

The many shapes of diversity: ecological and evolutionary determinants of biodiversity through time

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ABSTRACT

Question: Is it either necessary or useful to separate ecological and evolutionary factors as determinants of biodiversity pathways?

Organisms: The fossil record of 58 extinct marine invertebrate groups belonging to six different animal phyla, ranging from the early Palaeozoic to the early Cenozoic, and including a total of 21,554 species.

Methods: We tested six different models of biodiversity evolution by means of maximum likelihood estimation. The models reproduce familiar, long-standing hypotheses on biodiversity controls (such as adaptive radiation, Van Valen's Red Queen, and density-dependence).

Results: For nearly 90% of the fossil clades analysed, the best model includes an early diversification phase, and increased extinction rate over time. These features are consistent regardless of whether the main determinants of species diversity in the models are ecological or evolutionary. Clades terminated by mass extinctions did not have shorter duration than other clades but were characterized by earlier divergence and greater species richness than other clades.

Conclusion: An early rapid diversification, coupled with a late increase in extinction, is common to the majority of clades, and predicted by the most successful models of biodiversity evolution. This path is consistent with both evolutionary and ecological factors (or better, a combination of the two). The separation of ecological and evolutionary factors as determinants of biodiversity pathways seems neither justified nor necessary.

Keywords: adaptive radiation, diversification rate, diversity-dependence, diversity trend, key innovation.

INTRODUCTION

The path that diversity within clades takes through time is a major issue in palaeobiology. Most studies find that diversity follows a predictable course, with species richness peaking almost midway along a clade's existence and being symmetric around the peak. This surprising regularity was found repeatedly in a variety of fossil clades of different ages

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(Foote, 2007; Foote *et al.*, 2007; Quental and Marshall, 2013) and parallels an almost identical route for species occupancy or commonness, which is a composite measure of local abundance and geographic range (Jernvall and Fortelius, 2004; Hunt, 2007; Raia *et al.*, 2006; Waldron, 2007; Carotenuto *et al.*, 2010). While such regularity calls for explanation, some authors have suggested that a peaked diversity course and its tight association with range size evolution might simply be a statistical artefact (Pigot *et al.*, 2012).

There are several theories, and models based upon them, seeking to address the determinants of species diversity through time. These models differ from each other mainly in the relative importance they assign to ecological versus evolutionary factors. For instance, diversity-dependent models postulate that the rate of diversification slows down as the number of species increases. The rationale of this inverse relationship is based on ecological opportunity. As a clade diversifies, more and more niches become occupied, hence fewer remain free for further species to fill (Sepkoski, 1981, 1984; Alroy *et al.*, 2008; Phillimore and Price, 2008; Losos and Mahler, 2010; Etienne *et al.*, 2012; Rabosky, 2013; Rabosky and Hurlbert, 2015). This follows from the common observation that clade morphological diversity (hence the diversity of niches it encompasses) begins to grow earlier than the number of species (Benton *et al.*, 2014). The basic assumption of this class of models is that there is a limit to the number of species that can co-exist. Yet, this assumption has often been criticized (Benton, 1995; Benton and Emerson, 2007; Stanley, 2007; Alroy *et al.*, 2008; Erwin, 2008; Alroy, 2010; Harmon and Harrison, 2015). It has also emerged that diversity-dependent-like patterns may arise without any ecological factors being involved (Moen and Morlon, 2014).

The argument of ecological controls on diversity also pertains to the so-called long-fuse model (Bininda Emonds *et al.*, 2007). For some clades, diversity peaks late during their existence. This may happen because unfavourable environmental conditions, usually in the form of competition with a more diverse clade targeting the same set of niches, depress opportunities to diversify (Benton, 1987; Hallam, 1987, 1991; Vermeij, 1987). This dynamic was sought to explain the diversification of pleurodiran and cryptodiran chelonians (i.e. turtles capable of retracting the neck into the shell) at the expense of amphichelydians (Rozenzweig and McCord, 1991), the substitution of brachiopods by bivalves after the Permian mass extinction (Gould and Callaway, 1980; Liow *et al.*, 2015), major replacements within the mammalian order Carnivora (Van Valkenburgh, 1999), and the diversification of dinosaurs after the demise of crurotarsan archosaurs during the Late Triassic and Early Jurassic (Brusatte *et al.*, 2008). Whether or not diversity in these clades actually peaks in the late phases of their existence, the basic tenet that incumbent competitors of a different clade delayed the peak in diversification pertains to them all.

Perhaps the most famous theory linking diversification to standing diversity is Van Valen's Red Queen hypothesis (Van Valen, 1973; Benton, 2009). Under the Red Queen, the probability of extinction is constant over time, the result of a zero-sum game where increasing the fitness of one species is balanced by an equal loss in others. Therefore, a species is equally likely to go extinct wherever it appears during the clade's existence. The Red Queen hypothesis was originally proposed as an explanation of the empirically based *law of constant extinction* but has been disconnected from it in later Red Queen formalisms (Liow *et al.*, 2011; Vermeij and Roopnarine, 2013; Voje *et al.*, 2015), leaving only the basic idea that species have to evolve continuously just 'to keep in the same (ecological) place' (Quental and Marshall, 2013; Brockhurst *et al.*, 2014).

In all of the above, speciation and extinction rates, and hence net diversification, depend on ecological factors. Yet, many students of diversification patterns over time have indeed

posited that the effect of ecological interactions is not large enough to explain trends in diversity within clades. In contrast, this second (evolutionary) class of models gives much room to historical contingency as the key factor. The evolutionary model that best embodies this idea is Simpson's adaptive radiation (Simpson, 1944, 1953; Van Valen, 1980; Schluter, 2000). According to this, species diversification proceeds unbounded during the earliest phase of a clade's existence, to decrease afterwards as ecological niches become filled up with species and the opportunity for further speciation dwindles. Two reasons may justify the early explosive diversification phase. First, the extinction of an incumbent, dominant clade (a purely evolutionary cause) may vacate ecological niches for a new clade to settle in. A second truly evolutionary effect depends on key innovations. Clades may develop new traits with profound implications in terms of competitive ability. Such traits, once acquired, would bring about a sensible increase in diversification. A few among many examples of the former mechanism include the radiation of present-day mammalian orders at the end of the Palaeocene (Meredith *et al.*, 2011; Raia *et al.*, 2013), successive radiations in Cambrian trilobites (Taylor, 2006; Abe and Liebermann, 2012), the replacement of brachiopods by bivalves after the end Permian mass extinction (Gould and Calloway, 1980; Liow *et al.*, 2015), and the statistically significant increase in origination rates in bivalve clades after mass extinctions (Krug and Jablonski, 2012). Examples of key innovations spurring bursts in diversification are similarly common. They include mantle fusion in infaunal bivalve molluscs such as rudists (Stanley, 1968), the evolution of insect pollination in angiosperms (Sanderson and Donoghue, 1994), the development of the hypocone cusp in mammals (Hunter and Jernvall, 1995), hypsodont molars in ruminants (Raia *et al.*, 2011), and shell sculpturing coupled with narrow apertures in Mesozoic gastropods (Vermeij, 1977). Such 'early-burst' dynamics is commonplace among studies of diversification dealing with fossil clades, yet a comprehensive analysis of the diversification of living clades found little support for it (Harmon *et al.*, 2010).

Whereas these models may appear quite distinctive, they may not be entirely so. Three models share a pattern of rapid initial diversification followed by a decrease as niches become filled up: adaptive radiation (including *key innovation*), diversity-dependence, and the Red Queen (Van Valen, 1980). In keeping with Stanley (1979), Rabosky (2013) defined adaptive radiation as an exponential rise in species diversification that occurs when diversity-dependent controls are relaxed, either because a new adaptive zone is invaded (creating the opportunity to exploit new niches), or because of purely contingent factors, such as when a set of niches becomes vacated by a major extinction.

Although the above models conceive bursts in diversification as a product of adaptation, radiation can be non-adaptive as well (Gittenberger, 1991; Rundell and Price, 2009; Simões *et al.*, 2016). Furthermore, as in the case of diversity-dependence discussed above, the idea that the effective environment of a clade has a limited carrying capacity is merely an assumption. Such capacity is not usually measured (Rabosky, 2013), and there is no reason to believe it cannot change over time (Harmon and Hurlbert, 2015). The path of species diversity might therefore fail to reveal diversity-dependence even when such a factor is real (Moen and Morlon, 2014). The delayed-rise, adaptive radiation, and key innovation models all centre on the idea that the disappearance of incumbent competitors, or the appearance of a fitness-conferring trait, consistently increases diversification. Distinguishing between them might be impossible if the key innovation is not a clade apomorphy (i.e. it does not coincide with the clade birth). For some authors, clade age *per se* explains the rise of species diversity (McPeck and Brown, 2007), leaving no room for deterministic factors to affect diversification rate. The effect of clade age was specifically shown to matter in explaining the decay of diversity in

clades of terrestrial mammals (Quental and Marshall, 2013), yet it is often neglected. Most notably, diversity-dependent models are not explicit about what happens after the carrying capacity has been approached. Therefore, they do not predict clade extinction.

In order to better relate empirical data to different models, we tested the species richness path over time in 58 extinct marine animal clades, according to six different models of diversification, using maximum likelihood. Our approach was not to reproduce the diversification process (e.g. the birth–death model); rather, we designed models that describe different patterns of species appearance and disappearance in the fossil record. Although process-based approaches give fundamental insights on the factors producing diversity paths, theories such as adaptive radiation and the Red Queen were formulated from direct observation of the fossil record, such as the sudden appearance of many species in a geologically short time interval (Simpson, 1953) or plots of species numbers against age (Van Valen, 1973). We followed this fossil-record-oriented modelling approach and specifically asked whether any of our models is more likely than others to explain symmetric diversity paths.

MATERIALS AND METHODS

We collected data on the fossil record for 58 extinct clades belonging to six different animal phyla (Cnidaria, Mollusca, Brachiopoda, Arthropoda, Bryozoa, Echinodermata), downloaded from the Paleobiology Database (PaleoDB) in April 2015. We focused on fossil clades with a continuous stratigraphic range, containing at least 100 species, and with stable taxonomy (hence they presumably are monophyletic). Genera and species with uncertain classification (e.g. sp., cf.) were excluded.

Every database is bound to include entry errors such as incorrect taxonomy or age attribution. Whereas we could not fully control for the former, we strove to account for the latter by crosschecking age references with data reported in literature, and by asking for assistance from colleagues who are specialists on individual clades. After the data were cleaned, we divided species occurrence into time intervals of equal length. The length of such time bins was clade-specific, meaning that we applied bins of different lengths so as to maintain as many bins as possible (to attain maximum resolution) while avoiding producing bins containing no species. For each clade, we then computed both the absolute (per-interval) and cumulative species diversity curves.

Temporally, the clades range from early Cambrian trilobites (Ptychopariidae, Olenidae, Agnostidae), brachiopods (Acrotretida, Orthida), and echinoderms (Crinozoa) to Late Cretaceous bivalves (Inoceramidae, Radiolitidae, Hippuritidae), bryozoans (Cystoporida), and gastropods (Euomphalidae). Most of the species are Palaeozoic in age. Clade duration ranges from 9 to *c.* 400 million years. Species diversity of individual clades ranges from 103 species (Illaenidae, Trilobita) to 2247 species (Productida, Brachiopoda), with a mean of 372 species.

Models of diversification

We inquired whether any particular model is more likely than others to produce a symmetric species diversity curve over time, which happens to occur in more than half of all fossil clades (Foote, 2007). As such, whereas speciation and extinction rates are usually modelled as number of such events per lineage per unit time (Sepkoski, 1984; Foote, 2007; Foote *et al.*, 2007; Silvestro *et al.*, 2014) and along phyletic lineages (Nee, 2006; Stadler, 2013; Morlon, 2014), we started

from a reference distribution z where the distribution of species' first appearances per time bin is normally distributed:

$$z_i = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(x_i - \mu)^2}{2\sigma^2}} * s. \quad (1)$$

In equation (1), s represents a scalar fitted by maximum likelihood estimation so that the number of speciation events summed over all the time bins equals the number of species N in the clade. The mean (μ) and standard deviation (σ) of the vector of time bins x (which is a vector of integers including $i_1, i_2, i_3 \dots i_n$ time intervals of equal length) are used to yield z .

We produced six diversification models, which differ from each other in the timing of maximum number of new species per time bin, the pattern it takes over time, and in how extinction is computed. That is, we included both patterns of early and late diversification.

We started with a *neutral* model where the number of species appearing per interval Sp_i is a function of z and time, so that:

$$Sp_i = z_i * x_i, \quad (2)$$

where x_i is the i^{th} time bin (the scalar s is fitted by maximum likelihood estimation). The total number of species appearing over the interval x_1 to x_i (i.e. the cumulative species richness to bin i) is:

$$S_{\text{tot}_i} = z_i * x_i + S_{\text{tot}_{i-1}}. \quad (3)$$

From (1) and (3) we modelled the shape of the extinction curve as:

$$y_i = S_{\text{tot}_i} * c, \quad (4)$$

fitting the scalar c by means of maximum likelihood estimation. Under this approach, a constant proportion c of the total number of species that ever appeared in the clade go extinct in each interval under this model. This means that the number of extinctions will track the number of speciations.

The speciation and extinction curves can be used to compute the mean diversification at a given bin D_i :

$$D_i = \bar{z}_{1:i} - \bar{y}_{1:i}. \quad (5)$$

From (5) the species richness in the i^{th} interval S_i is derived as:

$$S_i = D_i * x_i. \quad (6)$$

From (6) the actual number of species going extinct in the i^{th} interval is calculated as:

$$Ext_i = S_{i-1} + Sp_i - S_i, \quad (7)$$

which implies that the change in diversity from one interval to the next is:

$$Div_i = Sp_i - Ext_i. \quad (8)$$

We defined this model as *neutral* since there is no particular theory behind the distribution of z and y , despite the fact it was conceived to produce a late-diversification curve (i.e. diversity curve S peaks during the second half of the life of the clade; Fig. 1).

Our second model was designed to represent an *adaptive radiation* (a pattern of high speciation immediately after the birth of the clade; Fig. 1). With this aim, we derived the speciation curve z from equations (1, 3) pertaining to the *neutral* model as:

$$z = \max_z * \left(1 - \frac{S_{\text{tot}t_i}}{\max_{S_{\text{tot}}}}\right) * S, \quad (9)$$

where \max_z and $\max_{S_{\text{tot}}}$ are the highest values that the z_i and S_{tot} curves, respectively, would take according to the *neutral* model.

The third model is tailored to represent the *delayed-rise* hypothesis (Bininda Emonds *et al.*, 2007). To produce such a model we warped the time axis according to an exponent e :

$$tsk_i = x_i^e, \quad (10)$$

which means the time intervals will take the values:

$$xsk_i = \frac{x_i * tsk_i}{\max(tsk_{1:i})}. \quad (11)$$

For $e > 0$ and substituting (11) in (1) produces a left-skewed distribution of z . Since the extinction curve is calculated as in models 1–2, the species diversity S will itself be

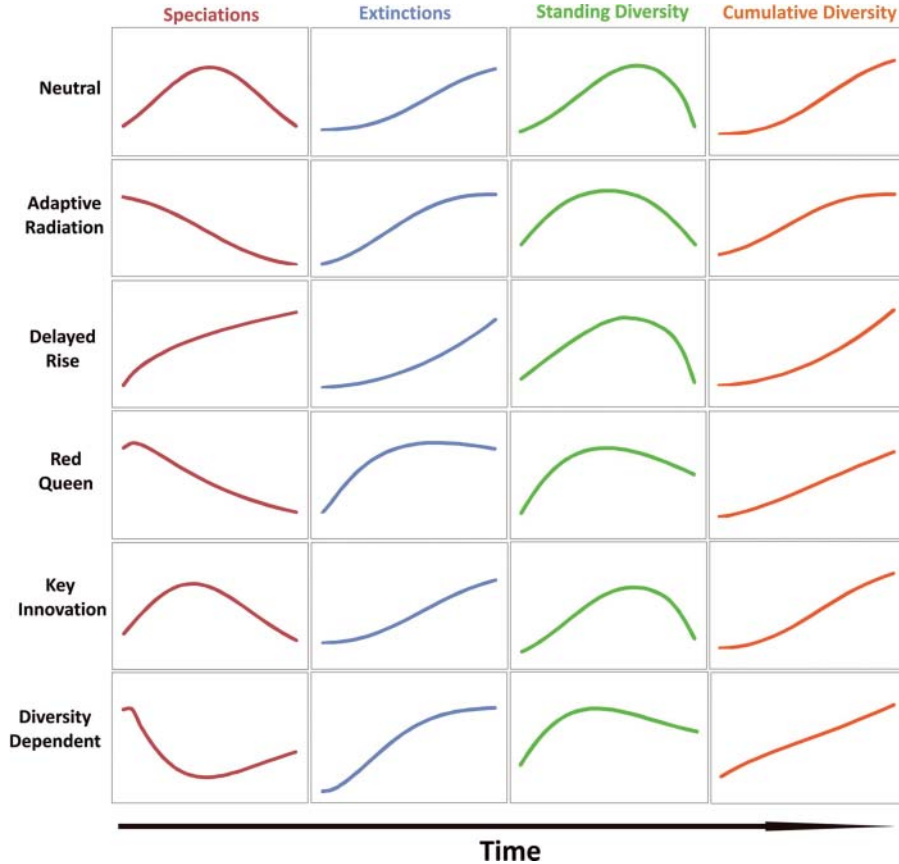


Fig. 1. For each model, we report the expected trajectory of the number of speciations per bin, the number of extinctions per bin, the standing diversity in each bin, and the total number of species to appear since the clade's inception. For each model we simulated a clade with 1000 species distributed over 20 bins of equal length. Time goes from left to right.

left-skewed (Fig. 1). The exponent e is fitted by maximum likelihood optimization and constrained within the range 0–1.

By constraining e to negative values and modifying equation (11) by using the minimum value of tsk :

$$xsk_i = \frac{x_i * tsk_i}{\min(tsk_{1:i})}, \quad (12)$$

it is possible to obtain a model with a right-skewed z distribution. Such a model represents a ‘soft’ version of the *adaptive radiation*, where the highest z value comes early during clade existence but it is not forced to coincide with the very first interval. We dubbed such a model the *key innovation*, meaning that we designed it to represent a situation where the evolution of a given trait promotes a rapid increase of the diversification rate early on during the history of the clade (Fig. 1).

The models presented so far assume extinctions y to be some quantity proportional to the cumulative diversity S_{tot} . Since the latter grows exponentially, y is bound to peak later than z .

By relaxing this assumption, we produced a constant-extinction model, in keeping with Van Valen’s (1973) Red Queen hypothesis. Under the Red Queen, biological interactions are presumed to control diversification, hence its components are just regulated by the intensity of the former in a zero-sum game. Therefore, the probability for a given species to go extinct is independent from the moment of its birth. From this, Van Valen derived his ‘law of constant extinction’ (Liow *et al.*, 2011; Brockhurst *et al.*, 2014). We formulated the Red Queen under the assumption that a constant proportion of a given cohort is always removed by extinction:

$$y_i = z_{i-1} * x_{i-1} * c, \quad (13)$$

where c is fitted by means of maximum likelihood estimation, as usual. Thus, the extinctions curve will have the same shape as the diversity curve (Fig. 1). In the Red Queen model, there is no explicit hypothesis about the shape of z , although it is commonly assumed that an inverse relationship between standing diversity and origination rate is consonant with any model assuming biological controls on species diversity (Walker and Valentine, 1984; Alroy *et al.*, 2008). We therefore decided to model z with the *key innovation* model (that is, z follows an early diversification phase) under the hypothesis that intense biological interactions promote extinction and depress speciation. It is worth noting, however, that whatever shape z takes, the Red Queen hypothesis is satisfied so long as the rate of species extinction per cohort is constant.

One major issue in studies of diversity trends through time is whether diversity itself controls diversification (Harmon and Harrison, 2015; Rabosky and Hurlbert, 2015). Diversity-dependence is not necessarily separated from the *adaptive radiation* model, and could in principle produce adaptive radiation-like diversity paths (Rabosky, 2013). Yet, it is the only model tested here which is explicit about the negative effect of diversity on diversification rate. To model such a relationship, we designed z to be:

$$z_i = s - s \left(\frac{S_{i-1}}{e} \right), \quad (14)$$

where e represents the carrying capacity and s is the diversity at the very first time bin. Both parameters are fitted by maximum likelihood. This implies that the number of species

appearing in a given bin i is inversely proportional to the standing diversity in the previous interval S_{i-1} (Fig. 1). In classic diversity-dependence, the extinction rate reaches its maximum at a given (high) diversity S . Yet, this naively means that S cannot be zero. Therefore, to model clade extinction, we added a positive time-dependence on y :

$$y_i = c + f(x_i * S_{i-1}), \quad (15)$$

where c and f are fitted parameters. The parameter c represents the baseline, and $f(x_i * S_{i-1})$ the time-dependent components of the rate. Under *diversity-dependence*, the function of S will thus be:

$$S_i = S_{i-1} + z_i - y_i. \quad (16)$$

Model discrimination

This work is about discriminating among models (potentially) producing a bell-shaped diversity curve over time. To select the best model among the six candidates clade by clade, we focused on their ability to reproduce the shape of both the absolute and cumulative paths of diversity curve (Fig. 1). We concatenated the S and S_{tot} curves, and minimized the distance between these curves and the real (concatenated S and S_{tot} for each clade) while fitting free parameters by means of maximum likelihood estimation. Model log-likelihoods were then compared by means of the likelihood ratio test and computing Akaike weights (Wagenmakers and Farrell, 2004).

RESULTS

In the fossil data, 25 out of 58 clades (43.1%) present a normal distribution of the diversity curve S , assessed with Lilliefors' test for normality. The models unsurprisingly produce a higher proportion of normal S curves (42 in 58, 72.4%) than the data. The likelihood ratio test strongly discriminates among models. In fact, 62 best models were selected for 58 clades overall (Tables 1, 2), meaning that almost all clades (54/58, 93.1%) are best fitted by a single model only (according to likelihood ratio tests). The frequency of success per model is statistically different from random, whether including (c^2 test $P = 0.0003$) or not including the neutral model (c^2 test $P = 0.0053$) that was the least successful, as expected. Akaike weights confirm the strong discrimination among models (Table 1). The distribution of model success also differs between clades that went extinct and clades that did not go extinct by a mass extinction (c^2 test $P = 0.0099$, Table 2). Overall, the Red Queen (19 times) and the key innovation (18 times) models are the most successful. In general, models including an early diversification phase (adaptive radiation, key innovation, Red Queen, and diversity dependence) are far more successful (54 times the best models collectively) than the neutral and delayed rise (8, out of $2/6 * 58 = 19.3$ expected; Fisher's exact test $P = 0.028$). Repeating tests for model success frequency distribution by removing clades covering less than 10 bins, gives qualitatively the same insight.

Interestingly, not only the distribution, but also the identity of the most successful models is influenced by mass extinctions (Table 2). The frequency of success for the adaptive radiation and diversity-dependent models, restricted to clades terminating by a mass extinction, is in fact higher than expected, while the delayed-rise model is less represented than expected for such clades. Clades terminated by a mass extinction do not have a shorter

Table 1. For each clade analysed, we report the major (most inclusive) clade it belongs to, which diversification model has the best fit (with Akaike weights indicated in parentheses), how many time bins of equal length the clade fossil record is divided into, how many species it includes, the clade's oldest (FA) and youngest (LA) available stratigraphic age, and its stratigraphic duration (which is FA age minus LA age)

Major clade	Clade	Best model	# Bins	# Species	FA	LA	Duration
Ammonites	Acanthoceratidae	Red Queen (100)	10	200	148.15	87.55	60.6
Ammonites	Brancoceratidae	Red Queen (59.3) Neutral (30.9)	8	184	110.8	85.35	25.45
Ammonites	Collignoniceratidae	Key innovation (100)	7	145	182.5	77.75	104.75
Ammonites	Desmoceratidae	Diversity-dependence (100)	19	209	133.2	77.75	55.45
Ammonites	Hildoceratidae	Red Queen (100)	10	321	189.75	153.25	36.5
Ammonites	Hoplitidae	Key innovation (100)	8	118	153.35	97.0	56.35
Ammonites	Neocomitidae	Red Queen (100)	10	172	153.35	117.53	35.82
Ammonites	Oppelidae	Delayed-rise (100)	15	231	173.6	102.5	71.1
Ammonites	Perisphinctidae	Red Queen (100)	10	282	169.65	142.85	26.8
Ammonites	Polyptychitidae	Key innovation (100)	3	134	142.85	133.2	9.65
Anthozoans	Auloporida	Key innovation (85.4) Red Queen (14.6)	37	234	455.2	256.5	198.7
Anthozoans	Cystiphyllida	Key innovation (99.9)	13	269	455.2	385.25	69.95
Anthozoans	Favositida	Delayed-rise (100)	37	903	455.2	233.5	221.7
Anthozoans	Helolitida	Key innovation (100)	15	240	457.75	382.1	75.65
Anthozoans	Stauriida	Key innovation (100)	42	2201	466.35	253.15	213.2
Belemnites	Belemnoidea	Red Queen (100)	16	108	328.75	77.75	251.0
Bivalves	Aviculopectinidae	Diversity-dependence (100) Key innovation (70.8) Red Queen (28.9)	22	118	397.2	106.15	291.05
Bivalves	Halobiidae	Red Queen (28.9)	6	126	244.6	203.6	41
Bivalves	Hippuritidae	Adaptive radiation (100)	4	158	91.8	68.3215	23.4785
Bivalves	Inoceramidae	Red Queen (100)	19	409	199.05	68.3215	130.7285
Bivalves	Myophoriidae	Diversity-dependence (100)	11	105	450.7	203.6	247.1
Bivalves	Pterineidae	Red Queen (100)	26	172	455.2	249.25	205.95
Bivalves	Radiolitidae	Adaptive radiation (100)	8	338	119.025	68.3215	50.7035
Brachiopods	Acrotretida	Delayed-rise (100)	9	114	518.0	432.1	85.9
Brachiopods	Athyridida	Key innovation (100)	28	784	455.2	182.5	272.7
Brachiopods	Atrypida	Red Queen (100)	12	609	466.0	329.8	136.2
Brachiopods	Orthis	Delayed-rise (100)	27	1136	515.15	251.8	263.35

continued overleaf

Table 1.—*Continued*

Major clade	Clade	Best model	# Bins	# Species	FA	LA	Duration
Brachiopods	Orthotetida	Diversity-dependence (100)	22	505	464.75	252.65	212.1
Brachiopods	Pentamerida	Adaptive radiation (100)	13	366	505.75	377.8	127.95
Brachiopods	Productida	Diversity-dependence (100)	23	2247	458.35	251.8	206.55
Brachiopods	Spiriferida	Red Queen (100)	20	1665	446.6	249.25	197.35
Brachiopods	Spiriferinida	Diversity-dependence (100)	25	482	427.2	178.85	248.35
Brachiopods	Strophomenida	Key innovation (100)	21	958	480.05	316.35	163.7
Bryozoans	Cryptostomata	Delayed-rise (100)	11	133	466.35	301.15	165.2
Bryozoans	Cystoporida	Diversity-dependence (100)	18	231	455.2	63.8715	391.3285
Bryozoans	Fenestrata	Adaptive radiation (100)	20	538	437.5	77.75	359.75
Bryozoans	Rhabdomesida	Key innovation (100)	23	196	455.2	213.55	241.65
Bryozoans	Trepostomida	Red Queen (100)	30	716	483.45	148.15	335.3
Echinoderms	Crinozoi	Red Queen (100)	13	190	507.0	385.9	121.1
Gastropods	Bellerophonitidae	Key innovation (95.6)	13	204	464.5	178.8	285.7
Gastropods	Euomphalidae	Delayed-rise (100)	19	180	483.45	68.3215	415.1285
Gastropods	Gosseletinidae	Key innovation (100)	16	288	464.65	102.5	362.15
Gastropods	Lophospiridae	Red Queen (99.6)	16	144	473.35	110.8	362.55
Gastropods	Murchisoniidae	Key innovation (71.3)	12	103	455.2	233.5	221.7
Gastropods	Platyceeratidae	Delayed-rise (100)	12	186	461.75	164.45	297.3
Trilobites	Agnostidae	Diversity-dependence (100)	4	151	515.15	475.2	39.95
Trilobites	Asaphidae	Adaptive radiation (100)	6	178	499.75	446.6	53.15
Trilobites	Bathyruridae	Diversity-dependence (98.1)	3	111	483.45	455.2	28.25
Trilobites	Calymenidae	Adaptive radiation (100)	8	120	475.2	398.0	77.2
Trilobites	Cheiruridae	Red Queen (50)	9	199	469.95	385.9	84.05
Trilobites	Illiaenidae	Key innovation (95.7)	6	103	483.45	422.1	61.35
Trilobites	Odontopleuridae	Red Queen (100)	8	187	464.75	390.0	74.75
Trilobites	Olenidae	Red Queen (97.9)	7	123	515.15	446.6	68.55
Trilobites	Phacopidae	Adaptive radiation (100)	10	115	462.2	362.7	99.5
Trilobites	Proetidae	Key innovation (100)	18	455	463.45	270.25	193.2
Trilobites	Ptychopariidae	Red Queen (100)	4	163	527.5	494.65	32.85
Trilobites	Styginidae	Key innovation (100)	10	136	475.2	379.9	95.3
Trilobites	Tropidocoryphidae	Adaptive radiation (100)	8	166	459.2	377.8	81.4

Table 2. Selection of best models per clade by means of likelihood ratio test

	Neutral	Adaptive radiation	Delayed-rise	Red Queen	Key innovation	Diversity-dependence	Totals
Best model	1	8	7	19	18	9	62
Mass	0	6	2	9	8	6	31
No mass	1	2	5	10	10	3	31

Note: The number of times each model was the best appears in the first row. In the second and third rows, clades (and resulting best models) were partitioned according to whether they went extinct (Mass) or did not go extinct (No mass) during a mass extinction event.

duration (151.7 Ma for mass extinction terminated clades vs. 157.2 Ma, t -test $P = 0.85$). Yet, mass extinction-terminated clades are far richer in species than others, if richness is tested in interaction with their containing clade (ANOVA, mass extinction*major clade: d.f. = 15, $F = 2.055$, $P = 0.031$) to account for intrinsic differences in richness between major clades.

DISCUSSION

Although common to many fossil clades (Foote *et al.*, 2007; Quental and Marshall, 2013), a normally distributed diversity trajectory over time is not a feature emphasized by any particular diversification model. The models we applied are almost equally probable to produce symmetric diversity paths. Whereas the models were specifically meant to produce peaked S trajectories, this indicates that such a pattern should be seen as a normal outcome of the diversification processes, and therefore is more consistent with statistical necessity than with biological explanations (Pigot *et al.*, 2012). In stark contrast, models differ in their fit to the real data. Models including an early burst in diversification are far more effective, in keeping with Quental and Marshall (2013), with the Red Queen and key innovation models being the most successful. In our design, these two models share similar speciation curve trajectories (a right-skewed distribution of the number of species appearing per time bin) but consistently differ in the path of extinction. Under the Red Queen, a constant proportion of species appearing in a given interval was removed in successive intervals, whereas in the key innovation model extinction per bin is a constant proportion of the cumulative diversity, hence accelerating towards younger time bins. Thus, a strong decline in diversification rate over time is predicted by key innovation as a consequence of both increased extinction and reduced speciation numbers, whereas the corresponding decline in diversification in the Red Queen model is much shallower as a consequence of reduced speciation events with time (Fig. 1). While declining diversification rate is commonly found in studies of clade diversification (Nee *et al.*, 1992; Zink and Slowinski, 1995; Harmon *et al.*, 2003; Raia *et al.*, 2013), the steep declining phase predicted by the key innovation model is consistent with evolutionary (historical) controls on diversification, whereas in the Red Queen the decline is modelled so as to depend on the effect of ecological interactions. Evolutionary determinants of species diversification are also pertinent to the adaptive radiation and delayed-rise models (8 and 7 times the best model, respectively, Table 2), while ecological controls pertain to the diversity-dependent model (9 times, Table 2). Thus, our data do not suggest any strong dominance of a class of factors (evolutionary or ecological) over others. Instead, it is worth emphasizing that early rapid speciation and a progressive increase of extinction intensity

over time are the most prominent features of the most successful models, irrespective of whether they were designed to be consistent with evolutionary versus ecological factors. The distinction between these classes of factors is in fact hard (cf. Rabosky, 2013) and possibly of difficult biological interpretation.

It is very interesting that the frequency of successful models depends on whether the clade was terminated by a mass extinction. Such major events wiped out clades before their natural decline, which implies that stratigraphic durations might have been truncated for them. Previous work also suggests that dominant clades are disproportionately affected by mass extinctions (Jablonski, 2001). Our data support the latter notion, but not the former: we found almost equal durations for the two categories, while clades terminating during a mass extinction are statistically more diverse when controlling for the major clade to which they belong.

Since extinction in a mass event is expected to be unrelated to clade viability, clades potentially showing a delayed rise in species diversity are more likely to go extinct before their peak diversity has been reached. Consequently, the likelihood of observing a delayed-rise path is lower for clades going extinct during a mass extinction, which is consistent with our results (Table 2). Similarly, for clades showing a rapid burst in diversification early on, it is more likely that the peak is observed, which translates to a better fit for the adaptive radiation and the density-dependent models when dealing with clades that died out in a mass extinction. Irrespective of mass extinction effects, the key innovation and Red Queen models remain the most successful overall. They share a similar speciation path, which was built so that the rate of species appearance in the record rises very rapidly early on and then declines gently. Since the key innovation and the Red Queen models are almost equally successful (and far more so than any other model) but differ from each other in terms of the path of extinction, we conclude that their path of speciation is a very robust generalization, shared by most animal clades. It is consistent with both evolutionary and ecological factors (or better a combination of the two, see above), and explained by the idea that the opportunity for speciation is inversely related to species (standing) diversity (Sepkoski, 1981, 1984; Alroy *et al.*, 2008; Phillimore and Price, 2008; Losos and Mahler, 2010; Etienne *et al.*, 2012; Rabosky, 2013; Rabosky and Hurlbert, 2015). This means that whatever the reason for the early burst is [either the acquisition of a key innovation, or relaxation from competition to an incumbent group via its extinction or decline (Simpson, 1944, 1953; Van Valen, 1973, 1980; Stanley, 1979; Benton, 1987; Hallam, 1987; Schluter, 2000; Rundell and Price, 2009; Liow *et al.*, 2011; Quental and Marshall, 2013)], such an early burst is a common and ubiquitous feature of clade history. Exactly because the trigger of the early burst can be either evolutionary or ecological, we argue that the separation of these two factors in explaining patterns of clade diversification may be of little significance. This would also account for the observation that for some models both these factors can equally likely be advocated [e.g. Rabosky (2013) on density-dependence]. An alternative interpretation is that in many instances evolutionary factors (e.g. the extinction of a competing, diverse group, the acquisition of a key innovation) might just characterize the early phase of clade diversification, whereas purely ecological factors (e.g. the negative effect of diversity on diversification) might come into play later on. Under both scenarios, the separation of ecological and evolutionary factors as determinants of the biodiversity path would appear unnecessary.

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