

TECHNICAL COMMENT

Demystifying the marine-terrestrial biodiversity gradient: response to Vermeij *et al.*

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

We respond to seven criticisms made by Vermeij *et al.* (2018) regarding Miller & Wiens (2017). Their criticisms generally reflect misunderstandings, unsupported speculations, and topics that were explicitly addressed in our paper.

Keywords

Amniotes, diversification rates, extinction, marine-terrestrial gradient, species richness, time-for-speciation.

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Vermeij *et al.* (2018); VEA) made seven criticisms regarding Miller & Wiens (2017; MW). Broadly speaking, most can be resolved with three clarifications:

- (1) The proper units to test the effect of time on species richness are lineages that underwent habitat transitions, not clades of similar rank or age (*contra* points 1, 5–6 of VEA).
- (2) The ‘deathtrap’ of MW refers to extinction of entire marine invasions, a process that was not detected from extinction rates estimated within extant clades. MW did not find or claim that marine extinction rates were higher than nonmarine rates (*contra* points 1, 3, 5–6). Instead, MW emphasised differences in the long-term survival of lineages colonising each habitat. Many marine colonisations have gone extinct throughout amniote history. Consequently, almost all surviving marine colonisations have relatively recent, Cenozoic origins. Thus, marine extinctions reduced the mean age of living marine invasions, explaining the low mean richness of these colonisations and of extant marine amniotes overall. In contrast, amniotes have persisted on land continuously for > 300 million years. This dramatic difference in persistence is true regardless of uncertainty in the exact number or timing of marine colonisations (*contra* points 5–6).
- (3) Effects of extinction may only become apparent over longer timescales (*contra* points 1, 5–6). The lack of consistent diversification-rate differences between habitats within younger extant clades (MW: Fig. 1) is not inconsistent with other findings. For example, extinction of older marine groups (e.g. ichthyosaurs) will not be reflected in diversification rates within extant families, but should instead be reflected in reduced diversification rates of larger clades (i.e. phyla; Wiens 2015). This is also consistent with simulations showing that the time-for-speciation effect explains richness patterns among habitats over shorter timescales, whereas diversification-rate differences dominate over longer timescales (Pontarp & Wiens 2017).

We respond to the seven points of VEA below.

- (1) VEA claim that we did not properly compare marine and nonmarine clades. However, the time-for-speciation hypothesis predicts that earlier *habitat transitions* will have greater richness than later transitions, not that *named clades* within one habitat will be older and more rich than clades in another habitat (Wiens 2011). Therefore, simply comparing ages of clades of similar rank between habitats (VEA’s proposal) would be highly misleading, because almost all terrestrial amniote diversity is descended from one ancient sea-to-land transition. VEA further claim that the terrestrial occupancy of land > 300 Mya is irrelevant to extant richness patterns. This is untrue. Terrestrial amniote diversity accrued continuously over 300 Myr, whereas extinction of marine colonisations has repeatedly halted the accumulation of marine richness.
- (2) VEA speculate that patterns found in amniotes are not broadly applicable. However, the mechanisms MW described (i.e. extinction with limited time to rebuild richness) should be broadly applicable to groups originating in either habitat. For ancestrally nonmarine groups (e.g. angiosperms, insects), extinction of older marine colonisations may lower marine richness by leaving only young, species-poor marine lineages, as in amniotes. For example, extant marine insects consist of single species or genera, not entire families or orders (Cheng 1976). For ancestrally marine groups, extinction may decrease their diversification relative to terrestrial groups (consistent with their lower diversification rates; Wiens 2015). Testing the generality of our findings will require similar quantitative analyses in other taxa.
- (3) VEA speculate that since molecular phylogenies do not include extinct taxa, overestimation of diversification rates could overturn our conclusions. However, our inference of the importance of extinction does not stem from diversification-rate estimates within clades, but rather the extinction of entire lineages that colonised marine habitats (MW: Figs 2–3).

- (4) VEA speculate that the young age of living marine clades reflects ecological opportunity. However, this does not conflict with MW. We referred to ‘replacement’ as the turnover of marine lineages in general (*sensu* Kelley & Pyenson 2015), not replacement of clades with similar ecological roles. Extant marine transitions are young because older marine invasions went extinct; this is true regardless of whether ecological opportunity facilitated colonisation.
- (5) VEA argue that our conclusions are flawed because of incorrect inference of the number of marine colonisations and their ages, and that similar clade durations in each habitat suggest no differences in extinction. We address these below:
- (i) *Durations*: Despite what VEA claim, MW did not calculate extinction frequencies using clade durations. Instead, MW compared the durations of lineages corresponding to habitat transitions. Unlike marine transitions, descendants of the initial sea-to-land transition have persisted for >300 Myr.
- (ii) *Counts*: VEA claimed that individual species were incorrectly counted as independent invasions, but this claim was without supporting evidence. Many marine invasions do consist of single species, based on ancestral-state reconstructions (i.e. many birds). Regardless, analyses excluding single-species transitions yield similar results (MW: Table S6).
- (iii) *Ages*: VEA do not provide evidence that our clade-age estimates from time-calibrated phylogenies are incorrect, nor do they show how incorrect ages would overturn our conclusions. Clade ages inferred from molecular phylogenies are often older than those inferred from fossils (Donoghue & Benton 2007), but this alone does not make them incorrect. Nevertheless, even large uncertainties in clade ages should not overturn our conclusions, given the striking difference in ages of surviving marine vs. terrestrial colonisations.
- (6) VEA argue that the limited number of marine transitions is sufficient to explain the marine-terrestrial richness gradient. However, among amniotes, sea-to-land transitions are even fewer than land-to-sea transitions (MW: Fig. 2). Thus, by their argument, there should be more marine than terrestrial species, the opposite of the observed gradient. Instead, the relative amount of time colonists have inhabited each habitat is more relevant than the number of colonisations alone. VEA further speculate that our results would be different had we analyzed Mesozoic taxa alone. Two lines of evidence suggest otherwise. First, terrestrial amniotes still had more time-for-speciation than marine amniotes by the Mesozoic, given that amniotes continuously occupied land since the Paleozoic. Second, many marine transitions went extinct during the Mesozoic (MW: Fig. 3). Therefore, similar mechanisms are relevant to both the Mesozoic and present.
- (7) VEA claim that we ignored ecological differences among habitats. Instead, we elucidated the potential roles that

extinction, speciation, and colonisation play in generating the richness gradient. These are the only processes that directly change species richness. We then suggested specific ecological mechanisms that may drive marine extinction (MW: p. 919).

NOTES

After this comment was accepted, a paper cited by VEA as “in progress” was published (Vermeij & Motani 2018; Paleobiology; doi: 10.1017/pab.2017.37). We performed the analyses in Figs. 2 and 3 of MW using their data (after removing 21 invasions not considered marine under the definition used in MW). These analyses produced similar results to those in MW (Fig. 2: $n=17$ invasions, $r^2=0.31$, $P=0.02$; MW: $n=58$, $r^2=0.51$, $P<0.001$; Fig. 3: $P<0.001$ for all analyses). Their data do not overturn our conclusions.

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REFERENCES

- Cheng, L. (1976). *Marine Insects*. North-Holland Publishing Company, Amsterdam.
- 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.
- Kelley, N.P. & Pyenson, N.D. (2015). Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science*, 348, 6232.
- Miller, E.C. & Wiens, J.J. (2017). Extinction and time help drive the marine-terrestrial biodiversity gradient: is the ocean a deathtrap? *Ecol. Lett.*, 20, 911–921.
- 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.
- Vermeij, G.J., Grosberg, R.K., Marshall, C.R. & Motani, R.M. (2018). The sea as deathtrap: comment on a paper by Miller and Wiens. *Ecol. Lett.*, 10.1111/ele.12886.
- 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.

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