to $\lambda - \mu$. Hidden states in HiSSE are denoted by A and B. For turtles, Null-Four was selected, and hidden states A–D are identical between habitats (Appendix S2). Full results are in Tables S3, S4 and S7, including transition rate estimates between habitats and hidden states.

Four clades met these criteria (hereafter 'trimmed' trees; see Appendix S1): (1) mammalian clade within Laurasiatheria containing carnivores and ungulates (618 species, 19% marine); (2) bird clade containing penguins, petrels and related orders (636 species, 24% marine); (3) the bird order Charadriiformes (278 species, 35% marine); (4) lepidosaur clade containing elapid snakes (280 species, 11% marine). Turtles were not reduced because BiSSE has low power with <200 species (Davis *et al*. 2013).

The trimmed trees have the added benefit of comparing marine colonisations with their closest non-marine relatives. For example, higher non-marine rates might be observed because a few non-marine clades have exceptionally high diversification rates, not because invading marine habitats *per se* reduces diversification (Maddison & FitzJohn 2014).

Frequency and timing of colonisation

Instead of differences in diversification rates, marine richness might be lower because amniotes colonised marine habitats more recently (time-for-speciation effect; Stephens & Wiens 2003). We compared the age of each phylogenetically independent transition (to either non-marine or marine habitats) with its present-day richness.

To identify independent marine colonisations and their ages, we performed ancestral reconstructions of habitat on the whole phylogeny of each group using maximum likelihood with the 'ace' function in *ape* version 3.4 (Paradis *et al*. 2004). We assumed a single transition rate between habitats. We did not perform reconstructions using HiSSE, nor models with asymmetrical transition rates, because these models produced highly problematic reconstructions (i.e. reconstructing the ancestor of all mammals as marine). This may be due to complications with rare states (Davis *et al*. 2013). We identified marine invasions by the oldest node with a proportional likelihood ≥0.95 for the marine state. This yielded reconstructions corresponding to known marine clades (Table S5). An exception was the ancestor of hippopotamuses and cetaceans ('whippomorpha'), which was reconstructed as marine. We instead used crown cetaceans.

We identified crown and stem ages of each independent marine colonisation and determined their richness in marine habitats (excluding secondarily non-marine members). Importantly, the stem and crown ages should encompass much of the uncertainty surrounding the timing of marine transitions. Monotypic colonisations do not have a crown age, so we performed analyses either excluding them or assuming habitat transitions occurred mid-branch (stem/2). Deviations from this assumption are unlikely to affect our conclusions, because monotypic invasions are relatively young, reducing the range of possible ages.

To compare the amount of time amniotes have diversified in each habitat, we also identified independent non-marine colonisations. All amniotes are ultimately descended from a single invasion of land. We used Amniota as a single non-marine transition with crown and stem ages of 330 and 350 Ma (Chiari *et al*. 2012). We estimated richness in non-marine habitats derived from this initial colonisation, including crocodilians (25 species; Uetz & Hosek 2015).

Additionally, we identified secondarily non-marine colonisations (nested within marine clades) and their richness, crown age and stem age as described above.

We tested for the time-for-speciation effect on marine and non-marine richness by fitting standard and PGLS regressions relating ages of habitat transitions to their present-day richness. We performed separate analyses using crown and stem ages, and among marine clades only. We log10-transformed richness but not age (following Hutter *et al*. 2013).

We used ages from molecular phylogenies because most living marine clades lack fossil records. Ages from fossil data for some clades (i.e. cetaceans) are younger than those used here (Donoghue & Benton 2007). Younger ages would further support our conclusions, by reducing the time-for-speciation in marine habitats.

Niche conservatism

Niche conservatism is crucial for the time-for-speciation effect by reducing successful transitions between habitats that would otherwise homogenise richness over time (Wiens *et al*. 2010; Hutter *et al*. 2013). Given niche conservatism, closely related species will share similar trait values, as indicated by phylogenetic signal (Wiens *et al*. 2010). We tested phylogenetic signal in habitat for each group using the D statistic (Fritz & Purvis 2010) with *caper*. D is $[\Sigma d_{obs} - \text{mean}(\Sigma d_b)]/[\text{mean}(\Sigma d_r) - \text{mean}(\Sigma d_b)]$, where Σd_{obs} is the observed count of sister clades differing in a binary trait, Σd_b is that under a simulated Brownian motion threshold model (high signal) and Σd_r is that under phylogenetic randomness (no signal). Means represent 1000 simulations of trait data on each tree. Values of $D < 1$ indicate high phylogenetic signal because there are few observed sister-clade differences (Table S7).

Extinct marine colonisations

Many extinct marine invasions are known only from the fossil record and may not be detectable from molecular phylogenies (Kelley & Pyenson 2015). We collected data on the temporal durations of extinct marine clades, and tested if living marine clades significantly overlap in time with extinct marine clades. A lack of overlap suggests frequent marine extinction, because older clades are less likely to persist (Bromham *et al*. 2016).

We searched the paleontological literature for independent marine colonisations within crown Amniota, confirmed using published phylogenies. For each extinct invasion, we determined the clade's first and last appearance using occurrence data from the Paleobiology Database (2016) (http://paleobiodb.org; see Appendix S3).

For comparison to living marine invasions, we used both crown and stem ages of extant marine clades determined from phylogenies (above). Again, these ages may be older than those suggested by fossil data. However, younger clade ages reduce the observed overlap with extinct clades. Therefore, clade ages from molecular phylogenies are conservative for our purposes.

We performed two-sample Welch's *t*-tests comparing the mean ages of origination and extinction with the mean stem and crown ages of living marine clades. This provides four

possible measures of temporal overlap. We performed alternative analyses: (1) including all clades, (2) removing 33 extant single-species colonisations (relatively young), (3) removing six colonisations that went extinct before the Cretaceous (relatively old), and (4) removing both categories 2 and 3. We log10-transformed ages to improve normality.

Simulations of marine extinction

We performed two sets of simulations informed by observations in the fossil record (above) to test if extinction or alternative factors can explain the young age of extant marine colonisations. First, we considered three factors that may explain why a given state will have young origins: increased extinction rate, increased lability (both gains and losses) and increased losses relative to gains (Bromham *et al.* 2016). We simulated trees with a binary trait under a BiSSE model, constraining the root as non-marine, using the package *diversitree* version 0.9–7 (FitzJohn 2012; see Appendix S4). Trees were constrained to contain 10 000 species and be over ≥ 105 Ma. We first considered a null model with speciation, extinction and transition rates identical between habitats. Starting values for the null were the mean speciation, extinction and transition rates across mammals, birds and lepidosaurs, estimated from BiSSE models assuming no state-dependent differences (Table S10). From this empirical value of ε (μ/λ; ~0.23), we increased ε of the marine state to 0.5 and 0.9. We simulated 12 sets of 50 trees each: three with each alternative ε value (null, 0.5, 0.9) and a single transition rate estimated from empirical phylogenies ('Baseline'), these three epsilon values with losses of marine habitat 10 × higher than gains ('High reverse'), three with a single transition rate set 3 × higher than the empirical rate ('Labile') and three with marine gains 3 × higher and losses 10 × higher ('Labile and high reverse').

For each simulated tree, we performed ancestral reconstructions to identify independent marine colonisations (see above). We performed ANOVA and Tukey post hoc pairwise comparisons to test for significant differences in means among the 12 models in total marine richness, number of marine colonisations and relative age of marine colonisations (crown age of marine clade divided by age of the whole tree, to accommodate differing ages of trees). We log10-transformed data to improve normality.

The second set of simulations tested if the observed pattern of non-overlapping geological durations of extinct and extant marine clades can be explained by high marine extinction rates or infrequent marine colonisation (causing a lag until recolonisation after an extinction event). We simulated trees as above but retaining extinct clades, under 12 models: 'Baseline' with the null gain/loss rate and marine ε = null, 0.5, 0.9 and 0.99 ('null' as above; Table S10), 'Labile' with a single transition rate 10 × higher with alternative ε values (above), and 'Very Labile' with this rate 20 × higher and alternative ε values (above).

Next, for each simulated tree, we determined the age of extinct and extant marine colonisations (defined as the oldest node with a proportional likelihood ≥ 0.95 for the marine state) and the time of extinction for extinct marine clades.

Due to low sample sizes of extinct marine clades, we simulated 150 trees under each model, and pooled data for three trees prior to age comparison (akin to combining multiple amniote groups as described above for durations). Ages were log10-transformed. We performed two *t*-tests comparing either ages of extinct and extant clades or comparing the time of extinction with ages of extant marine clades. We performed tests on 50 sets of three trees each.

We caution against literal comparison of metrics between empirical and simulated data. Empirical phylogenies will differ from phylogenies simulated under simple models, especially when trees are large (Pennell *et al.* 2012). Birds, mammals and lepidosaurs include clades with many different diversification rates (Database S2). Rather than attempting to simulate clades exactly matching empirical ones (impossible given only two sets of rates across all trees), we instead use simulations to understand the general roles that extinction and transition rates may play in generating the observed patterns.

RESULTS

Diversification rate differences

We found little support for the hypothesis that differences in diversification rates between extant marine and non-marine clades explain the marine-terrestrial richness gradient in amniotes. The proportion of marine species per clade did not have a significant effect on net diversification rates for any group, except for marine elapids having higher diversification rates using crown ages ($r^2 = 0.20$, $P = 0.04$; Fig. S1; Table S2; Database S2). Non-marine clades had a wide range of diversification rates. In mammals and turtles, marine clades had low or intermediate diversification rates. However, in elapid snakes and birds, marine clades had among the highest rates.

HiSSE analyses also showed little support for higher non-marine diversification rates (Fig 1). BiSSE-equivalent models and models assuming equal transition rates had poor fit in all clades (Table S3). Mammals (whole tree) and trimmed bird clade 1 were the only groups with higher non-marine diversification rates. In the trimmed mammal clade, trimmed bird clade 2, lepidosaurs (whole tree) and turtles, the null HiSSE models could not be rejected with ΔAIC ≤ 4 (diversification rate differences driven by hidden states, not habitat). In the whole bird tree and trimmed lepidosaur clade, marine clades had higher net diversification rates. While extinction rate estimates were often near-zero, there was no consistent trend for lower speciation or higher extinction rates in marine clades (Table S4).

Time and relative richness of habitats

Our results suggest that higher non-marine richness is explained by a time-for-speciation effect, with lower extant richness in marine habitats because of recent colonisation, and limited dispersal between habitats due to niche conservatism.

Extant marine colonisations were strikingly young relative to the timeframe amniotes have been evolving on land (Fig. 2). The mean crown age of marine clades was 10.4 Ma
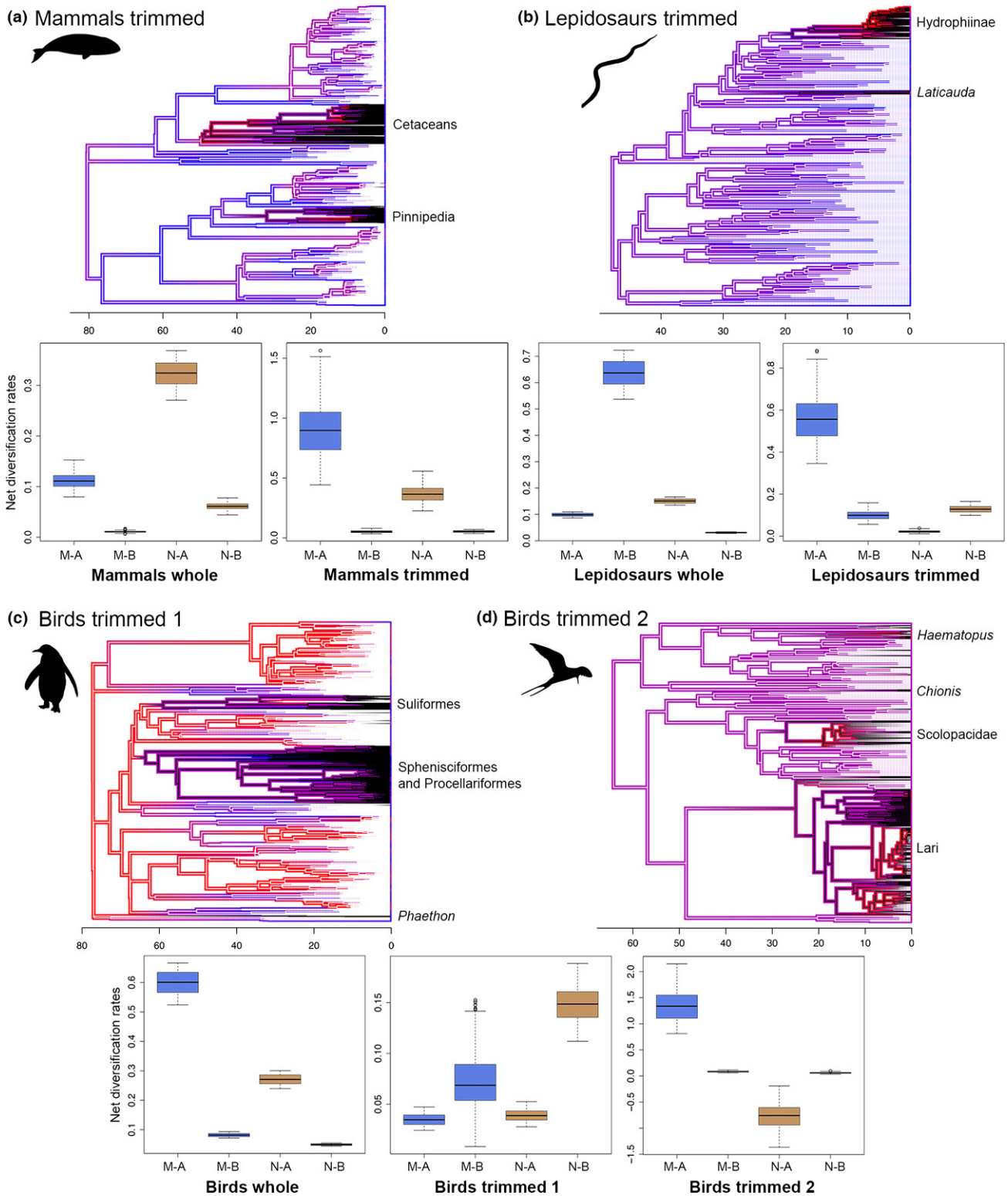
Figure 1 Ancestral state reconstructions of trimmed clades, and boxplots of confidence distributions of net diversification rates among observed states (M = marine, blue, and N = non-marine, brown) and hidden states (A and B). Figures are derived from best-fit HiSSE models (highest Akaike weight). Colours inside branches represent habitat reconstruction (black = marine and white = non-marine). Colours outside of branches represent net diversification rates (warmer = faster relative to all rates across the tree). Scale bars show time in millions of years before present, Ma. Silhouettes are from Phylopic [phylopic.org] (Appendix S5 for credits). Turtles are not pictured because the null model had the best fit. Full results are in Tables 1, S3 and S4. Results show that net diversification rates are generally inconsistent with observed richness differences between marine and non-marine amniotes. Ancestral state reconstructions shown here are for visualisation of diversification rates, and not used to identify marine clades (see Methods).

(0.2–68.5 Ma) vs. 330 Ma for Amniota. We identified 58 living marine colonisations (33 single-species) and 26 secondarily non-marine colonisations (15 single-species). The relationship between colonisation times and present-day richness from each colonisation event was highly significant (crown ages: $P < 0.001$, $r^2 = 0.65$, Fig. 2; stem ages: $P < 0.001$, $r^2 = 0.59$). Alternative analyses among marine clades only and excluding monotypic colonisations were also highly significant (Table S6; Fig. 2; Fig. S2).

Phylogenetic signal in habitat was high across all four groups (negative D; Table 1; Table S7). In addition, HiSSE models estimated low transition rates from non-marine to marine (Table S4). Reverse transition rates were higher in mammals, birds and lepidosaurs, seemingly because freshwater transitions are common within marine clades. Although there were more overall transitions from non-marine to marine, these freshwater transitions were all relatively young, yielding high rates (Table S5).
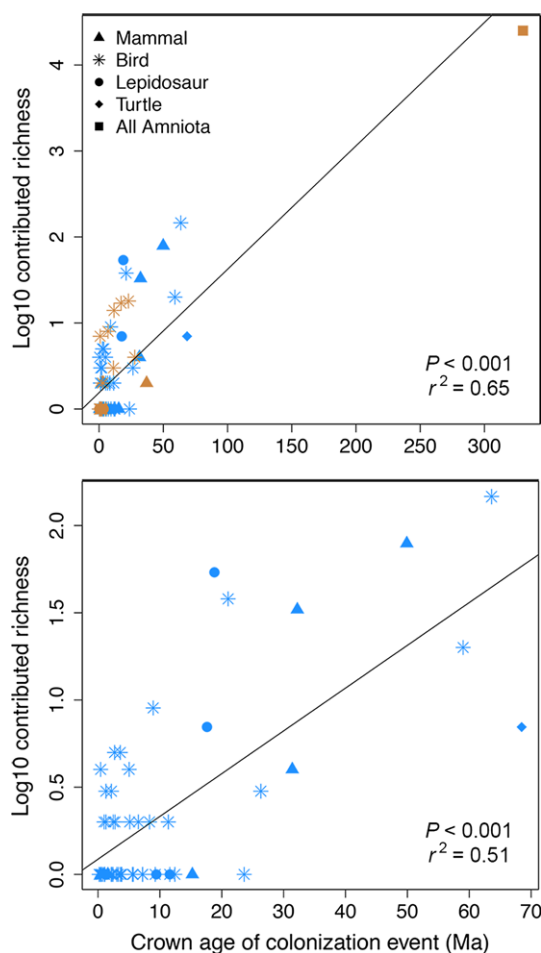

Figure 2 Evidence for the time-for-speciation effect on present-day richness in each habitat: amniotes colonised non-marine habitats (brown) much earlier than living marine clades (blue; top panel), and older marine clades contributed more richness to marine habitats than younger clades (bottom panel). We performed linear regression of ages associated with colonisation events (marine or non-marine) vs. richness contributed by each event. Here, we used crown ages and assumed monotypic clades had a crown age = half the stem age (alternative analyses also significant; Fig. S2; Table S6).

Insights from fossils and simulations

There was little temporal overlap between extinct and extant marine clades, suggesting that extant marine clades are young and replaced older, extinct marine lineages (Fig. 3). We summarised phylogenetic and temporal information for 26 extinct marine colonisations (Table S8). The origin of extinct clades was always significantly older than that of extant clades (crown and stem ages), even when removing exceptionally old or young marine invasions (Table S9). The time of extinction was significantly older than crown ages (mean extinction time = 109 Ma, crown age = 10.4 Ma; $P = 0.0002$) except when both old and young clades were removed, and stem ages when all clades were included (mean stem age = 17.1 Ma; $P = 0.003$).

Simulations showed that high marine extinction rates can explain young extant marine clades, because older marine invasions do not persist. Our first set of simulations (Fig. 4; Table S11) showed that: (1) only increasing marine extinction yielded significantly younger marine colonisations relative to null extinction rates (estimated from phylogenies); (2) increasing transition rates from marine to non-marine did not consistently reduce marine richness or the number or age of marine invasions; and (3) increasing the rate of marine colonisation dramatically increased marine richness by producing more marine clades, but not older marine clades. Similarly, in our second set of simulations, non-overlapping durations of extinct and extant marine clades were driven by high marine extinction rates (Fig. 5). The mean time of extinction deviated significantly from the mean age of extant clades most frequently with $\varepsilon \geq 0.9$.

Two patterns in the simulated data differ somewhat from our empirical data. First, extant marine clades can be much older than those simulated under empirical parameters (Baseline model; Figs 2 and 5). We simulated trees under constant transition rates for each state, which should yield more transitions on recent branches (most branches in a phylogeny are young). However, adaptive radiation theory predicts relatively early transitions in habitat (Schluter 2000), consistent with older marine clades. This discrepancy does not overturn our conclusions, because older marine clades should generate higher marine richness, but instead empirical and simulated marine richness is comparable (Table S1; Table S11). Extinction is known to have reduced richness in older extant marine clades, like cetaceans (Pyenson *et al.* 2014).

Second, significant gaps between durations of extinct and extant clades are more common under high lability, seemingly in conflict with strong phylogenetic signal in habitat in empirical phylogenies (Table 1). Importantly, mean temporal durations deviate when $\varepsilon \geq 0.9$ under all transition scenarios, but standard deviations surrounding extinction times remain wide under Baseline models (Fig. 5). Increasing lability increases the sample size of marine invasions, leading to more frequent detection of significant gaps in duration.

DISCUSSION

The higher species richness of non-marine relative to marine environments is one of the most dramatic patterns in global
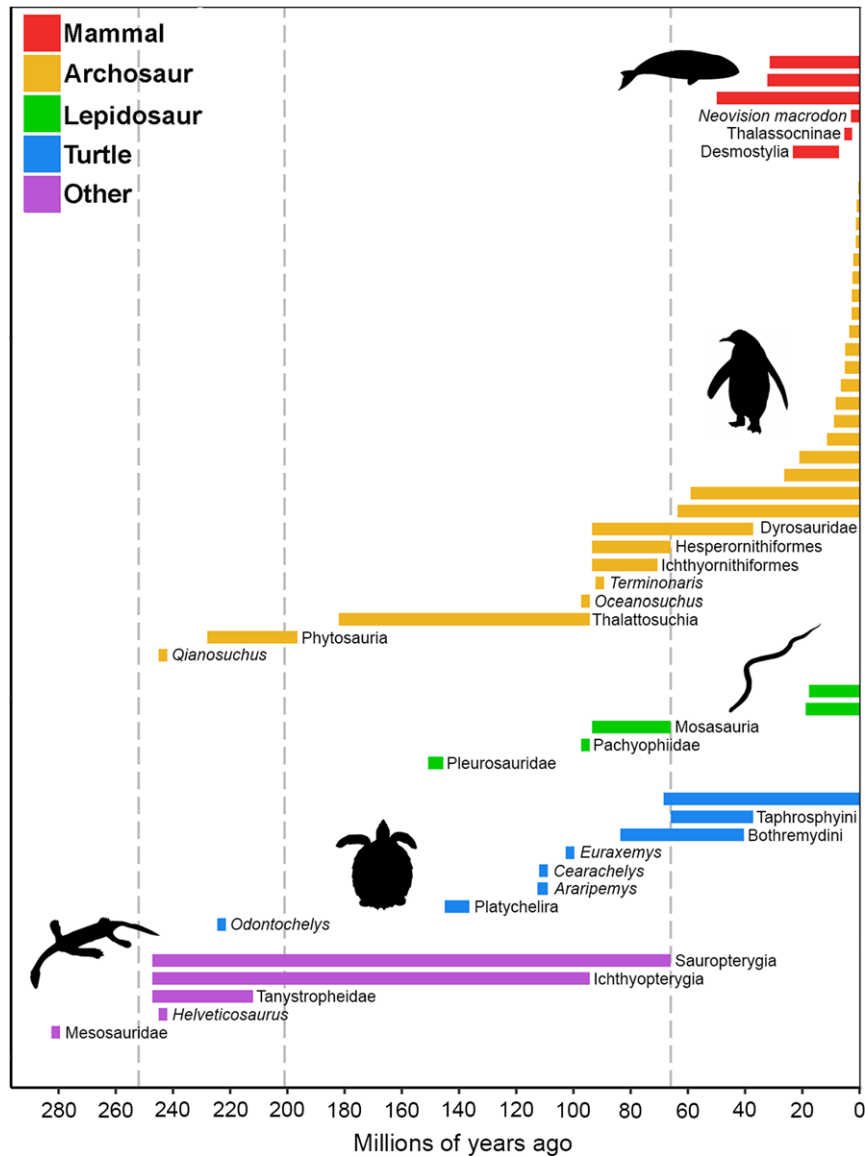
Figure 3 Stratigraphic ranges of 26 extinct clades (with names) vs. extant marine clades. On average, extinct clades originated and went extinct prior to the mean age of extant clades (Table S9). This suggests that extant clades are relatively young, and the oldest marine clades have failed to persist. Extinct clades were identified from published phylogenies (Table S8) and dates obtained from PaleoDB (http://paleobiodb.org). Ages of extant clades were obtained from molecular phylogenies because most extant clades do not have a fossil record (Table S5). These ages are generally older than those estimated from fossils. Extant single-species clades are omitted for clarity. Grey dashed lines indicate mass extinction events: Permian (252 Ma), Late Triassic (201 Ma) and Cretaceous (66 Ma). Extinct clades with an estimated stratigraphic range < 3 Ma were elongated for visibility (+ 3 Ma). See Appendices S3, S5 and Tables S5 and S8 for details of clades, ages and Phylopic silhouette credits.

biodiversity. Recent analyses across animals showed that this pattern is caused by higher diversification rates in terrestrial lineages (Wiens 2015), but the mechanisms underlying this difference were unclear (e.g. speciation vs. extinction, and the factors acting on each). Here, we integrate detailed phylogenies, paleontological data and simulations to gain insights into these mechanisms. Our results are surprising for several reasons. We find no consistent difference in diversification rates between habitats in major amniote clades. Instead, lower marine richness is explained by niche conservatism, limited time-for-speciation in extant marine lineages and extinction of older marine lineages across > 250 million years. Thus, our results suggest that: (1) the time and diversification rate hypotheses can act synergistically to explain richness patterns, especially when there is limited time for speciation to compensate for past extinction events, (2) frequent marine extinction is a major factor contributing to lower marine richness, a hypothesis that is not clearly related to any of the widely discussed ecological mechanisms previously hypothesised to explain the marine-terrestrial richness gradient, and (3) unsuccessful colonisations ending in extinction over long geological time scales can be an important (but underappreciated) component of the time and niche conservatism hypotheses. We discuss these ideas below.
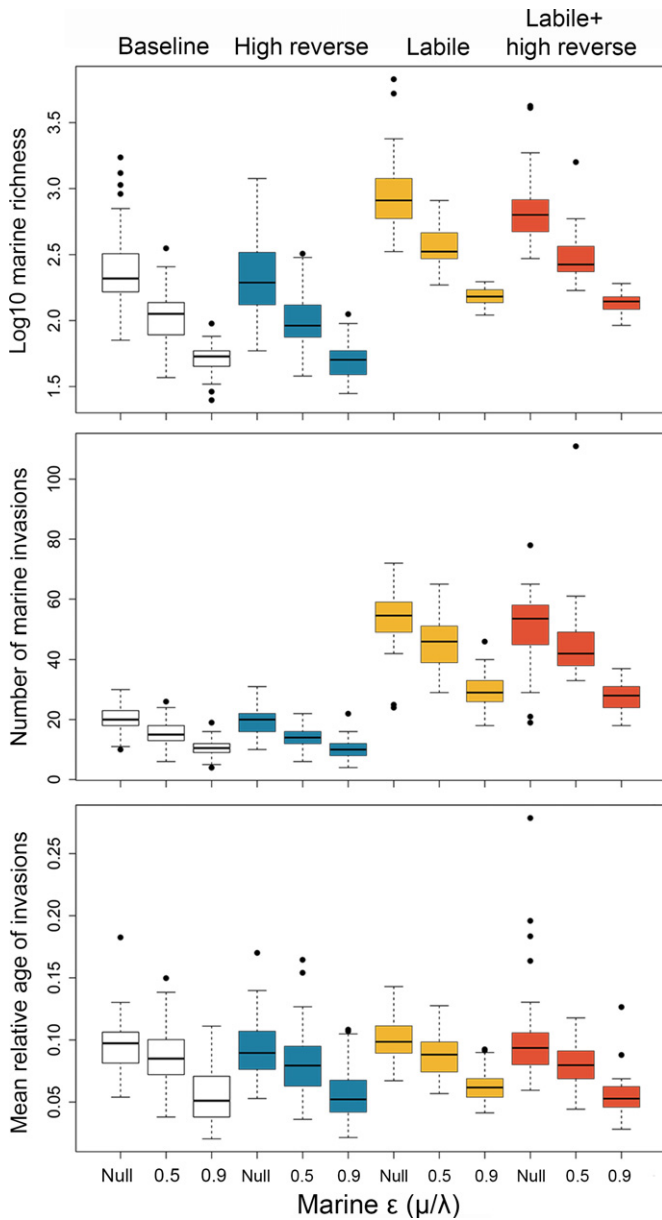
Figure 4 Simulated distributions of marine richness (log10-transformed; top), number of independent marine invasions (middle) and relative age of extant marine clades (bottom). White boxes = 'Baseline' models; blue boxes = 'High reverse' models; yellow boxes = 'Labile' models; and red boxes = 'Labile and high reverse' models (see Methods; Appendix S4; Table S11). The extinction fraction (ratio of extinction to speciation) of the marine state was increased from the null model (rates from empirical phylogenies; Table S10) to 0.5 and 0.9. Boxplots show upper and lower quartiles, medians and outliers. Tukey post hoc pairwise comparisons suggest: (1) increasing marine extinction creates younger extant marine invasions relative to the null; (2) increasing the rate of marine to non-marine transitions does not affect richness, number or age of invasions; and (3) increasing the rate of non-marine to marine transitions increases marine richness and number of invasions, but does not influence the age of invasions.

Extinction and time interact

Our results suggest that higher non-marine species richness in amniotes is driven (in part) by a combination of extinction of
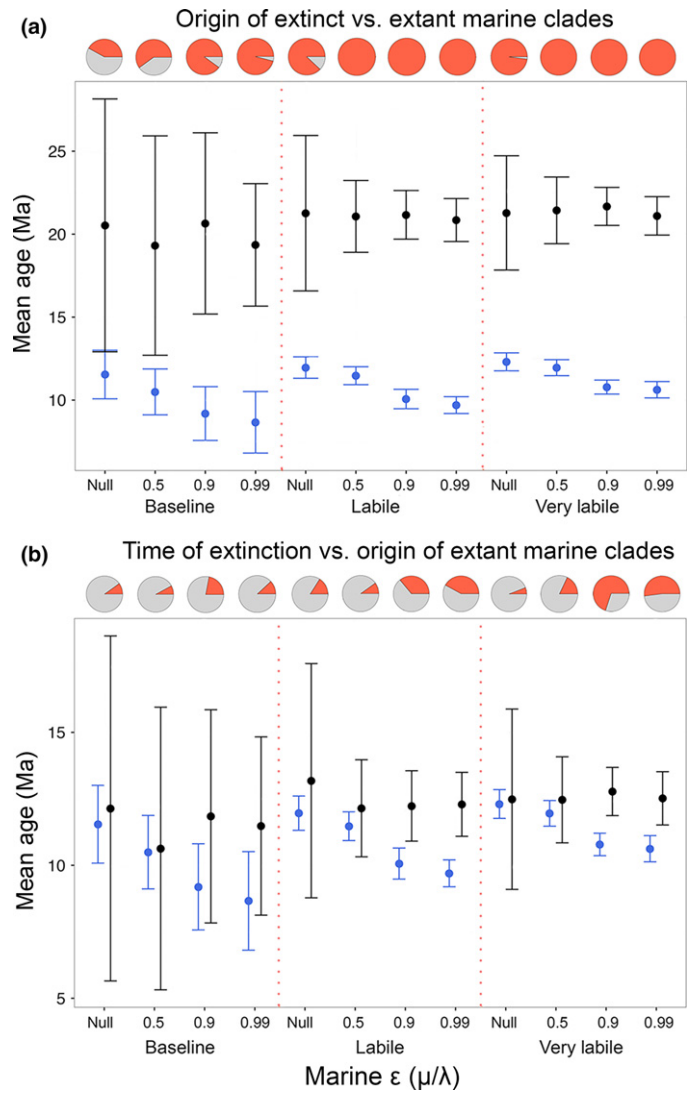

Figure 5 Simulated distributions of (a) mean ages of extinct (black) and extant (blue) marine clades, and (b) mean time of extinction of extinct clades and age of extant clades. We pooled data from three simulated phylogenies and performed *t*-tests to assess significance of temporal overlap of extant and extinct invasions (following our empirical analyses of fossil amniotes in Table S9). Data represent means and standard deviations among 50 pools of three trees each. Pie charts show the number of significant *t*-tests (orange) out of 50 tests after log10-transforming ages. Models include: 'Baseline', 'Labile' and 'Very Labile', with the extinction fraction (ratio of extinction to speciation) of the marine state increased from the null (rates from empirical phylogenies) to 0.5, 0.9 and 0.99 (Appendix S4; Tables S10, S11). Durations of extinct and extant marine invasions deviated most frequently with high marine extinction rates ($\varepsilon \geq 0.9$), and this deviation is significant most often when marine invasions are common (Labile and Very Labile models).

marine clades and limited time for recolonisation to rebuild marine richness, rather than just differences in speciation and extinction rates among extant lineages. Diversification rates (speciation–extinction) and time are generally seen as competing but non-exclusive explanations for biodiversity gradients (Wiens 2011), and most studies examining both factors find strong support for one over the other (Pontarp & Wiens 2017

and references therein). We show that diversification rates and time can work synergistically to produce richness patterns. Importantly, this pattern was not apparent from molecular phylogenies alone because they do not include ancient marine extinctions.

Amniotes show a striking pattern of replicated marine extinctions and recolonisations. Across all major clades, ancient marine invasions have ended in extinction but have been replaced by extant groups (Fig. 3; Pyenson *et al.* 2014; Kelley & Pyenson 2015). Remarkably, a similar pattern occurred in the largest fish radiation (actinopterygians), with extinction of ancient marine lineages and replacement by re-invasion from freshwater (Carrete Vega & Wiens 2012; Betancur-R *et al.* 2015).

Our results demonstrate that mechanisms explaining large-scale patterns might only be apparent over sufficiently long time scales. Extinction of only a few lineages during the Mesozoic could have important consequences for species richness. Some marine colonisations, such as ichthyosaurs, are so old that with an identical net diversification rate to their nearest extant sister clade (Motani *et al.* 2015; Table S8), they could contribute tens of thousands of marine species. Of course, this richness has not been realised due to differences in diversification rates. Simulations show that diversification rates dominate richness patterns over longer timescales, whereas time dominates over shorter timescales (Pontarp & Wiens 2017). Thus, our overall results are consistent with broad-scale analyses showing lower diversification rates in marine clades (Wiens 2015), although our fine-scale diversification results are not.

Ecological mechanisms underlying the marine-terrestrial gradient

This study may be the first to provide evidence for a strong role for extinction in the marine-terrestrial biodiversity gradient. Our findings on the importance of extinction and time for the marine-terrestrial biodiversity gradient contrast strongly with traditional ecological explanations, which imply reduced speciation rates in marine clades. These hypotheses for low marine richness include reduced primary productivity, less habitat heterogeneity and fewer opportunities for geographic isolation in marine environments (May 1994; Benton 2001; Grosberg *et al.* 2012).

We show that a few clade-level extinction events may have great consequences for extant marine richness in amniotes, due to the interaction between extinction and time-for-speciation (Figs 2 and 3). However, it remains unclear whether marine lineages have higher extinction rates than non-marine lineages, especially at the species level. High marine extinction rates are supported by our simulation results (Figs 4 and 5), but the effect of extinction on non-marine clades is not addressed in our simulations. Of course, many non-marine groups have also gone extinct. Previous studies have suggested that marine clades experience lower extinction rates than terrestrial clades, given the greater longevity of marine invertebrate genera (McKinney 1997). However, at higher taxonomic levels, non-marine amniote clades have greater longevity than marine clades (lepidosaurs and archosaurs, vs. their sister clades containing marine colonisations;

Motani *et al.* 2015; Table S8). Understanding how extinction changes with phylogenetic scale may be important for explaining the marine-terrestrial biodiversity gradient.

Future work on the marine-terrestrial gradient may benefit by focusing on ecological mechanisms driving frequent extinction in marine lineages (rather than reduced speciation). For example, extinctions of major marine groups coincide with fluctuations in sea level (Benson & Butler 2011; Pyenson *et al.* 2014; Tennant *et al.* 2016). Coastal lineages may be especially vulnerable to extinction over long time scales due to the ephemeral nature of coastal habitats. In fact, open-ocean marine amniotes were better able to survive the Late Triassic mass extinction than their coastal counterparts (Benson & Butler 2011).

Since most macroscopic marine species inhabit coastal habitats (Tittensor *et al.* 2010), high turnover in coastal lineages might underlie the marine-terrestrial biodiversity gradient in general. Infrequent transitions from non-marine to marine habitats are relevant for ancestrally non-marine groups (such as tetrapods, angiosperms and insects), but might also result from marine extinction (see below). Importantly, marine extinction could drive the gradient in all clades, especially ancient, ancestrally marine clades (Kenrick *et al.* 2012; Wiens 2015). Additional reasons for frequent extinction of marine taxa may be the trend for larger body sizes (Clauset 2013) and greater dependency on consumers for food (Tucker & Rogers 2014) than non-marine taxa.

Mechanisms of niche conservatism

Low rates of marine colonisation alone were insufficient to explain the deviance in age between extinct and extant marine clades, but they clearly play a strong role in reducing marine richness. In our simulations, increasing lability increased the number of marine clades, whereas increasing extinction reduced their ages (Fig. 4).

Niche conservatism is implicated here by the strong phylogenetic signal and low transition rates (Table 1; Table S4). This signal arises because successful transitions between marine and non-marine habitats are relatively rare (Vermeij & Dudley 2000). This rarity could occur through at least three, non-exclusive factors: (1) individuals rarely attempt habitat transitions, (2) individuals attempting this transition have reduced fitness, and (3) when lineages successfully transition, they are more likely to go extinct. Our simulation results illustrate this third factor. Extinction reduces the number of surviving marine colonisations even when the transition rate is increased (Fig. 4). Additionally, the observation that single-species marine colonisations are more common than colonisations that have diversified may exemplify this role of extinction (Table S5).

Role of speciation rates

In contrast to previous hypotheses (e.g. Grosberg *et al.* 2012), extant marine clades often had high speciation rates (Figs 1, S1; Table S4). These include hydrophiine snakes and charadriiform birds. These clades may have experienced little extinction because they are young (Fig. 2; Table S5). Their high diversification rates may also be driven by invasion of novel niche space (Schluter 2000).

However, speciation rate differences may still be relevant for explaining the marine-terrestrial richness gradient. Most non-marine species richness within mammals and birds is contained within a few terrestrial clades with high diversification rates (e.g. rodents, bats, passerine birds). We found that analyses of trimmed clades tended to reduce or reverse differences in diversification rates between marine and non-marine clades by excluding these exceptional terrestrial clades (Fig. 1). Perhaps opportunities for rapid and sustained diversification are greater on land (also exemplified by angiosperms and insects), although not realised by all non-marine clades (Fig. S1). This might be due to stronger effects of density-dependent diversification due to reduced niche availability in marine environments (Sahney *et al.* 2010).

Additionally, when alive, all extinct marine clades were much less rich than co-occurring terrestrial amniote clades (Tennant *et al.* 2016). However, extinct marine clades may have periodically high speciation rates but maintain low net diversity because extinction rates are also high, such that they experience frequent turnover with sea-level fluctuations (Benson & Butler 2011). Future studies should examine temporal patterns of wax and wane (Silvestro *et al.* 2014) in related marine and non-marine clades.

CONCLUSION

In conclusion, we show that the marine-terrestrial biodiversity gradient in amniotes is explained by a synergy between frequent extinction of marine lineages and the young age of extant marine clades. This synergy is observed only by integrating molecular phylogenies, paleontological data, and simulations. More broadly, we show how time and diversification rates can be intertwined to explain richness patterns, that extinction can play an important role in niche conservatism, and that future ecological studies should consider marine extinction as a major mechanism for low marine richness.

ACKNOWLEDGEMENTS

AUTHORSHIP

ECM and JJW designed the study and wrote the paper. ECM performed the analyses.

REFERENCES

Beaulieu, J.M. & O'Meara, B.C. (2016). Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Syst. Biol.*, 65, 583–601.

Benson, R.B.J. & Butler, R.J. (2011). Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. *Geol. Soc. London Spec. Publ.*, 358, 191–208.

Benton, M.J. (2001). Biodiversity on land and in the sea. *Geol. J.*, 36, 211–230.

Betancur-R, R., Orti, G. & Pyron, R.A. (2015). Fossil-based comparative analyses reveal ancient marine ancestry erased by extinction in ray-finned fishes. *Ecol. Lett.*, 18, 441–450.

Boxshall, G.A., Mees, J., Costello, M.J., Hernandez, F., Bailly, N., Boury-Esnault, N. et al. (2016). World register of marine species. Available at: http://www.marinespecies.org. Last accessed 10 May 2016.

Bromham, L., Hua, X. & Cardillo, M. (2016). Detecting macroevolutionary self-destruction from phylogenies. *Syst. Biol.*, 65, 109–127.

Burnham, K.P. & Anderson, D.R. (2002). Information and likelihood theory: a basis for model selection. In: *Model Selection and Multimodel Inference* Springer-Verlag, New York, NY, pp. 49–97.

Carrete Vega, G. & Wiens, J.J. (2012). Why are there so few fish in the sea? *Proc. R. Soc. Lond. B*, 279, 2323–2329.

Chiari, Y., Cahais, V., Galtier, N. & Delsuc, F. (2012). Phylogenomic analyses support the position of turtles as the sister group of birds and crocodiles (Archosauria). *BMC Biol.*, 10, 65.

Clauset, A. (2013). How large should whales be? *PLoS ONE*, 8, e53967.

Davis, M.P., Midford, P.E. & Maddison, W. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evol. Biol.*, 13, 1.

Donoghue, P.C.J. & Benton, M.J. (2007). Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends Ecol. Evol.*, 22, 424–431.

FitzJohn, R.G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods Ecol. Evol.*, 3, 1084–1092.

Fritz, S. & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv. Biol.*, 24, 1042–1051.

Grosberg, R.K., Vermeij, G.J. & Wainwright, P.C. (2012). Biodiversity in water and on land. *Curr. Biol.*, 22, R900–R903.

Hutter, C.R., Guayasamin, J.M. & Wiens, J.J. (2013). Explaining Andean megadiversity: the evolutionary and ecological causes of glassfrog elevational richness patterns. *Ecol. Lett.*, 16, 1135–1144.

Jaffe, A.L., Slater, G.J. & Alfaro, M.E. (2011). The evolution of island gigantism and body size variation in tortoises and turtles. *Biol. Lett.*, 7, 558–561.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012). The global diversity of birds in space and time. *Nature*, 491, 444–448.

Kelley, N.P. & Pyenson, N.D. (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science*, 348, 6232.

Kenrick, P., Wellman, C.H., Schneider, H. & Edgecombe, G.D. (2012). A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 367, 519–536.

Kozak, K.H. & Wiens, J.J. (2016). Testing the relationships between diversification rates, species richness, and trait evolution. *Syst. Biol.*, 65, 975–988.

Maddison, W.P. & FitzJohn, R.G. (2014). The unsolved challenge to phylogenetic correlation tests for categorical characters. *Syst. Biol.*, 64, 127–136.

Maddison, W.P., Midford, P.E. & Otto, S.P. (2007). Estimating a binary character's effect on speciation and extinction. *Syst. Biol.*, 56, 701–710.

Magallón, S. & Sanderson, M.J. (2001). Absolute diversification rates in angiosperm clades. *Evolution*, 55, 1762–1780.

Martins, E.P. & Hansen, T.F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.*, 149, 646–667.

May, R.M. (1994). Biological diversity: differences between land and sea. *Phil. Trans. R. Soc. Lond. B*, 343, 105–111.

McKinney, M.L. (1997). Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.*, 28, 495–516.

Motani, R., Jiang, D.Y., Chen, G.B., Tintori, A., Rieppel, O., Ji, C. *et al.* (2015). A basal ichthyosauriform with a short snout from the Lower Triassic of China. *Nature*, 517, 485–488.

Orme, D. (2013). The caper package: comparative analysis of phylogenetics and evolution in R. R package version 0.5.2

Paleobiology Database. (2016). Available at: http://fossilworks.org/. Last accessed 20 March 2017.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.

Pennell, M.W., Sarver, B.A.J. & Harmon, L.J. (2012). Trees of unusual size: biased inference of early bursts from large molecular phylogenies. *PLoS ONE*, 7, e43348.

Pontarp, M. & Wiens, J.J. (2017). The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate, and carrying capacity. *J. Biogeogr.*, 44, 722–735.

Pyenson, N.D., Kelley, N.P. & Parham, J.F. (2014). Marine tetrapod macroevolution: physical and biological drivers on 250 Ma of invasions and evolution in ocean ecosystems. *Palaeogeogr. Palaeoclimatol. Palaeroecol.*, 400, 1–8.

Ricklefs, R.E. (1987). Community diversity: relative roles of local and regional processes. *Science*, 235, 167–171.

Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014). Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biol.*, 12, e1001775.

Sahney, S., Benton, M.J. & Ferry, P.A. (2010). Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biol. Lett.*, 6, 544–547.

Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.

Silvestro, D., Salamin, N. & Schnitzler, J. (2014). PyRate: a new program to estimate speciation and extinction rates from incomplete fossil data. *Methods Ecol. Evol.*, 5, 1126–1131.

Stephens, P.R. & Wiens, J.J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.*, 161, 112–128.

Tennant, J.P., Mannion, P.D. & Upchurch, P. (2016). Sea level regulated tetrapod diversity dynamics through the Jurassic/Cretaceous interval. *Nat. Commun.*, 7, 12737.

Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V. *et al.* (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466, 1098–1101.

Tucker, M.A. & Rogers, T.L. (2014). Examining predator-prey body size, tropic level, and body mass across marine and terrestrial mammals. *Proc. R. Soc. B*, 281, 20142103.

Uetz, P. & Hosek, J. (eds.). (2015). The Reptile Database. Available at http://www.reptile-database.org. Last accessed 15 January 2015.

Vermeij, G.J. & Dudley, R. (2000). Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biol. J. Linn. Soc.*, 70, 541–554.

Wiens, J.J. (2011). The causes of species richness patterns across space, time, and clades and the role of 'ecological limits'. *Q. Rev. Biol.*, 86, 75–96.

Wiens, J.J. (2015). Faster diversification on land than sea helps explain global biodiversity patterns among habitats and animal phyla. *Ecol. Lett.*, 18, 1234–1241.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* (2010). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecol. Lett.*, 13, 1310–1324.

Wilson, D.E. & Reeder, D.M. (2005). *Mammal Species of the World, a Taxonomic and Geographic Reference*, 3rd edn. John Hopkins University Press, Baltimore, MD.

Zheng, Y. & Wiens, J.J. (2016). Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. *Mol. Phylogenet. Evol.*, 94, 537–547.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.