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1 **The challenges to inferring the regulators of**
2 **biodiversity in deep time**

3

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1 **Abstract**

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

19

1 **1. Introduction**

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

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

29 Traditionally, deep-time regulators of biodiversity have polarised into biotic vs.
30 abiotic controls [6], with biotic interactions argued to dominate in the near term and
31 abiotic upheaval imparting the clearer signal over long time scales [10]. The biotic,
32 organismal, ecological perspective is commonly associated with the Red Queen
33 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 generating mechanisms. We begin with how our analytical
29 choices affect the results we obtain.

30

31

32 **2. Individuals, populations, species and genera**

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

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

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

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

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

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

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

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

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

29

30

31 **3. Biotic and abiotic contributions to stochastic macroevolutionary** 32 **dynamics**

1 Sepkoski argued that a stochastic version of his fixed finite upper limit to taxon
2 diversity was “probably more typical of natural systems” than the deterministic
3 analytical solutions [4]. Population ecologists have long used year-to-year fluctuations
4 in abundance to reveal that environmental stochasticity acts on a density-dependent
5 framework [9, 49]. One simplistic partitioning [49, 50] is that the cause of any deviation
6 from a deterministic density-dependent framework is either due to an environmental
7 factor that affects the realised fitness of all individuals concurrently (environmental
8 stochasticity: σ_e^2), or due to winners and losers from particular individual interactions
9 that average out in the long term (demographic stochasticity: σ_d^2). Taken together, year-
10 to-year fluctuations in population abundance can be written as:

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

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

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

1 why some groups of species are winners and others losers, beyond the patterns that can
2 be generated assuming neutral dynamics [56, 57].

3 The stochastic population theory used above [49, 51] predicts that environmental
4 stochasticity will dominate dynamics for sufficiently large populations (i.e. N large) such
5 that the differences among individuals can therefore be neglected. The species-area
6 relationship is one of the best ecological laws in determining the number of species that
7 can co-exist within a given biome, but, in terms of driving macroevolutionary
8 diversification shifts in deep time, the fragmentation of an area has been argued to be as
9 influential as area per se [58, 59]. In this volume, Jordan et al. [60] find that neutral
10 theory, in which all species are assumed to be functionally equivalent [56] on a
11 fragmenting super-continent cannot explain the post-Jurassic increase in terrestrial
12 species richness. The results suggest a role for some biotic factors, either a competitive
13 advantage or some other founder effect over and above geographic isolation, in the
14 subsequent adaptation and expansion of the clade, even if the precise generating
15 mechanism remains to be identified.

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

31 The biased distribution of fossils in time and/or space motivated the development
32 of methods to “correct” for the vagaries of the rock record [62-65]. Commonly used
33 sampling proxies, such as counts of collections, localities, or formations, accrue in close

1 connection with the species count [66]. Residuals-based approaches [64, 65] compare a
2 sampling proxy (e.g. formations count; rock outcrop area) and then identify and remove
3 a sampling trend, with the residuals interpreted as the true biological signal.
4 Acknowledging the limitations of formation counts as a sampling indicator, it remains
5 controversial whether the correlation between rock and species counts, or the residuals
6 from that correlation, represents the holy grail of biological truth [66]. Rarefaction [62]
7 and shareholder quorum subsampling [27] have proven less controversial methods, but
8 still imply that the geological drives the biological. Integrated approaches, which
9 calculate the error due to incomplete preservation and biological diversity
10 simultaneously, promise to place both on an even footing [24, 67-70].

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

22 The difficulty of extracting the biological signal from the geological noise was
23 formalised by Raup *et al.*'s [72] pioneering work simulating phylogenetic diversification.
24 At a given point in time, Raup *et al.* [72] assumed that each species has an equal
25 probability of going extinct and an equal probability of giving rise to a descendant
26 daughter species. These assumptions evoke the equal-rates Markov model of
27 diversification [57] and Hubbell's Neutral Theory [56] for a clade fluctuating around its
28 supposed equilibrium (assuming, in the latter case, that the birth and death rates are
29 similar). A simple null model with constant rates was able to recover the diversity
30 trajectories seen in the fossil record [72]. "Familiarity with the 'patterns' that random
31 processes create is ... essential" for all scientists [57] because "it is fatally easy to read a
32 pattern into stochastically generated data" [73]. Systematic geological structure can
33 generate seductive impressions on macroevolutionary signals, such as bursts of genus

1 origination [26], the clumping of last occurrence dates into apparently accelerated
2 extinction events [74] as the ranges of higher-taxa are bounded by mass extinctions
3 [75].

4 Despite this warning for any literal reading of the fossil record [72], running the
5 same simulations using empirically defined parameter estimates suggested that the
6 fluctuations in fossil taxon counts most likely result from changes in the diversification
7 dynamics rather than a constant-rate stochastic process [76]. Asserting a role for
8 ecological regulators of biodiversity requires the rejection of appropriate null models
9 that incorporate the temporal inconsistencies of fossilisation [57].

12 **4. The regulators and their signatures**

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

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

32 Competitive interactions might be the most commonly discussed biotic driver of
33 diversification rate changes. Both origination and extinction rates have been reported as

1 diversity-dependent and both can generate equilibrium dynamics in biodiversity [4, 81,
2 82]. At a finer taxonomic resolution than assumed by Alroy [81] or Foote [82],
3 speciation rate seems to respond more closely than extinction rate to changes in within-
4 clade diversity [Fig. 3, see also 13, 46], but this balance of influence need not be constant
5 for all time [82]. Species interactions are increasingly being recognised as capable of
6 leaving an impact on clade diversification through a variety of modes [83, 84] and not
7 simply slowdowns in diversification rate with increasing levels of standing diversity
8 [85, 86].

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

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

32 Biogeographical variation fundamentally restricts such global-level analyses. The
33 latitudinal diversity gradient is one of the most frequently described macroecological

1 patterns [90], but has not been constant through time [91]. The tropics are cited as
2 acting as both a cradle of and a museum for diversity [92, 93], with the consequence
3 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 If specialist species depend intimately on their native biome to persist, then any
13 climate change that alters the spatial extent of these biomes will rapidly lead to their
14 extinction. Exploring the interactions of species and their geographic ranges over
15 ecological and evolutionary time scales has been hard. In this volume, Villalobos *et al.*
16 [97] explore how species co-occur with other species, and find that in the long term
17 species respond individualistically to major climatic shifts, while more stable climates
18 allowed less phylogenetically variable, yet richer palaeocommunities to settle. The
19 authors calculate phylogenetic fields, the co-occurrence patterns among species and
20 their phylogenetic structure within individual species ranges, for living and extinct
21 mammal species over long spans of time, to explore how individual species interact with
22 predators, prey, and competitors, and with major changes in physical environments.

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

1 extinction and temporal changes in the asymmetry of dispersal rates. Silvestro *et al.*
2 [98] applied their method to a genus-level empirical dataset of Cenozoic terrestrial
3 plants. Their empirical results suggest a predominant dispersal from Eurasia to North
4 America in the Eocene climatic cooling period, but a higher dispersal from North
5 America to Eurasia during the more stable climatic period between 32 and 14 Ma. The
6 most recent 10 My are characterized by a more symmetric dispersal between both
7 continents, although higher extinction rates in Eurasia.

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

18
19

20 **5. Beyond counts and towards ecological significance.**

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

1 Missa & Morlon [111] use computer simulations to show, under Neutral Theory
2 [56] with alternative modes of speciation, that species-area relationships and species-
3 abundance distributions reach their equilibriums after species richness. Phylogenetic
4 patterns of biodiversity either do not (e.g. phylogenetic diversity) or take far longer (e.g.
5 tree imbalance and gamma statistics) to converge. The authors also show that the mode
6 and magnitude of speciation strongly affect the time taken for ecological patterns to
7 reach their equilibrium. The authors conclude: “Given that real metacommunities may
8 not have reached equilibrium in terms of species richness, it would be unwise for users
9 of the Neutral Theory of Biodiversity to continue assuming that other biodiversity
10 patterns, which take even longer to converge to equilibrium, are themselves at
11 equilibrium.”

12 One of the reasons for the resurgence of interest in higher taxa is that they, if
13 robustly defined, are more intimately linked to environmental change than species. The
14 environment moderates both the number of ways that organisms can persist, and also
15 the efficiency of the chosen method: the number of hypercarnivores has been roughly
16 constant through time, despite ongoing turnover in named species [112]. The principal
17 way in which functional types are defined in deep time is by assigning roles to particular
18 characters [113]. Mass extinction events generate high levels of species extinction, but
19 can either slightly reduce [114] or considerably change [115] ecological functioning in
20 the clade. Although taxon diversity and morphological disparity are not always coupled
21 [116], morphological disparity typically saturates more rapidly than taxon diversity
22 counts [117]. Obtaining accurate estimates of intraspecific variation is fundamental to
23 adoption of trait-based approaches for their use in inferring niche breadth and stability,
24 as well as the strength of ecological interactions [118, 119]. Understanding changes in
25 the ecological role of a given species, and studying how trait distributions change more
26 broadly, therefore could reveal species interactions. In this volume, Hsiang et al. [120]
27 describe algorithmic procedures to rapidly extract size and shape phenotypic data in
28 microfossil communities, providing the robust sample sizes from which trait
29 (co)variation can be accurately estimated. Hsiang et al. [120] use their workflow to
30 compare and contrast dendrograms obtained through morphological, ecological, and
31 phylogenetic data. Another potential use is to compare the multivariate morphological
32 data that underpins the dendrograms and so assess the relative contributions of
33 evolutionary or ecological processes via simultaneous alterations to phylogeny,

1 environment and species abundance. A focus on morphological traits promises to “bind
2 the past and present together” [121] as a common analytical currency for analysis in
3 deep time and the present day. The challenge ahead is therefore to identify ecologically
4 meaningful traits that are incompletely rendered by higher taxon definitions [121, 122].

5 Although the fossil record is the most direct way to access the role of different
6 regulators [78], it has also, until recently, been blind to preservation of certain body
7 parts and physiological functions that might be ecologically very relevant. Here,
8 Trueman *et al.* [123] review ecogeochemical methods to recover individual scale
9 information from macrofossil remains, and thus study food web structure, nutrient
10 fluxes and population connectivity in contemporary deep sea fish systems. Deep-sea
11 fishes share with fossils many of the problems in extracting trait data: difficult-to-access
12 material and vanishingly rare evidence of direct interactions among individuals. The
13 authors provide a balanced perspective of the potential impact of the approach. While
14 evidence exists that symbiosis influences macroevolutionary dynamics in deep time
15 [13], other areas are less well understood: trace element analysis can indicate
16 population connectivity in the focal modern deep sea fishes, but remain unproven in
17 deep time [123]. Adoption of such techniques to yield data on behaviour and physiology
18 promises a more holistic (beyond morphology) view of the interplay between organism
19 and its environment in deep time.

20 Selection pressure and long-term rates of evolution are regulated by ecological
21 opportunity [124], but any response to selection depends on individual form [125, 126].
22 Individual form matters because individuals in species are characterised by a distinctive
23 set of traits, many of which covary. It is not individual traits that survive, reproduce and
24 die, but whole individuals. Selection on one trait can generate a response to selection in
25 others [126], implying that we need multivariate approaches within functional modules
26 [127]. The decoupling of size and wing shape, for example, differs among distinct
27 subfamilies of fossil birds and occurred as a precursor to flight [128]. Despite Simpson’s
28 evocative “choppy sea” metaphor of a dynamic adaptive landscape [129], there are
29 “dismally few” empirical estimates of how the constraints imposed by trait covariance
30 evolves during a species’ existence [130].

31 Multivariate changes in ecologically relevant traits offer strong potential to better
32 understand the processes that bridge micro- and macroevolution [131]. If there are no
33 strictly macroevolutionary processes [132], then we need a finer resolution to unpick

1 the circumstances that promote ecological divergence to become fixed through some
2 speciation events, but not in others. Coarse macroecological proxies, even when
3 calculated as integrated variables over the whole duration of each lineage [133], show
4 negligible explanatory power to predict molecular divergence, albeit among a very
5 limited number of species [134] evoking the hypothesis that molecular divergence is
6 accelerated during speciation events [135]. It is now widely accepted that evolutionary
7 divergence can be rapid [14, 136], and its rate covaries negatively with the interval
8 being studied [14]. While diversity dynamics need the fossil record to understand the
9 dual roles of speciation and extinction [78], fine temporal resolution might reveal that
10 the ecological regulators of biodiversity actually operate chiefly in a punctuated fashion
11 during post-speciation divergence, rather than throughout a species' existence once its
12 ecological role is, to a large extent, established.

13

14 **6. Conclusion**

15 *"It is my hope that future work will not reject the question of competition*
16 *in macroevolution out of hand, but will explore it with new models that*
17 *are more sophisticated than coupled logistic equations and can use these*
18 *accumulating paleontological data to produce far more predictive, and*
19 *therefore testable, statements about how species replace one another*
20 *over the vast spans of evolutionary time". [137]*

21

22 The challenge is not to find a dynamic signature of ecological interactions in
23 macroevolutionary dynamics, but rather to isolate a particular generating mechanism
24 from the many sources of bias, the role of random chance and the disparity of potential
25 outcomes. Continued dialogue and ever-closer union of fossil and modern approaches
26 will prove essential in maintaining this momentum [138]. Price & Schmitz [138] extend
27 the argument that morphological traits "bind the past and present together" [121] to an
28 explicitly functional context, arguing that this focus alongside greater integration across
29 biodiversity research silos will enable scientists to better understand how lower-level
30 ecological and evolutionary processes scale up, and vice versa. It is difficult to separate
31 the role of the biotic and abiotic environments, but recent methodological and data
32 advances showcased within this Theme Issue offer increased hope for a brighter future
33 in which we gain a better understanding of how ecological mechanisms regulate the

1 interplay between organismal biology and environmental change to drive
2 macroevolutionary dynamics.

3

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13

1 **Short Biographies**

2

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

11

12

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

21

22

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

30

31

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9

10 **Figure Legends**

11

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

20

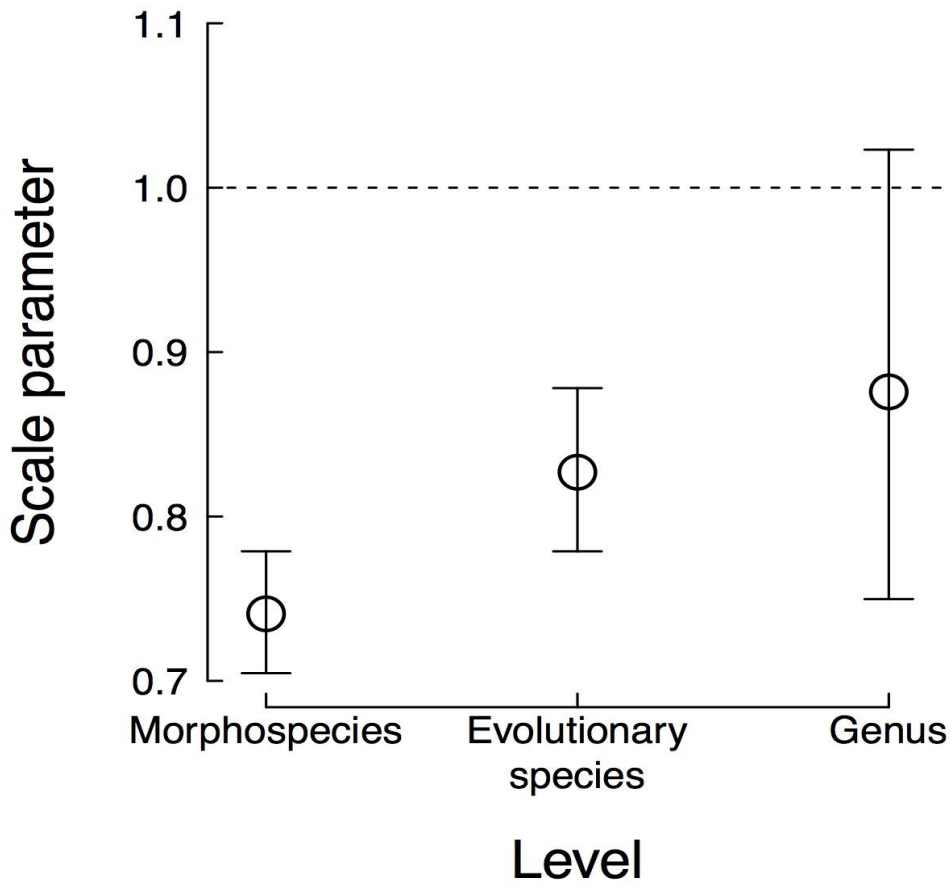
21 **Fig. 2.** Simplified schematic of the main regulators of biodiversity during a snapshot in
22 deep time for a given clade. The strength and existence of interactions can change
23 through time. We do not indicate the impacts of space in the schematic because it is
24 assumed that if species are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

27

28 **Fig. 3.** Diversity-dependent controls acts more strongly through speciation than
29 extinction in Cenozoic Era planktonic foraminifera [33] and Canidae over the last 40
30 Myr [53]. Number of species was calculated at the start of each bin and regressed
31 against speciation or extinction rate in the next 1 Myr. Regression lines correct for
32 overdispersion and non-constant variance with the mean. Solid lines indicate
33 statistically significant relationships ($p < 0.01$) while dashed lines indicate non-
34 significant ($p > 0.05$) relationships. See also Table S1 for parameter values.

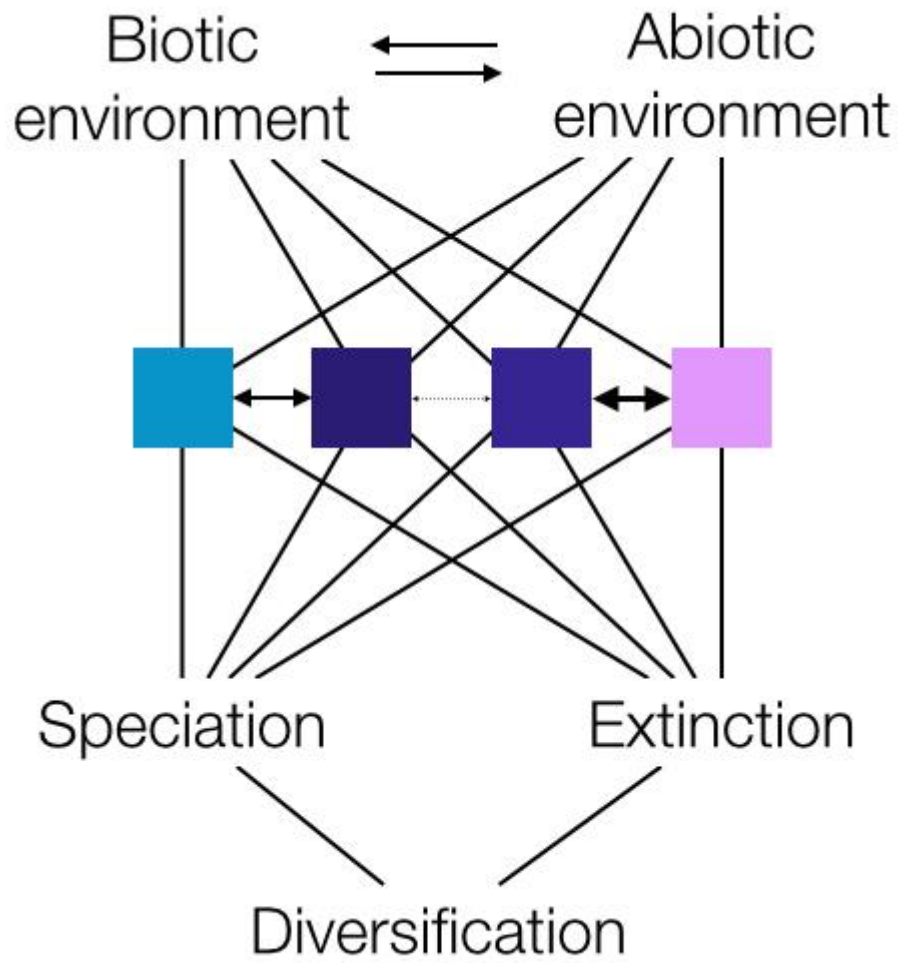
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1
2 **Figures**
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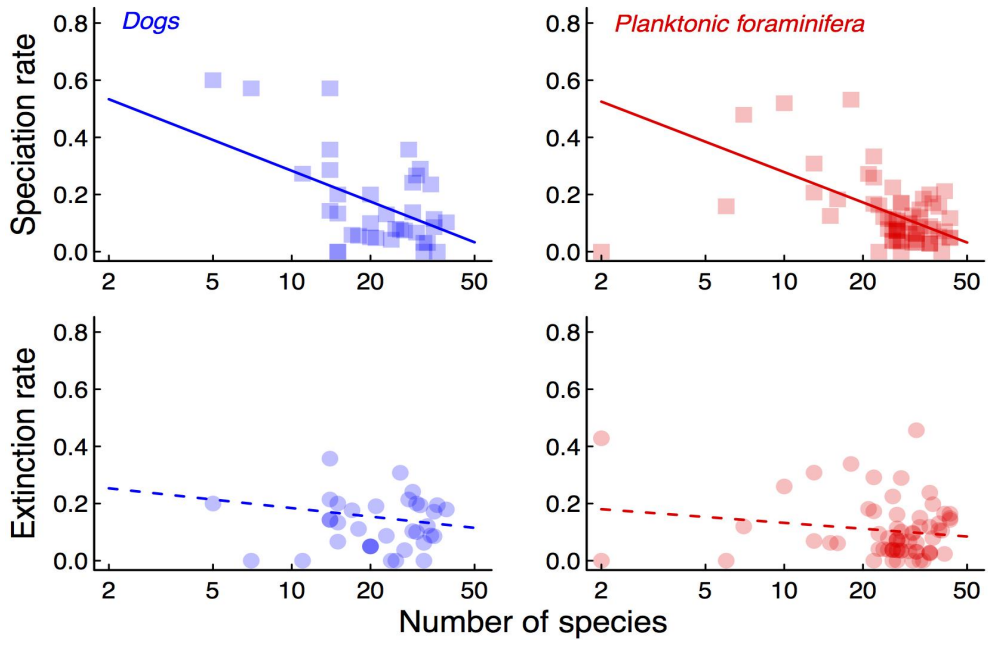
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Figure 1.



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Figure 2.



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Figure 3.

	Morphospecies				Evolutionary Species				Genera			
	coef.	SE	z	p	coef.	SE	z	p	coef.	SE	z	p
Intercept	2.17	0.07	29.39	***	2.33	0.1	22.66	***	3.677	0.349	10.539	***
ln(scale)	-0.3	0.05	-6.48	***	-0.19	0.06	-3.08	**	-0.133	0.155	0.853	
ln(density)	-0.32	0.15	-2.19	*	-0.74	0.26	-2.88	***				
climate	0.11	0.05	2.15	*	0.15	0.08	1.9		-0.132	0.287	-0.458	
spines	0.39	0.09	4.12	***	0.41	0.14	2.86	***	-1.316	0.502	-2.623	***
symbionts												
keels	-0.33	0.14	-2.42	*	-0.39	0.24	-1.63					
ln(density):climate	-0.83	0.14	-5.82	***	0.84	0.32	2.58	**				
keels: climate					0.63	0.23	2.73					
spines:climate									0.873	0.44	1.983	*

1

- 2 Table S1. Coefficients (coef.) with standard errors (SE), z-values and p-value codes for explanatory variables correlated with extinction
- 3 risks of morphospecies (N=339), evolutionary species (N=210) and genera in planktonic foraminifera (N=48). P-value codes are p >
- 4 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001. Where no values are given, this variable was not significant for that model; where no p-value
- 5 code is given, that term was not statistically significant on its own. These tables for morphospecies and evolutionary species were first
- 6 published in [29]; the genus level analyses are new. The maximum likelihood estimate of the ln(scale) coefficient for the full model, i.e.
- 7 without model simplification, is -0.304 with a standard error of 0.158 for a 95% confidence interval on the original scale of (0.537,
- 8 1.014). According to the parameterization of the Weibull distribution used, the instantaneous risk (hazard) h of extinction at age x is