K-Pg events facilitated lineage transitions between terrestrial and aquatic ecosystems

Şerban Proches¹,², Gianluca Polgar² and David J. Marshall²

¹Discipline of Geography, University of KwaZulu-Natal, Westville Campus, PO Box X54001, Durban 4000, South Africa
²Environmental and Life Sciences Programme, Universiti Brunei Darussalam, Jalan Tungku Link 1410, Brunei Darussalam

We use dated phylogenetic trees for tetrapod vertebrates to identify lineages that shifted between terrestrial and aquatic ecosystems in terms of feeding or development, and to assess the timing of such events. Both stem and crown lineage ages indicate a peak in transition events in correspondence with the K-Pg mass extinction. This meets the prediction that changes in competitive pressure and resource availability following mass extinction events should facilitate such transitions.

1. Introduction

Transitions between the terrestrial, freshwater and marine realms are undoubtedly some of the most spectacular events associated with the evolution of life [1]. Reconstructions of the evolutionary histories and the initial colonization of land by early aquatic lineages (such as the Devonian prototetrapods) have captured both the interest of researchers and the imagination of the public [2,3]. Novel terrestrial colonizations and reversions to the aquatic realm have nonetheless occurred throughout the history of life [4]. Although the ecological and evolutionary drivers of such realm transitions are complex and variable among lineages relative to geographical distributions and geological timeframes, their proliferation conceivably relates to periods of physical and biological turmoil. While volcanism, glaciation and eustatic sea-level change have triggered large-scale extinctions through effects on seawater chemistry, environmental temperature and habitat loss [5], the biological upheaval that has followed extinctions seemingly presents extraordinary opportunities for realm transitions [6].

Mass extinctions are succeeded by considerable reorganization of ecological processes as a consequence of the redistribution of resources and changes in competitive and predation pressures [6]. The significance of an extinction event on ecological interactions is, however, unlikely to be equitable across realms [7]. Reduced competition or predation in one realm should favour the adaptive evolution and colonization of lineages from a juxtaposed realm, where these are greater [4,8–10].

The prediction that realm transition proliferation corresponds with mass extinction events has not been tested before, to the best of our knowledge. Here, we determined the incidence of transitions in terms of feeding and development within a geological timeframe. Our study is based on dated phylogenetic trees for extant tetrapod vertebrates, arguably the best studied animal group.

2. Material and methods

For each major tetrapod clade with extant representatives, we coded the primary environment for feeding in adults and the development of early life stages [11–16]. In segments of the phylogenetic tree where these traits showed high variability (e.g.
multiple clades within Neobatrachia, Charadriiformes), coding was performed at the genus or species level, depending on data availability. This information was used to reconstruct the ancestral states for each node in the tree (Mk1 likelihood option in the MESQUITE software, ‘Trace Character Over Trees’ facility) [17]. Probability values for the three possible character states (terrestrial, freshwater and marine) were calculated twice (feeding and development) for each node. A transition event was defined as a change in the type of environment where adult feeding predominantly takes place, or where the youngest independent life stages occur. This was identified as any situation where two consecutive nodes had different character states with probability greater than 50%, in the ancestral character reconstruction (e.g. at one node early development was most likely terrestrial, but at the next node, marine). Where this criterion was met, but probability values assigned to states at either node did not exceed 50%, we viewed this as a transition, but the relevant environments as equivocal. To clarify some of these transitions of equivocal directionality, we consulted information on extinct taxa, which was otherwise not considered in the study. For example, both crocodiles and turtles are listed here as derived from terrestrial common ancestors with their respective sister taxa, whereas this would be unclear if only phylogenies based on extant species were considered.

For each transition event, we recorded the date when the clade performing the transition became separated from its sister clade (stem age value). Additionally, we recorded the earliest diversification date, and the reconstructed environments relevant to development and feeding for both the clade that performed the transition and the sister clade. The earliest diversification date (based on extant lineages) of the clade that performed the transition was used as the crown age value. The dates were derived from the OneZoom online engine [18], accessed 11–19 September 2013. This was at the time incomplete for Squamata, so information was in this case retrieved from published papers (see the electronic supplementary material). To limit any biases resulting from the variable availability of

![Figure 1. A phylogenetic tree of the major tetrapod lineages relevant to transitions in feeding and development between terrestrial, freshwater and marine environments, and their sister lineages (topology: \([17]\)). Hollow horizontal bars indicate the intervals between the crown age and stem age values for each transition event, with the actual transition presumably taking place within this interval (see Material and methods). Grey vertical bar: period of heavy biotic turmoil relevant to the K-Pg mass extinction. Blue, fully aquatic; green, adults with predominantly terrestrial feeding, but aquatic young stages; red, adults with predominantly aquatic feeding, but terrestrial young stages; brown, fully terrestrial. Sister lineages both in red refer to marine/freshwater shifts.](http://rsbl.royalsocietypublishing.org/)

rsbl.royalsocietypublishing.org
Biol. Lett. 10:
20140010

on June 20, 2017http://rsbl.royalsocietypublishing.org/Downloaded from
habitat and phylogenetic data in small clades (especially in amphibians), transition events were considered only where the transiting lineage contained at least ten extant species. Additionally, we excluded ambystomatid salamanders, which exhibit high intraspecific variability for the presence of terrestrial adults—in a sense representing transitions in progress. We then plotted the number of transitions for 10 Ma intervals, using both stem and crown age values.

3. Results

Forty transition events were identified, of which 10 represented cross-realm transitions in development (all in amphibians), 27 in feeding and three (Typhlonectidae, Whippomorpha and Hydrophiinae) in both. Ten transitions were from aquatic to terrestrial environments, 18 in the opposite direction, four were between marine and freshwater systems, while directionality could not be determined with reasonable certainty in the remaining eight. In some cases, based on node-level reconstruction, it appears that multiple back-and-forth transitions had occurred. For instance, tortoises (Testudinidae) are a fully terrestrial group derived from an aquatic-feeding chelonian ancestor, which in turn is derived from a fully terrestrial reptilian of amphibian descent; likewise, some amphibious salamanders (Plethodontidae: Spelerpinae) are derived from ancestors with secondarily acquired direct development. The transitions are mapped onto the tetrapod tree of life in figure 1, and the data are presented in full in the electronic supplementary material. Given the limited representation of transitions between freshwater and marine systems, further analyses only considered transitions between terrestrial and pooled aquatic systems.

The scarcity of old (more than 100 Ma) transition events with surviving descendants (as well as the great differences between stem and crown age in those cases) meant that we could assess the importance of only one mass extinction event (K-Pg; 66 Ma). Since bird diversification followed shortly after the K-Pg event, and given the large number of feeding transitions in birds, our analyses included or excluded birds (figure 2a,b). The incidence in realm transition events peaked at 70–40 and 20 Ma both with and without birds, and to varying degrees in both feeding and development, and in the case of water–land transitions (figure 2a–c,e,f). The first peak is less obvious for land–water transitions (figure 2d). A K-Pg peak is observed even in this latter case when transitions of equivocal directionality are added (not presented), but these could not have all taken place from land to water (having to include switches and reversals).

4. Discussion

The patterns observed here are influenced by at least two biases. First, the inclusion of lineages with surviving descendants only means that older transitions are underrepresented. Numerous lineages that shifted to a new realm, such as

Figure 2. Numbers of transition events in tetrapod vertebrates for 10 Ma intervals (filled bars, using stem age values; unfilled bars, crown age values). (a) All transitions, (b) excluding birds, (c) water to land transitions, (d) land to water transitions, (e) reproductive/development transitions and (f) feeding transitions.
mosasaurs, plesiosaurs and various fish-feeding birds, represent secondary users of aquatic resources derived from fully terrestrial ancestors that subsequently became extinct (some in the very mass extinction event discussed here). Second, the inclusion of only large clades (10 extant species or more) means that very recent transitions, which had little opportunity to become large, are also excluded. However, neither of these biases nor their combination explains the sharp 70–40 Ma peak or the bimodal pattern observed in some subsets of the transitions (figure 2a,c,f). We suggest that the first peak (70–40 Ma) is best explained by the physical and biological turmoil associated with the K-Pg mass extinction event. While we know of no other studies documenting realm shifts following mass extinctions, a variety of other types of shifts have been documented to occur under such circumstances, some referring to food chain structure and others to ecosystem complexity, within realms [19,20].

The second peak (20–10 Ma) could simply be derived from better chances of survival in more recent transitions. However, this peak also coincides with the Paleogene/Neogene boundary, which, without representing one of the major mass extinctions, was also marked by a degree of biotic turmoil [21].  Older transitions, although too few to draw any reliable conclusions, are also in some cases coincident with the Jurassic/Cretaceous and Permian/Triassic boundaries.

The increased incidence of realm transitions following the K-Pg event could be attributable to at least two ecological phenomena: an increased availability of vacant niches, and an increase in habitats facilitating such transitions. The former can be exemplified by birds, which represent a substantial proportion of the transition events included in our data (figure 2a,b), and which are considered to have diversified as a direct result of K-Pg extinctions [22]. As an example of the latter, angiosperm diversification resulted in increased areas of transitional habitat, such as mangroves and seagrass beds [23–25].

When examining the directionality of transition events, the increased terrestrial biodiversity around the times of the K-Pg extinction [26] might be expected to have led to a greater number of land–water transitions. Our observations were, however, contrary to this expectation, and we propose that the more limited distribution ranges of terrestrial species [26] resulted in comparatively reduced opportunities for realm shifts.

Our results are based on a single mass extinction, raising questions as to whether our conclusions are relevant to older events. It has been suggested that dramatic changes in aquatic ecosystems following previous mass extinction events have indirectly promoted the initial colonization of land by plants and vertebrates [2]. These are, however, single transitions, and as such difficult to explain without invoking multiple factors [27]. It would, therefore, be useful to also test our hypothesis for groups such molluscs and arthropods—the former having a remarkably good fossil record [6], and the latter still awaiting a solid understanding of directionality in major transitions [28].

Acknowledgement. We thank John Measey and one anonymous referee for comments.

Funding statement. We are grateful to UBD, UKZN and the National Research Foundation (South Africa) for support.

References


