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# The challenges to inferring the regulators of biodiversity in deep time

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3 **Abstract**  
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5 Attempts to infer the ecological drivers of macroevolution in deep time have long drawn  
6 inspiration from work on extant systems, but long-term evolutionary and geological  
7 changes complicate the simple extrapolation of such theory. Recent efforts to  
8 incorporate a more informed ecology into macroevolution have moved beyond the  
9 descriptive, seeking to isolate generating mechanisms and produce testable hypotheses  
10 of how groups of organisms usurp each other or co-exist over vast timespans. This  
11 Theme Issue was planned to exemplify this progress, providing a series of case studies  
12 of how novel modelling approaches are helping infer the regulators of biodiversity in  
13 deep time. In this Introduction, we explore the challenges of these new approaches.  
14 First, we discuss how our choices of taxonomic units have implications for the  
15 conclusions drawn. Second, we emphasize the need to embrace the interdependence of  
16 biotic and abiotic change, because no living organism ignores its environment. Third, in  
17 the light of parts 1 and 2, we discuss the set of dynamic signatures that we might expect  
18 to observe in the fossil record. Finally, we ask whether these dynamics represent the  
19 most ecologically informative foci for research efforts aimed at inferring the regulators  
20 of biodiversity in deep time. The papers in this Theme Issue contribute in each of these  
21 areas.  
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## 1. Introduction

Organisms respond to their environments. This link regulates biodiversity, but its complexity complicates efforts to provide unequivocal evidence for supposedly simple expectations. The challenge is to disentangle how environmental, ecological and evolutionary processes interact in deep time when they cannot be observed directly. Palaeobiology and evolutionary biology have long drawn inspiration from methods initially developed for population ecology [1, 2], where the chief regulator of biodiversity is often purported to be density-dependence: population growth rate falls as population size increases due to resource limitation [3]. The co-option of population ecological theory into palaeobiology has a distinguished history [4], but a simple re-interpretation of elementary ecology to the macroecological and macroevolutionary scale is compromised by the vast timespans, which provide scope for environmental, (micro)evolutionary and geological change. Simple plots of species' diversity through time reveal coarse dynamical patterns of how the diversity of life on Earth has fluctuated [5], but do not uncover which underlying mechanisms generate such higher-level patterns [6].

The outcomes of interactions among living organisms can be experimentally manipulated to tease apart direct causes of births and deaths. These interactions can have negative (competition, predation) or positive (mutualism, symbiosis) consequences for a focal species. The outcome of the interactions depends on the abiotic arena in which those species co-exist: the victorious species in ecological competition is the one that can persist on the lowest amount of the limiting resource [7]. It is difficult to move from small-scale experiments to large temporal and spatial scales [8] because of substantial changes in the terms of reference: carrying capacities in population biology restrict population growth directly by resource limitation [3, 9], whereas an analogous limit at supraspecific level, and over hundreds of thousands or millions of years, would be an emergent higher-level phenomenon from genuine interactions among individuals moving together through space and time.

Traditionally, deep-time regulators of biodiversity have polarised into biotic vs. abiotic controls [6], with biotic interactions argued to dominate in the near term and abiotic upheaval imparting the clearer signal over long time scales [10]. The biotic, organismal, ecological perspective is commonly associated with the Red Queen hypothesis originally proposed by Van Valen to explain the apparently age-independent

1 extinction probabilities among ecologically homogeneous groups [11]. In his original  
2 formulation, Van Valen considered the deterioration of the environment to include both  
3 the biotic and abiotic environment, but palaeontologists have usually credited most  
4 biodiversity change to abiotic factors [10, 12]. The false dichotomy between the  
5 supposed superiority of biotic versus abiotic factors in regulating biodiversity [6, 10,  
6 13] echoes the analogous debate in population ecology [9]. While population ecologists  
7 concluded that the abiotic environment acts as soft tissue on top of a hard density-  
8 dependent “skeleton” [9], ecologists working in deep time have to accept that any  
9 purported diversity dependent analogy is an emergent property from accumulating  
10 organismal responses to the biotic and abiotic environments with which they interact.  
11 These organismal responses are liable to evolve substantially through time.

12 Evolutionary rates multiply by many orders of magnitude when measured at  
13 laboratory scales of days and months, when compared to historical time spans of years  
14 and decades and palaeontological spans of millions, or hundreds of millions, of years  
15 [14]. Analysts are in effect measuring different aspects of a single fractal phenomenon  
16 where some rates are generational changes, while others are the outcomes of  
17 phenomena averaged over long-term environmental change. Most palaeontologists will  
18 never be as confident as experimental biologists that the individuals and species they  
19 study genuinely interacted at a given time in a given location, but that does not mean  
20 that it is impossible to study biotic interactions in deep time. Indeed, progress towards  
21 more ecologically informed macroevolution has shifted over the past five years from a  
22 predominantly descriptive pattern-based approach [15], to one in which we now aim to  
23 isolate which ecological mechanisms determined the origination, proliferation and  
24 extinction of biodiversity.

25 This Theme Issue aims to synthesize this progress. Our introduction to the  
26 manuscripts, which reviews the state of the art and showcases advances in  
27 contemporary modelling and data extraction techniques, lays the foundations required  
28 for methods to extract the mechanisms that regulate biodiversity in deep time. We  
29 begin with how our analytical choices affect the results we obtain.

## 30 31 32 **2. Individuals, populations, species and genera**

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3 1 Although ecologists can characterize biodiversity more broadly than simply counting  
4 2 species, most deep-time studies cannot directly quantify abundance or biomass data. A  
5 3 few notable exceptions exist: coarse estimates suggest that biomass [16] and primary  
6 4 productivity [17] might have increased during the Phanerozoic. While a few taxon-free  
7 5 approaches infer the structure and stability of food webs [18] or characterize the  
8 6 patterns of ecospace occupancy [19, 20], deep-time investigations into the regulators of  
9 7 biodiversity are, for the most part, limited to counting taxonomic units through time.

10 8 Linnaeus wrote in *Fundamenta Botanica* that both genus and species are genuine  
11 9 entities of nature [21]. Mayr [22] argued that species, now considered the canonical unit  
12 10 for macroevolution, obey ecological rules, but conceded that genera also represent a  
13 11 biological reality. The integrated taxonomic evidence that distinct genera occupy  
14 12 morphospace discontinuously and rarely hybridize among themselves due to their long  
15 13 histories of separation [23] support the basic tenet for reproductively isolated  
16 14 taxonomic units. The same could be argued for any higher, clade-based taxa, whatever  
17 15 category names one might wish to apply, provided they reflect fundamentally different  
18 16 organismal constructions.

19 17 Acknowledging all the vagaries of matching category terms to clades, Benton [5]  
20 18 showed broadly similar genus and species diversity curves, both of which differed  
21 19 markedly from the corresponding higher order and family curves [See also 24 for an  
22 20 updated version on the Carnivora]. The smoothness at higher taxonomic levels (e.g.  
23 21 families and orders) and the apparent evidence for upper limits to diversity [4, 5] is, in  
24 22 part, a function of artificial constructs (naming by scientists), in part incompleteness  
25 23 and structure of the rock record [25, 26] and also some genuine biotic interactions. A  
26 24 logistic curve at the level of orders or classes might mask increasing diversification at  
27 25 species level within a continuously branching tree [5], but need not correspond in any  
28 26 simple way to lower-level processes: the marine invertebrates, for example, reach a  
29 27 single equilibrium without the component clades doing so [27].

30 28 Given that morphology and species classification within taxa are not necessarily  
31 29 coupled [28], the different diversity trajectories among different levels of the taxonomic  
32 30 hierarchy [5] result in part from taxonomic practices that influence extinction risk [29].  
33 31 Raup [30] proposed that if species follow Van Valen's law [11] of random extinction  
34 32 with respect to age among homogeneous groups, then genera cannot. There is a  
35 33 difference between the durations of species and genera because species' longevity is

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3 1 determined solely by extinction, assuming genuine speciation occurred in the first  
4 2 instance, whereas the longevity of a genus is determined by both speciation and  
5 3 extinction of the constituent species. Additional confusion of macroevolutionary  
6 4 longevity arises through pseudospeciation and pseudoextinction [31], which occur  
7 5 when sufficient anagenetic change causes scientists to award a new name to a novel  
8 6 morphological form despite a lack of cladogenetic lineage splitting. Such  
9 7 pseudospeciated morphospecies are therefore often named from the anagenetic  
10 8 appearance of a novel character rather than post-speciation divergence from an  
11 9 ancestral species.

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20 To illustrate how taxonomic practices and taxonomic resolution impact our ability  
21 11 to reject fundamental evolutionary laws, we analysed durations of Cenozoic Era  
22 12 macroperforate planktonic foraminifer genera, evolutionary species *sensu* Simpson  
23 13 [defined by the first appearance of a morphological gap, i.e. post-speciation divergence,  
24 14 between sister taxa, 29, 31, 32]) and morphospecies (defined by the first appearance of  
25 15 a novel character) compiled by Aze *et al.* [33]. To ensure we were comparing  
26 16 homogeneous groups of species [11], we followed Ezard *et al.* [13] in assigning  
27 17 morphological innovations associated with feeding ecology and depth habitat to each  
28 18 species or genus, and accounted for the changing Cenozoic climate using the Zachos *et*  
29 19 *al.* [34, 35]  $\delta^{18}\text{O}$  oxygen isotope compilation of deep sea benthic carbonates and the  
30 20 changing biotic environment using the natural logarithm of the number of  
31 21 contemporaneous morphospecies, evolutionary species or genera (as appropriate). All  
32 22 these explanatory variables were fixed at origination, which encodes the idea that  
33 23 conditions early in a species' or genus' existence leave long-lasting signatures on its  
34 24 duration [36]. Morphospecies and evolutionary species show age-specific patterns of  
35 25 extinction: extinction risk increases with the age of each species [See also 37 for  
36 26 morphospecies. These morphospecies and evolutionary species' results were published  
37 27 in 29.]. The genus durations, on the other hand, cannot be distinguished from Van  
38 28 Valen's law of constant extinction (Fig. 1), although part of that failure to reject is likely  
39 29 due to the much lower sample size of genus vs. species counts. Interpreting these  
40 30 numbers, including the possibility that the age-specific extinction patterns arise due to a  
41 31 veil line (implying we fail to document the shortest-lived species), demonstrates how  
42 32 analysing different levels of the Linnaean hierarchy can generate different extinction



1 risks during a taxon's existence. Altered extinction risks change species longevities,  
2 which, as a consequence, change the strength of any inferred diversity-dependent  
3 regulation [29].

4 The empirical correspondence between the species and genus diversity curves [5]  
5 should not therefore be taken to imply that analyses at either species or genus level are  
6 equivalent. Genus-level origination encodes substantially more divergent ecologies than  
7 those perceived by speciation: higher taxonomy is, in one sense, a crude index of  
8 morphological disparity through time [38]. If speciation is in fact a rather easy and  
9 common process that perpetually produces ecologically similar species [39], then it  
10 could be argued that the limits to long-term equilibrium models of diversification [40]  
11 are not regulated by speciation but rather by origination of evolutionarily significant  
12 units at higher taxonomic levels [41-44]. Equilibrial assumptions are more common for  
13 species-level analyses performed by neontologists than analyses on higher taxa [45],  
14 which contradicts the empirical paleontological evidence [5] and standard  
15 palaeontological practice [4, 27, 46-48].

16 The assumption of the species as the canonical unit of study has long held, but the  
17 inconvenient truth is that a species, like all higher-order taxa in the Linnaean system,  
18 contains heterogeneous amounts of intraspecific variation through the spatial  
19 organisation of populations and distribution of cryptic genetic types. The reality is that  
20 genera and species both contain relevant, but distinct, information for what regulates  
21 biodiversity over long time scales. The re-emergence of the biological reality of higher  
22 taxa has in part been stimulated through the increasing size of molecular phylogenies,  
23 and thus statistical power, to identify multiple thresholds which reveal that molecular  
24 diversification cannot be explained by species-level divergences alone [41, 42]. The  
25 more resolved level exhibits greater fluctuations [4], which may or may not be of  
26 genuine biological interest for identifying the principles behind patterns of biodiversity.

### 27 28 29 **3. Biotic and abiotic contributions to stochastic macroevolutionary** 30 **dynamics**

31 Sepkoski argued that a stochastic version of his fixed finite upper limit to taxon  
32 diversity was "probably more typical of natural systems" than his deterministic  
33 analytical solutions [4]. Population ecologists have long used year-to-year fluctuations



1 in abundance to reveal that environmental stochasticity acts on a density-dependent  
2 framework [9, 49]. One simplistic partitioning [49, 50] is that the cause of any deviation  
3 from a deterministic density-dependent framework is either due to an environmental  
4 factor that affects the realised fitness of all individuals concurrently (environmental  
5 stochasticity:  $\sigma_e^2$ ), or due to winners and losers from particular individual interactions  
6 that average out in the long term (demographic stochasticity:  $\sigma_{\square}^2$ ). Taken together, year-  
7 to-year fluctuations in population abundance can be written as:

$$\sigma_{\lambda}^2 = \sigma_e^2 + \frac{\sigma_{\square}^2}{\square}$$

8  
9 Demographic stochasticity is defined by a sum of squares statistic for the relative  
10 variation among individual fitnesses in a given time interval. Environmental  
11 stochasticity is calculated by the residual of observed vs. expected change, minus the  
12 difference caused by individual interactions [51], and therefore assumes a uniform  
13 response in all individuals (e.g. in our context here, an increase in background  
14 origination rates). While this binary classification forms a crass straw man, this  
15 simplistic polarisation echoes the palaeobiological dichotomy into either the biotic,  
16 organismal Red Queen school [11, 52], or the supposed alternative of an abiotic,  
17 environmental Court Jester [12]. The mutual dependence between the hypotheses has  
18 only recently been acknowledged [6, 10, 13].

19 Assuming that the number of species saturates following logistic growth [4],  
20 calculating environmental and demographic stochasticity statistics for evolutionary  
21 species of Cenozoic Era macroperforate planktonic foraminifera [33] suggests that  
22 differential responses among species explains, on average, about three times as much  
23 variation as the changing environment (0.087 vs. 0.029). This result is unsurprising. The  
24 waxing and waning of relative abundance reported at species [13, 53] and genus levels  
25 [27, 54], as well as among higher taxa [55], is evidence that there are always winners  
26 and losers from environmental change. In deep time, the key challenge is to identify  
27 why some groups of species are winners and others losers, beyond the patterns that can  
28 be generated assuming neutral dynamics [56, 57].

29 The stochastic population theory used above [49, 51] predicts that environmental  
30 stochasticity will dominate dynamics for sufficiently large populations (i.e.  $N$  large) such

1 that the differences among individuals can therefore be neglected. In our example,  
2 demographic stochasticity dominates because the units are species, which are much less  
3 abundant than individuals. The species-area relationship is one of the best ecological  
4 laws in determining the number of species that can co-exist within a given biome, but  
5 the fragmentation of an area has been argued to be as influential as area per se in terms  
6 of driving macroevolutionary diversification shifts [58, 59]. In this volume, Jordan et al.  
7 [60] find that neutral theory, in which all species are assumed to be functionally  
8 equivalent [56] on a fragmenting super-continent cannot explain the post-Jurassic  
9 increase in terrestrial species richness. The results suggest a role for some biotic factors,  
10 either a competitive advantage or some other founder effect over and above geographic  
11 isolation, in the subsequent adaptation and expansion of the clade, even if the precise  
12 generating mechanism remains to be identified.

13 After demographic and environmental stochasticity, the third fundamental cause  
14 of fluctuations in population dynamics is measurement error [50]. Palaeontologists  
15 have to worry about which fossils enter the rocks and which fossils are found [61].  
16 Preservation biases include organismal factors (skeletons or not; slow or fast  
17 reproducers; population size), their habitats (marine, river, and lake settings are more  
18 often preserved than coasts, uplands and forests), and the subsequent history of the  
19 rock (is it eroded or buried; is it metamorphosed or not; is it covered by younger  
20 rocks?). Human biases include accessibility (is the rock at the surface; is the rock in  
21 reach of people?), geographic location (e.g. Europe vs. South America), and research  
22 interest (e.g. diatoms vs. dinosaurs). On the whole, older rocks are less available than  
23 younger rocks because the chances of burial under younger rocks increase with age.  
24 Much emphasis has been placed on this temporal pattern: Raup [61] and Alroy [27]  
25 argue that this burial bias explains nearly all of the substantial rise in biodiversity  
26 through the Phanerozoic, and tie this to a model in which global biodiversity reached  
27 modern levels over 400 Myr ago.

28 The biased distribution of fossils in time and/or space motivated the development  
29 of methods to “correct” for the vagaries of the rock record [62-65]. Commonly used  
30 sampling proxies, such as counts of collections, localities, or formations, accrue in close  
31 connection with the species count [66]. Residuals-based approaches [64, 65] compare a  
32 sampling proxy (e.g. formations count; rock outcrop area) and then identify and remove  
33 a sampling trend, with the residuals from the trend line interpreted as the true

1 biological signal. Acknowledging the limitations of formation counts as a sampling  
2 indicator, it remains controversial whether the correlation between rock and species  
3 counts, or the residuals from that correlation, represents the holy grail of biological  
4 truth [66]. Rarefaction [62] and shareholder quorum subsampling [27] have proven less  
5 controversial methods, but still imply that the geological drives the biological.  
6 Integrated approaches, which calculate the error due to incomplete preservation and  
7 biological diversity simultaneously, promise to place both on an even footing [24, 67-  
8 70].

9 In this volume, Starrfelt & Liow [71] propose a method to identify true levels of  
10 bias, and so true levels of historical biodiversity, for particular clades in the fossil  
11 record. Their new TRiPS method (True Richness estimated using a Poisson Sampling  
12 model) is based on the assumption that a particular fossil species, if observed multiple  
13 times in a given time interval, has a relatively high probability of fossilization and  
14 discovery by palaeontologists. Starrfelt & Liow apply their method to the fossil record of  
15 dinosaurs, and estimate that there were 1536 genera and 1936 species of dinosaurs in  
16 all, and that the numbers tramping across the Earth at any time ranged up to 300 in the  
17 latest Cretaceous, when diversity was highest. The method could revolutionise the ways  
18 in which palaeontologists and evolutionists in general treat fossil record data on ancient  
19 biodiversity.

20 The difficulty of extracting the biological signal from the geological noise was  
21 formalised by Raup *et al.*'s [72] pioneering work simulating phylogenetic diversification.  
22 At a given point in time, Raup *et al.* [72] assumed that each species has an equal  
23 probability of going extinct and an equal probability of giving rise to a descendant  
24 daughter species. These assumptions evoke the equal-rates Markov model of  
25 diversification [57] and Hubbell's Neutral Theory [56] for a clade fluctuating around its  
26 supposed equilibrium (assuming, in the latter case, that the birth and death rates are  
27 similar). A simple null model with constant rates was able to recover the diversity  
28 trajectories seen in the fossil record without recourse to ecological explanation [72].  
29 "Familiarity with the 'patterns' that random processes create is ... essential" for all  
30 scientists [57] because "it is fatally easy to read a pattern into stochastically generated  
31 data" [73]. Asserting a role for ecological regulators of biodiversity requires the  
32 rejection of appropriate null models that incorporate the temporal inconsistencies of  
33 fossilisation [57]. Systematic geological structure can generate seductive impressions

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3 1 on macroevolutionary signals, such as bursts of genus origination [26], the clumping of  
4 2 last occurrence dates into apparently accelerated extinction events [74] as the ranges of  
5 3 higher-taxa are bounded by mass extinctions [75]. Despite this warning for any literal  
6 4 reading of the fossil record [72], running Raup *et al.*'s simulations using empirically  
7 5 defined parameter estimates suggested that the fluctuations in fossil taxon counts most  
8 6 likely result from changes in the diversification dynamics rather than a constant-rate  
9 7 stochastic process [76].  
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#### 10 **4. The regulators and their signatures**

11 Macroevolutionary diversification is the net outcome of speciation and extinction. The  
12 regulators of biodiversity act differentially through these two rates as different  
13 ecologies compete with each another, filtering global biotic and abiotic environmental  
14 change, to shape variation among contemporaneous species in their speciation  
15 probability and extinction risk (Fig. 2). Understanding the interplay between  
16 organismal biology and environmental change holds the key to identifying the  
17 generating mechanisms of macroevolutionary dynamics [13].

18 Although fossil data are increasingly being used in phylogenetic comparative  
19 methods [69, 70, 77], the key interaction between biology and the environment is still  
20 rarely incorporated. This is in part explained by the lack of methods, but also by the  
21 nature of the data. Phylogenetic studies using only extant taxa often reconstruct  
22 evolutionary history from a single time slice and are therefore blind to dynamic  
23 associations between biological and environmental change, as well as sequential  
24 evolutionary changes that influence the evolutionary fate of lineages [78]. This coupling  
25 of the biotic response to abiotic environmental change emphasises one limitation of a  
26 simple extrapolation of population ecology theory into a macroevolutionary context.  
27 Sepkoski [4] assumed a single fixed equilibrium level of species diversity through  
28 hundreds of millions of years, which is a strong assumption if we hypothesise that  
29 environmental resources affect the outcome of competition [79] in deep time [46, 80].

30 Competitive interactions might be the most commonly discussed biotic driver of  
31 diversification rate changes. Both origination and extinction rates have been reported as  
32 diversity-dependent and both can generate equilibrial dynamics in biodiversity [4, 81,  
33 82]. At a finer taxonomic resolution than assumed by Alroy [81] or Foote [82],

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3 1 speciation rate seems to respond more closely than extinction rate to changes in within-  
4 2 clade diversity [Fig. 3, see also 13, 46], but this balance of influence need not be constant  
5 3 for all time [82]. Species interactions are increasingly being recognised as capable of  
6 4 leaving an impact on clade diversification through a variety of modes [83, 84] and not  
7 5 simply slowdowns in diversification rate with increasing levels of standing diversity  
8 6 [85, 86].

9 7 The dominant mode of macroevolutionary competition likely depends on how we  
10 8 define its arena. Unlike the case in Figure 3, which analyses the whole Canidae family as  
11 9 a homogeneous unit, Silvestro *et al.* [53] reported little diversity-dependent speciation  
12 10 within each Canidae subfamily as a distinct guild [87] and evoked interspecific  
13 11 competition among subfamilies in a broader species pool, in which all species compete  
14 12 for similar resources. Under such a scenario, clade replacement selectively drives less  
15 13 competitive guilds to extinction [87]. This difference between Figure 3 and Silvestro *et*  
16 14 *al.* [53] leads to the more refined hypothesis that biotic competition *between* closely  
17 15 interacting groups of species will leave a signature in extinction rates, whereas  
18 16 competition *within* closely interacting groups of species will leave a signature in  
19 17 speciation probability.

20 18 Developing this line of thought, Marshall & Quental [88] explore the hotly debated  
21 19 question of limits on diversification [40, 80]. Verbal interpretations of a diversity  
22 20 dependence mechanism built into a dynamic carrying capacity exist [40, 89], but an  
23 21 environmental regulator of such dynamic limits has not been identified statistically.  
24 22 Marshall & Quental [88] argue that an appropriate definition of the species pool and the  
25 23 consideration of time-variable carrying capacities could reconcile evidence of bounded  
26 24 versus unbounded diversification. The authors propose a diversity-dependent  
27 25 modelling framework with a carrying capacity varying through time as a result of  
28 26 changing either intrinsic diversification rates or the strength of the diversity-dependent  
29 27 effect. Importantly, their approach allows resolution of a long-standing debate about  
30 28 whether total global biodiversity has been held at equilibrium levels for long spans of  
31 29 time, or whether global biodiversity never reaches such levels.

32 30 Global-scale analyses are fundamentally restricted by biogeographical variation.  
33 31 The latitudinal diversity gradient is one of the most frequently described  
34 32 macroecological patterns [90], but has not been constant through time [91]. The tropics  
35 33 are cited as both a cradle of and a museum for diversity [92, 93], with the consequence

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3 1 being that these biomes act as net exporters of biodiversity to other regions [93, 94]. In  
4 this volume, Fenton *et al.* [95] investigate when and how the modern latitudinal  
5 diversity gradient in calcareous zooplankton became established. The authors construct  
6 latitudinal diversity gradients in deep time as an independent dataset to assess whether  
7 any putative driver has a dominant underlying cause or reflects multiple factors acting  
8 in concert [92, 93], including the statistical artefact of the mid-domain effect [96].  
9 Fenton *et al.* [95] demonstrate no latitudinal diversity gradient at the beginning of the  
10 Eocene epoch, but that the modern day pattern was established by the Eocene-  
11 Oligocene Transition 33.7 Mya.

12  
13 If specialist species depend intimately on their native biome to persist, then any  
14 climate change that alters the spatial extent of these biomes will rapidly lead to their  
15 extinction. Exploring the interactions of species and their geographic ranges over  
16 ecological and evolutionary time scales has been hard. In this volume, Villalobos *et al.*  
17 [97] explore how species co-occur with other species, and find that in the long term  
18 species respond individualistically to major climatic shifts, while more stable climates  
19 allowed less phylogenetically variable, yet richer palaeocommunities to settle. The  
20 authors calculate phylogenetic fields, the co-occurrence patterns among species and  
21 their phylogenetic structure within individual species ranges, for living and extinct  
22 mammal species over long spans of time, to explore how individual species interact with  
23 predators, prey, and competitors, and with major changes in physical environments.

24  
25 Although these methods can be readily applied in deep time, reconstructing  
26 species interactions is only useful when the spatial distribution of communities can be  
27 accurately estimated. The preservational biases of the fossil record are exacerbated  
28 when variations through space and time require analytical attention. In this volume,  
29 Silvestro *et al.* [98] develop flexible new dispersal-extinction approaches that use fossil  
30 data to infer macroevolutionary and biogeographical processes while taking into  
31 account the incompleteness (temporal and spatial) of the fossil record [99, 100]. The  
32 impact of migration is not symmetric [98, 101], implying a role for biotic interactions  
33 among already existing species and the new invaders in determining macroevolutionary  
34 fates. A major problem with most methods that use extant data only is the fact that  
35 ancestral geographic ranges inferred from phylogenies might be blind to local past  
36 extinction and temporal changes in the asymmetry of dispersal rates. Silvestro *et al.*  
37 [98] applied their method to a genus-level empirical dataset of Cenozoic terrestrial



1 plants. Their empirical results suggest a predominant dispersal from Eurasia to North  
2 America in the Eocene climatic cooling period, but a higher dispersal from North  
3 America to Eurasia during the more stable climatic period between 32 and 14 Ma. The  
4 most recent 10 My are characterized by a more symmetric dispersal between both  
5 continents, although higher extinction rates in Eurasia.

6 Empirical studies focus increasingly on geographical range as a predictor of  
7 extinction, but evidence is mixed: large geographic range buffers fossil taxa against  
8 background extinction [102] and contemporary extinction risk [103], but might be futile  
9 in the face of mass extinction [104]. Geographic range forms a composite trait not  
10 expressed by individuals but by the populations they form, i.e. is, like a putative upper  
11 limit to species richness, another emergent phenomenon from lower-level processes.  
12 While space can reveal the extent of a given ecological interaction, and different spatial  
13 extents impact the probability of speciation [105] and extinction [49], unpicking any  
14 ecological catalyst of macroevolution requires identification of the characters that  
15 define a species' functional role in their communities [20].

## 18 **5. Beyond counts and towards ecological significance.**

19 While most deep-time studies on biodiversity dynamics focus on counting taxa  
20 (however defined), such counts have limited ability to indicate ecosystem functioning  
21 [106]. Phenotypic traits provide this ecosystem functioning and determine the  
22 ecological redundancy of given species within a community [107]. Experimental studies  
23 indicate that initial species losses have relatively little impact on the healthy functioning  
24 of the ecosystem, but that increasing drops in species richness provoke increasing  
25 declines of functioning through non-linear feedbacks [108]. The limitations of taxon  
26 counts as a coarse presence/absence metric for inferring the link between organism and  
27 its environment have long been acknowledged, as have those of simply measuring  
28 abundance. "It is time we stopped simply counting taxa and tracking their numbers over  
29 time, and began looking at them, measuring them and estimating their ecological roles"  
30 [109]. Mass extinction events generate high levels of species extinction, but might  
31 slightly reduce [110] or fundamentally change [111] ecological functioning in the clade.  
32 More informative dimensions exist and better describe the state of a given assemblage  
33 or community [95, 106, 112].



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3 1 Missa & Morlon [113] use computer simulations to show, under Neutral Theory  
4 2 [56] with alternative modes of speciation, that species-area relationships and species-  
5 3 abundance distributions reach their equilibriums after species richness. Phylogenetic  
6 4 patterns of biodiversity either do not (e.g. phylogenetic diversity) or take far longer to  
7 5 converge (e.g. tree imbalance and gamma statistics). The authors also show that the  
8 6 mode and magnitude of speciation strongly affect the time taken for ecological patterns  
9 7 to reach their equilibrium. The authors conclude: "Given that real metacommunities  
10 8 may not have reached equilibrium in terms of species richness, it would be unwise for  
11 9 users of the Neutral Theory of Biodiversity to continue assuming that other biodiversity  
12 10 patterns, which take even longer to converge to equilibrium, are themselves at  
13 11 equilibrium."

14 12 One of the reasons for the resurgence of interest in higher taxa is that they, if  
15 13 robustly defined, are more intimately linked to fundamental morphological  
16 14 reconfiguration than species [38]. The principal way in which functional types are  
17 15 defined in deep time is by assigning ecological roles to certain characters [114]. The  
18 16 environment moderates both the number of ways that organisms can persist, and also  
19 17 the efficiency of a particular method: the number of hypercarnivores, defined by a  
20 18 common dental morphology [115], has been roughly constant through time, despite  
21 19 ongoing turnover in named species [116]. Although taxon diversity and morphological  
22 20 disparity are not always coupled [117], morphological disparity within a clade typically  
23 21 saturates more rapidly than taxon diversity counts [118]. Obtaining accurate estimates  
24 22 of this disparity is fundamental to adoption of trait-based approaches for their use in  
25 23 inferring niche breadth and stability, as well as the strength of ecological interactions  
26 24 [119, 120]. In this volume, Hsiang et al. [121] describe algorithmic procedures to rapidly  
27 25 extract size and shape phenotypic data in microfossil communities, providing the robust  
28 26 sample sizes from which trait (co)variation can be accurately estimated. Hsiang et al.  
29 27 [121] use their workflow to compare and contrast dendrograms obtained through  
30 28 morphological, ecological, and phylogenetic data. Another potential use is to compare  
31 29 the multivariate morphological data that underpins the dendrograms and so assess the  
32 30 relative contributions of evolutionary or ecological processes via simultaneous  
33 31 alterations to phylogeny, environment and species abundance. A focus on  
34 32 morphological traits promises to "bind the past and present together" [122] as a  
35 33 common analytical currency for analysis in deep time and the present day. The

1 challenge ahead is therefore to identify ecologically meaningful traits that are  
2 incompletely rendered by higher taxon definitions [122, 123].

3 Although the fossil record is the most direct way to access the role of different  
4 regulators [78], it has also, until recently, been blind to preservation of certain body  
5 parts and physiological functions that might be very relevant ecologically. In this  
6 volume, Trueman *et al.* [124] review ecogeochemical methods to recover individual  
7 scale information from macrofossil remains, and thus study food web structure,  
8 nutrient fluxes and population connectivity in contemporary deep sea fish systems.  
9 Deep-sea fishes share with fossils many of the problems in extracting trait data:  
10 difficult-to-access material and vanishingly rare evidence of direct interactions among  
11 individuals. The authors provide a balanced perspective of the potential impact of the  
12 approach. While evidence exists that symbiosis influences macroevolutionary dynamics  
13 in deep time [13], other areas are less well understood: trace element analysis can  
14 indicate population connectivity in the focal modern deep sea fishes, but remain  
15 unproven in deep time [124]. Adoption of such techniques to yield data on behaviour  
16 and physiology promises a more holistic (beyond morphology) view of the interplay  
17 between organism and its environment in deep time.

18 Selection pressure and long-term rates of evolution are regulated by ecological  
19 opportunity [125], but any response to selection depends on individual form [126, 127].  
20 Individual form matters because individuals in species are characterised by a distinctive  
21 set of traits, many of which covary. Selection on one trait can generate a response to  
22 selection in others [127], implying that we need multivariate approaches within  
23 functional modules [128]. The decoupling of size and wing shape, for example, differs  
24 among distinct subfamilies of fossil birds and occurred as a precursor to flight [129].  
25 Despite Simpson's evocative "choppy sea" metaphor of a dynamic adaptive landscape  
26 [130], there are "dismally few" empirical estimates of how the constraints imposed by  
27 trait covariance evolves during a species' existence [131].

28 Multivariate changes in ecologically relevant traits offer strong potential to better  
29 understand the processes that bridge micro- and macroevolution [132]. If there are no  
30 strictly macroevolutionary processes [133], then we need a finer resolution to unpick  
31 the circumstances that promote ecological divergence to become fixed through some  
32 speciation events, but not in others. Coarse macroecological proxies, even when  
33 calculated as integrated variables over the whole duration of each lineage [134], show

1 negligible explanatory power to predict molecular divergence, albeit among a very  
2 limited number of species [135] evoking the hypothesis that molecular divergence is  
3 accelerated during speciation events [136]. It is now widely accepted that evolutionary  
4 divergence can be rapid [14, 137], and its rate covaries negatively with the interval  
5 being studied [14]. While diversity dynamics need the fossil record to understand the  
6 dual roles of speciation and extinction [78], fine temporal resolution might reveal that  
7 the ecological regulators of biodiversity actually operate chiefly in a punctuated fashion  
8 during post-speciation divergence, rather than throughout a species' existence once its  
9 ecological role is, to a large extent, established.

## 10 11 **6. Conclusion**

12 *"It is my hope that future work will not reject the question of competition*  
13 *in macroevolution out of hand, but will explore it with new models that*  
14 *are more sophisticated than coupled logistic equations and can use these*  
15 *accumulating paleontological data to produce far more predictive, and*  
16 *therefore testable, statements about how species replace one another*  
17 *over the vast spans of evolutionary time". [138]*

18  
19 The challenge is not to find a dynamic signature of ecological interactions in  
20 macroevolutionary dynamics, but rather to isolate a particular generating mechanism  
21 from the many sources of bias, the role of random chance and the disparity of potential  
22 outcomes. Continued dialogue and ever-closer union of fossil and modern approaches  
23 will prove essential in maintaining this momentum [139]. Concluding this volume, Price  
24 & Schmitz [139] extend the argument that morphological traits "bind the past and  
25 present together" [122] to an explicitly functional context, arguing that this focus  
26 alongside greater integration across biodiversity research silos will enable scientists to  
27 better understand how lower-level ecological and evolutionary processes scale up, and  
28 vice versa.

29 It is difficult to separate the role of the biotic and abiotic environments. Recent  
30 methodological and data advances, many showcased within this Theme Issue,  
31 nonetheless offer increased hope for a brighter future in which we gain a better  
32 understanding of how ecological mechanisms regulate the interplay between  
33 organismal biology and environmental change to drive macroevolutionary dynamics.

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For Review Only

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3 **1 Short Biographies**  
4 2

5 3 **Thomas H.G. Ezard** is NERC Advanced Research Fellow across Ocean & Earth Sciences  
6 4 and the Centre for Biological Sciences at the University of Southampton. He leads a group  
7 5 that investigates the interaction of environmental change and population structure,  
8 6 attempting to contextualise evolutionary and ecological dynamics through a demographic  
9 7 lens. His interdisciplinary group most often develops the interface of mathematical and  
10 8 statistical methods for application in the life sciences. Current projects include an individual-  
11 9 based perspective on macroevolution using fossilised foraminifera, and the drivers of  
12 10 transient booms and busts in human population growth.  
13 11  
14 12

15 13 **Tiago B. Quental** is Assistant Professor at the Department of Ecology of University of São  
16 14 Paulo. He leads a research group focused on understanding spatial and temporal patterns of  
17 15 biodiversity and the mechanisms involved in generating species diversity. His research  
18 16 interests are not limited to a specific taxonomic group but are instead motivated by a range  
19 17 of questions and structured around them. At the moment he is particularly interested on  
20 18 understanding the role of biotic interactions on biodiversity changes in deep time. The main  
21 19 tools used to approach those questions are molecular phylogenies, fossil record, ecological  
22 20 data and numerical simulation.  
23 21  
24 22

25 23 **Michael J. Benton** is Professor of Vertebrate Palaeontology at the University of Bristol. He  
26 24 researches fossil reptiles of the Triassic, including the origin of the dinosaurs, and is  
27 25 particularly interested in the deep-time evolution of life, especially the roles of mass  
28 26 extinctions and adaptive radiations. He is currently investigating questions concerning the  
29 27 quality of the fossil record, the meaning of long-term global diversity curves in terms of  
30 28 models for the evolution of life, the nature of the Permo-Triassic mass extinction and its role  
31 29 in extinction and in opening opportunities for a massive recovery of life in the Triassic.  
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## Figure Legends

**Fig. 1.** Rejection of Van Valen's law in Cenozoic Era macroperforate planktonic foraminifera [33] depends on the level of biological organisation used in analysis. We define the homogeneous group for analysis by controlling for morphotype (presence/absence of keels, symbionts and spines), depth habitat, changes in overall climate [34, 35] and overall standing diversity. The scale parameter determines the curvature in extinction risk according to the Weibull distribution; a value of 1 reduces the Weibull to its simpler exponential distribution of constant extinction risk. Maximum likelihood estimates and 95% parametric confidence intervals are shown. . See also Table S1 for parameter values.

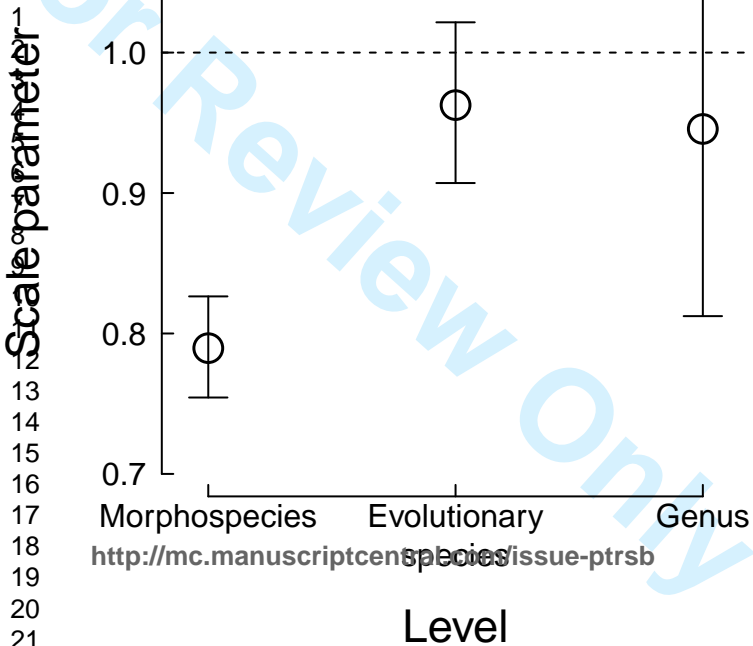
**Fig. 2.** Simplified schematic of the main regulators of biodiversity during a snapshot in deep time for a given clade. The strength and existence of interactions can change through time. We do not indicate the impacts of space in the schematic because it is assumed that if species are interacting, then, to some extent, their ranges must overlap. Coloured boxes denote distinct ecological types, which compete amongst each other and respond differentially to the same biotic and abiotic signals.

**Fig. 3.** Diversity-dependent controls acts more strongly through speciation than extinction in Cenozoic Era planktonic foraminifera [33] and Canidae over the last 40 Myr [53]. Number of species was calculated at the start of each bin and regressed against speciation or extinction rate in the next 1 Myr. Regression lines correct for overdispersion and non-constant variance with the mean. Solid lines indicate statistically significant relationships ( $p < 0.01$ ) while dashed lines indicate non-significant ( $p > 0.05$ ) relationships.

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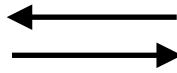
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Biotic

Abiotic



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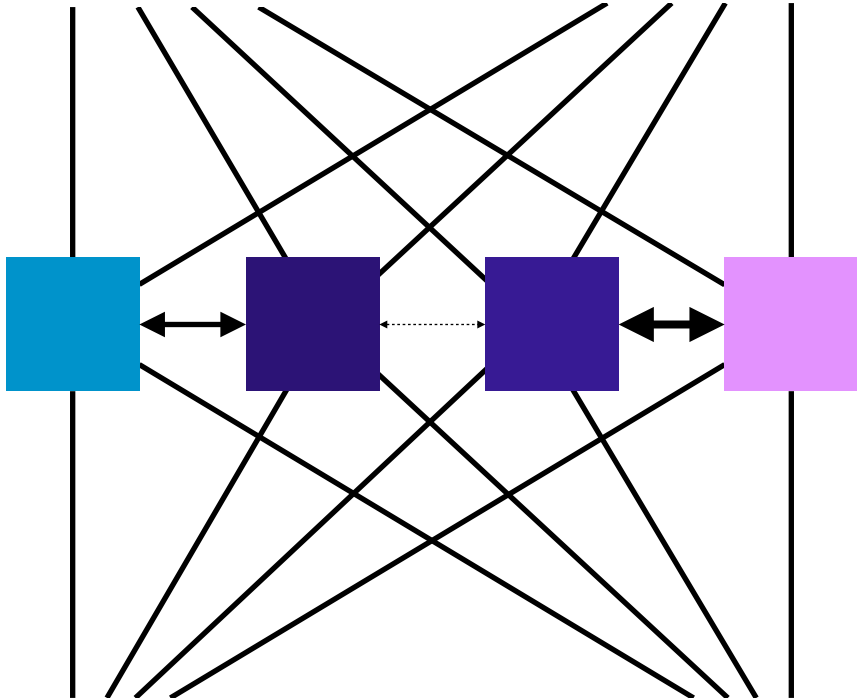
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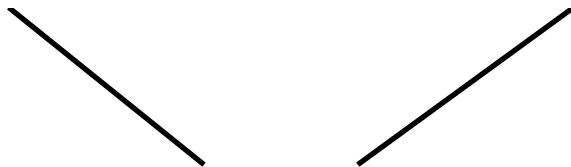
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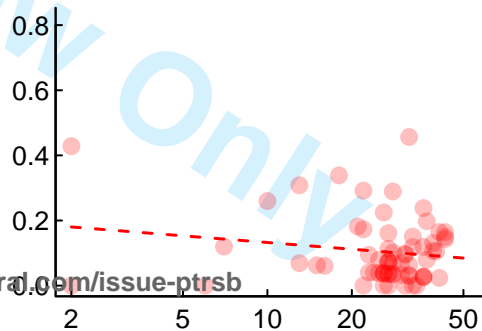
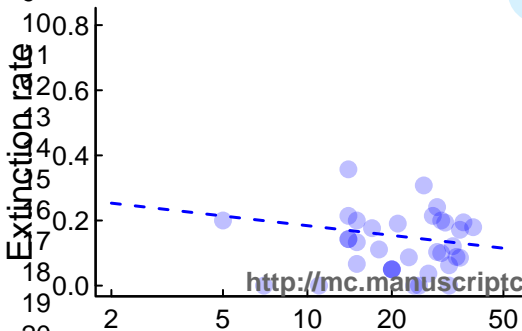
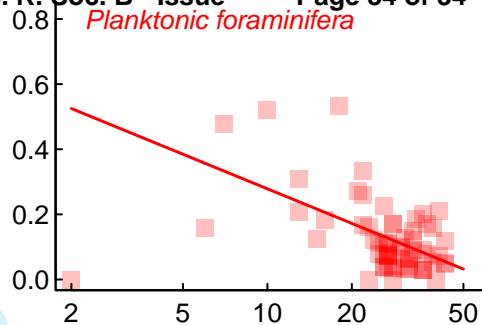
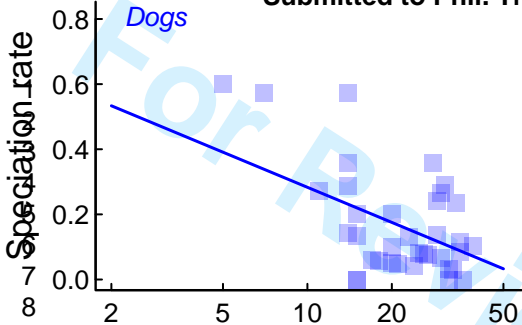


Speciation

Extinction



Diversification



Number of species