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Evolutionary macroecology



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Abstract. Macroecology focuses on ecological questions at broad spatial and temporal scales, providing a statistical description of patterns in species abundance, distribution and diversity. More recently, historical components of these patterns have begun to be investigated more deeply. We tentatively refer to the practice of explicitly taking species history into account, both analytically and conceptually, as ‘evolutionary macroecology’. We discuss how the evolutionary dimension can be incorporated into macroecology through two orthogonal and complementary data types: fossils and phylogenies. Research traditions dealing with these data have developed more-or-less independently over the last 20–30 years, but merging them will help elucidate the historical components of diversity gradients and the evolutionary dynamics of species’ traits. Here we highlight conceptual and methodological advances in merging these two research traditions and review the viewpoints and toolboxes that can, in combination, help address patterns and unveil processes at temporal and spatial macro-scales.

Keywords. Comparative methods, evolutionary dynamics, integrative approach, palaeobiology, phylogenetics.

Introduction

The term ‘macroecology’ was devised (Brown and Maurer 1989) to describe an emerging research programme focusing on ecological questions at broad spatial and temporal scales, particularly to provide a statistical description of patterns in species abundance, distribution and diversity. The macroecological research programme expanded quickly and gradually enfolded several other programmes in ecology that were also concerned with broad-scale patterns in diversity, such as island biogeography, species–area relationships, ecogeographical rules and latitudinal diversity gradients, to name just a few (Gaston and Blackburn 2000).

In macroecology, species can be viewed as ‘particles’ diffusing in a multi-dimensional geographical, environmental and trait space (Brown et al. 2003). Species evolve in a changing environment and expand or contract their geographic ranges, and their multiple biological traits are driven by—but also constrain—these shifts. These space–time dynamics explain the transition from

ancestral states to current states for all biological traits and distributional patterns. Palaeoecology has always been concerned with these transitions and has used species’ attributes to infer palaeoenvironment and environmental changes through time. As a consequence, the distribution of such ‘particles’ along any geographical or environmental gradient, or trait space, at a particular time is conditional on each species’ state at the time of origin from its ancestors and the stochastic and adaptive evolutionary mechanisms driving its dynamics since then. This can be further complicated if we attempt to explicitly join space and time to address the space–time dynamics of species across dynamic environments. Although this conceptual reasoning can be traced back to Darwin’s time, its full operational development is in its infancy. The theoretical and methodological tools needed to explore the space–time dynamics of macroecological particles, as well as the understanding of how the evolution of species’ traits affects these dynamics, are still under development (Jablonski 2009, FitzJohn 2010, Fritz et al.

2013).

The phylogenetic relationships among species are critical for analysing the temporal dynamics of diversity and the underlying macroecological and macroevolutionary processes (Hernández et al. 2013, Pennel and Harmon 2013). However, there is no guarantee (quite the contrary) that missing (extinct) species are only intermediate states of extant species. Actually, extinct species can possess unique combinations of traits that are no longer found in extant species. There can be hidden information on diversity patterns, adaptations, life-history patterns and body plans that are no longer found on Earth (e.g., Aze et al. 2011); some of this can only be recovered from fossil data. Therefore, ignoring fossils can bias our understanding of patterns and processes based on extant species alone (Slater et al. 2012, Slater & Harmon 2013).

Only recently have macroecologists begun to explicitly incorporate the evolutionary dynamics of species, although this situation is changing quickly. The historical component can be recovered both by reconstructing phylogenies and by assembling fossil data. Here, we focus on the particularities of phylogeny- and fossil-based perspectives in macroecological analyses, which may aid in the understanding of broad-scale patterns and processes. We refer to the practice of explicitly taking species' histories into account as 'evolutionary macroecology', providing explicitly theoretical and methodological links between macroecology and macroevolution. For simplicity, we tentatively refer to evolutionary approaches to dealing with extant species and extinct species as 'phylogenetic macroecology' and 'palaeo-macroecology', respectively. We consider that these two research traditions for incorporating historical processes into macroecological analyses developed more-or-less independently over the last 20–30 years (see Harrington 2010). Surely it is time to combine them more, in a joint effort to improve macroecology! Our main goal here is to provide some critical literature that can reciprocally illuminate these research traditions and improve their future integration, to better understand patterns of diversity on Earth.

The two research traditions

The trajectories of diversity in time can be (partially) recovered either by reconstructing phylogenies or by assembling fossil data. Phylogenies emulate the arrangement of relatedness and the sequence of divergence of current forms, whereas the fossil record explicitly identifies the temporal and spatial positions of transient and extinct states. Nonetheless, both are incomplete and present their own challenges to revealing historical patterns. Detailed phylogenies are not well known for most organisms and may reveal patterns biased toward survivors, whereas the fossil record relies on fortuitous events that result in preservation (Paul 2009).

Because the research traditions aimed at understanding the historical patterns of diversity through phylogenetics and palaeontology have developed more-or-less independently, it is not surprising that they have assembled their own toolkits to address analogous questions about evolutionary trends in biological traits and diversification patterns. Of course, a more recent collaboration of phylogenetics and fossil data in macroecological analyses is slowly being established, and in fact, some literature addresses this joining and suggests a set of practices that may benefit both research traditions (e.g., Dornburg et al. 2011, Morlon et al. 2011, Slater et al. 2012, Fritz et al. 2013, Pennel and Harmon 2013).

Phylogenetic Macroecology

Phylogenetic trees are now commonly used in macroecological studies for a number of purposes. Phylogenetic applications are used for testing hypotheses about the coexistence and partitioning of trait space in the assembling of communities, understanding the origins and maintenance of biotic interactions, assessing broad-scale patterns of diversity and developing evolution-oriented conservation plans. (See Mouquet et al. 2012 for a review of what has been called "ecophylogenetics" in an attempt to combine in a single framework more traditional phylogenetic comparative methods, community phylogenetics and diversification analyses based on phylogenies).

Also of great interest in macroecology is the amount of phylogenetic signal in many key ecological components, usually referred to as ‘niche conservatism’ (Wiens et al. 2010). Niche conservatism can provide an interesting framework for explaining several diversity patterns, including a compromise between ecological and historical explanations for broad-scale diversity patterns (Wiens & Donoghue 2004, Ricklefs 2006, Wiens et al. 2010). It also plays an important role in explaining patterns at the community level, usually expressed by phylogenetically clustered or overdispersed assemblages along environmental gradients (e.g., Graham et al. 2009).

Niche conservatism is usually analysed by inferring a phylogenetic signal (e.g., Münkemüller et al. 2012) and fitting evolutionary models (such as Brownian motion or Ornstein–Uhlenbeck processes) for traits and niche components (Hernández et al. 2013, Pennel and Harmon 2013). An important conceptual issue, still partially unsolved, is how to relate phylogenetic signal, evolutionary models and niche conservatism. The main question is whether niche conservatism can be defined only by the existence of a phylogenetic signal in these ecological components (indicating only that variation in ecological traits is ‘inherited’ from ancestors) or if a real ‘evolutionary constraint’, reflecting stabilising selection or persistence in sub-optimal environmental conditions, is needed to define niche conservatism (see Losos 2008, Wiens 2008, Cooper et al. 2010). There are also important discussions on how (and whether) fitting evolutionary models using phylogenetic comparative analyses allows the recovery of mechanistic process (evaluating the relative roles of natural selection, drift and mutation; Revell et al. 2008, Pennel and Harmon 2013).

Another important consequence of a phylogenetic signal is that it increases the Type I error rate of statistical analyses because of non-independence among observations (see Felsenstein 1985). This can lead to biased inferences of correlated evolution among traits and of an adaptive process inferred from the correlations between these traits and components of environmental variation (see Diniz-Filho & Torres 2002;

Hernández et al. 2013). In fact, this was the first reason for beginning to work with phylogenies in macroecological analyses almost two decades ago (see Blackburn and Gaston 1998, Blackburn 2004).

Phylogenetic patterns have been used since the late 1990s to understand the dynamics of speciation and extinction (see Stadler 2013 for a recent review). In short, the overall idea is to estimate diversification (speciation and extinction) rates by fitting models to the relationship between the number of lineages at a given depth in a time-calibrated phylogeny and the time (the lineage-through-time plots [LTTs]; see Figure 1). These rates, as well as their variation in space, can also be used to infer the geographical components of diversification (e.g., Ricklefs 2004). Similar reasoning was applied to the development of more complex models of range dynamics throughout the phylogeny, which may allow the distinction of macroevolutionary models explaining geographic variation in diversity patterns (e.g., Goldberg et al. 2011; see also below on latitudinal diversity gradients) and the linkage of morphological traits with diversification (Ricklefs 2012, Hunt 2013).

Palaeomacroecology

In the research tradition we are referring to as palaeomacroecology, the dynamics of a system are investigated primarily through the temporal trends of speciation and extinction and how they shape the spatial patterns of diversity based on fossil records. This research tradition appeared even before Brown and Maurer (1989) coined the term macroecology in the sense of dealing with species dynamics at broad temporal scales and trying to uncover the overall processes underlying these patterns (see Valentine 1985). Additionally, there is a long tradition of focusing on how traits and morphological variability (disparity) evolve within and among clades (see Pennel and Harmon 2013). Fossils and palaeoclimates provide direct evidence of ancestral attributes and environmental conditions, which may provide new or different insight into patterns of trait evolution and modes of speciation (Hunt 2006, 2012, Hernández et al. 2012). The models of evolution discussed above (i.e., Brownian motion and the Ornstein–

Uhlenbeck process) can also be fitted to fossil data to allow an explicit evaluation of the tempo and mode of trait evolution (Hunt 2006, 2012) and how these patterns are related to extinction dynamics through time (Roy et al. 2009). In addition, ancestral trait reconstruction can be better estimated using theoretical models of trait evolution that are fitted based on phylogenies but explicitly incorporate fossil data (Slater et al. 2012, Slater & Harmon 2013).

There is a long research tradition of estimating diversification patterns through time that

dates back to the early days of the ‘palaeobiology revolution’ (see Valentine 1985, Sepkoski and Ruse 2009). Because of the lack of fossil records for many groups of organisms, as well as taphonomic issues, these estimates have been widely discussed and questioned. It is important to highlight that, despite the popularity of LTT plots for estimating diversification rates, recent work reveals that such estimates can be seriously biased if fossil data are not explicitly taken into account (Quental and Marshall 2010), reinforcing the need for better fossil records to accurately

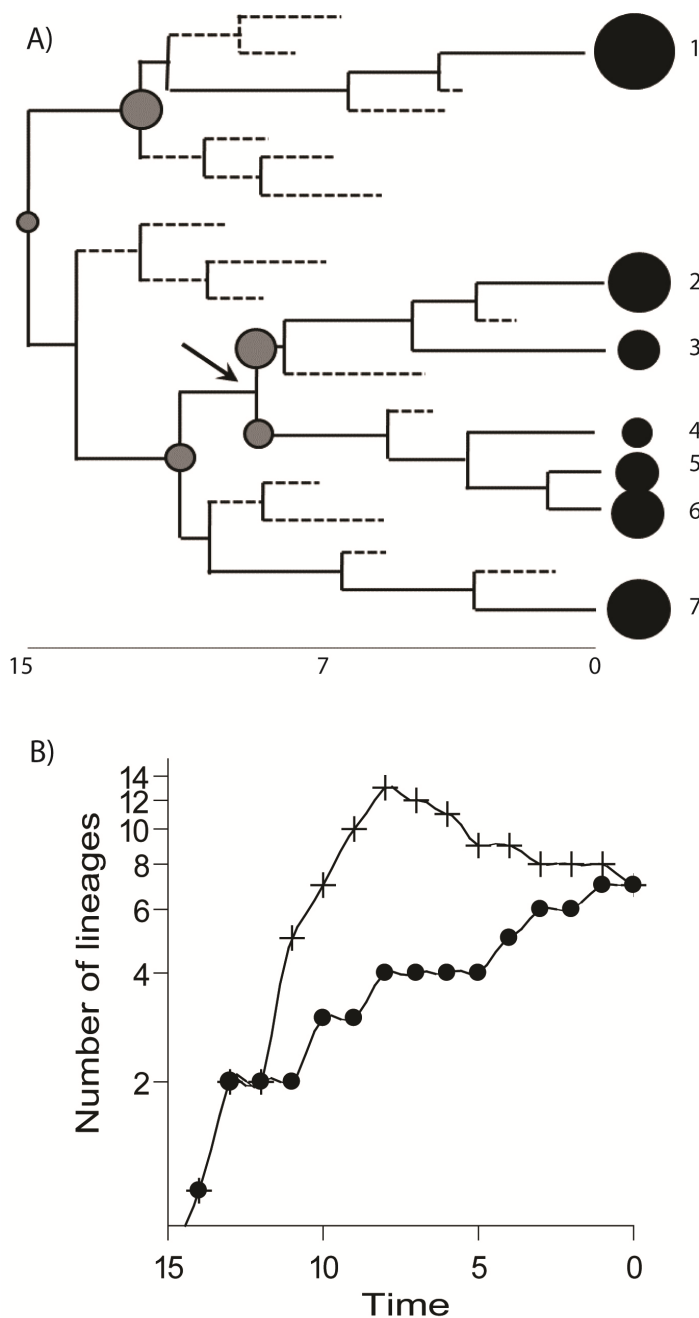


Figure 1. Some issues related to using phylogenies of extant species, only, to infer patterns in macroecological traits and diversification rates. A) Phylogeny of a hypothetical clade with 7 extant species, whose phylogenetic relationships are shown by solid lines, and several extinct lineages (dashed lines), illustrating a high early diversification followed by a concentrated extinction period that eliminated several lineages and subclades. Because extinction and speciation did not occur randomly through time, there is (B) a huge difference between lineage-through-time plots (LTT) when dealing with diversification based on relationships between extant species only (circles) and all lineages (crosses) (also see Quental and Marshall 2010, Stadler 2013). For traits, similar problems appear. A macroecological trait (e.g., body size) is overlaid on the phylogeny shown in (A), with the sizes of the circles proportional to trait values (black circles represent extant species and some key extinct species are in grey). There is typically a clear trend towards increasing body size during evolution of the clade (see Vrba 1985, her Figs 1c,d), unrelated to speciation/extinction dynamics. However, by not including extinct species one cannot infer the correct trend: phylogenetic signal does not allow recovery of this pattern, and any statistics will furnish an intermediate value of signal based on extant species only (i.e., closely related species are similar, such as species 5–6 or 2–3, but distantly related species, such as 1–2–7, will be also similar). Also, because body size did not increase during the speciation event at the root of the subclade with most of extant species (arrow), this subclade has species with smaller body size than others. At the same time, the most basal species (1) in the clade has the largest body size among the extant species; ancestral reconstructions will neither detect that the clade originated from a small-bodied species, nor that there is support for Cope’s rule. Both examples reinforce the need to couple fossil and extant data, where possible, to better infer macroecological patterns.

estimate diversification (particularly speciation) patterns (see Figure 1).

A recent research line that can be fitted into palaeomacroecology (although usually working with relatively young fossil records) involves analyses of temporal dynamics in species' geographic distributions using niche modelling and palaeoclimatic simulations (e.g., Nogués-Bravo 2009, Svenning et al. 2011). Evaluating temporal shifts in species' geographical distributions and occupancy is a common approach among palaeontologists using only fossil records (e.g., Foote et al. 2008, Raia et al. 2013), but the integration of geographic range dynamics with niche modelling has yielded a fresh perspective in ecological modelling that can provide more insight into evolutionary macroecology. This integrative approach has been used to test the role of climatic changes through time, and to evaluate how geographic ranges and niches shift and are conserved (e.g., Martinez-Meyer et al. 2004). In niche modelling, fossils can be used either as direct evidence of species' occurrence, to fit the niche models in a given past period, or as independent test data to evaluate model predictions (e.g., Macias-Fauria and Willis 2013).

Another recent approach in palaeomacroecology combines palaeodistribution modelling with molecular analyses of ancient DNA to recover species' demographic histories (i.e., the potential distribution and effective population sizes of species; e.g., Lorenzen et al. 2011). Although this is a powerful approach that can aid in disentangling the different mechanisms involved in these extinction patterns, it requires high-quality fossil and palaeoenvironmental data, coupled with sophisticated technologies for analysing ancient DNA, which limits its broad application in the near future. In tropical environments, for instance, DNA degrades quickly after the death of individuals, thus limiting the preservation of ancient DNA in these regions.

Furthermore, we suggest that expanding the temporal dimension will be very important for further coupling niche modelling and palaeomacroecology—at the forefront of this new integration. However, this will fundamentally depend on

the possibility of performing reasonable palaeoclimatic simulations for deeper timespans (see Rosenbloom et al. 2013).

Evolutionary macroecology: towards an integrative framework

Some questions in macroecology have been separately addressed by the phylogenetic and palaeomacroecological research traditions, and this appears to be a good starting point for better integration (Fritz et al. 2013). Some efforts to join both toolboxes have been made, such as the estimation of phylogenetic signals directly from traits measured from fossil data (Hunt 2006, Carotenuto et al. 2010, Pennel and Harmon 2013) or using fossil data to improve the modelling of trait evolution (Slater et al. 2012). Additionally, it is possible to evaluate shifts in the statistical distribution of traits (such as body size; e.g., Smith and Lyons 2011) in both the past and present and infer how extinction affects macroecological patterns or how macroecological patterns reflect extinction dynamics and their causes (e.g., Lyons et al. 2010, Ricklefs 2012, Hunt 2013).

Evaluating the phylogenetic signals of macroecological traits, such as body size and geographic range size, using both fossil and phylogenetic approaches is now straightforward (see Münkemüller et al. 2012 and Hernández et al. 2013 for recent reviews and methodological issues). When dealing with phylogenetics, the basic idea is to compare similarity among species for a given trait relative to their phylogenetic relationship (i.e., distances). For the fossil record, in many cases, there are temporal sequences of trait data within a lineage that can be fitted using time-series approaches (Hunt 2006), thus decoupling trends, shifts and short-distance autocorrelation in the trait throughout time. In some cases, it is possible to analyse the phylogenetic patterns of fossil data as well (e.g., Brusatte et al. 2012, Raia et al. 2013).

Although evolutionary models can be fitted to both phylogenetic and palaeontological datasets, it is important to understand that the patterns (and processes) evaluated with each one may be different. Phylogenetic signals estimated

from extant species reveal only the similarity of species as a function of their relatedness (Figure 1). Although this may be informative for evolutionary models, and it is particularly important for correctly inferring adaptations by correlations with other traits or with components of environmental variation, this does not allow the inference of macroevolutionary trends. These can be inferred only if independently known ancestral states (i.e., from fossils) are available (see Slater et al. 2012).

Body size, for example, usually retains a strong phylogenetic signal, and when analysing its correlation with other traits or its geographical patterns (e.g., Bergmann's rule), this drawback must be taken into account (e.g., Diniz-Filho et al. 2009). However, in a macroevolutionary context, an interesting body-size pattern is Cope's rule, or the tendency toward increasing body size over time. However, simply detecting a phylogenetic signal in body size does not allow the estimation of such directional patterns. It is now clear that a better understanding of the patterns and processes related to Cope's rule and analogous macroevolutionary trends can only be achieved by coupling phylogeny and the fossil record, in which these patterns are inferred from the dynamics of traits in different subclades and lineages (see Vrba 1985, Raia et al. 2012). Another promising research avenue is the question of exactly how geographical and evolutionary trends in body size (Bergmann's and Cope's rules) can be coupled (see Hunt and Roy 2006, Diniz-Filho et al. 2009).

From a more mechanistic point of view, there have been interesting discussions around phylogenetic patterns in geographic range size, which can be investigated based on phylogenetic signals (e.g., Diniz-Filho and Torres 2002) or from ancestor–descendant patterns in the fossil record (Jablonski 1987, Hunt et al. 2005, Jablonski and Hunt 2006, Foote et al. 2008). The implications of phylogenetic signals in geographic range size are conceptually deep, because such signals in this emergent trait can provide evidence for the hierarchical expansion of natural selection theory (Diniz-Filho 2004, Jablonski 2008). Thus, macroecological patterns can be understood as a re-

sult of species selection or sorting (see Lieberman and Vrba 1985, Jablonski 2008) in terms of how emergent or aggregate macroecological traits (such as geographic range size and body size) drive speciation and extinction rates (Rabosky and McCune 2009, FitzJohn 2010).

Another promising subject for evolutionary macroecology is the analysis of latitudinal diversity gradients. These patterns have been known since the eighteenth century (Hawkins 2001), and their investigation was quickly absorbed into the macroecology research program. There is a long debate regarding the relative roles of historical components (especially geographic variation in diversification rates and age along the gradients, niche conservatism) and current drivers (usually climate) in structuring such gradients (see Mittelbach et al. 2007). Several attempts to evaluate the balance between these components based on the phylogenetic patterns of species along the gradients have recently been published (e.g., Jablonski et al. 2006, Hawkins et al. 2007, Davies and Buckley 2011, Goldberg et al. 2011, Jansson et al. 2013). It is also possible to infer the broad-scale temporal stability of gradients using the fossil record, although relatively few attempts have been made to combine neontological and palaeontological approaches (e.g., Archibald et al. 2010). Clearly, the stability of diversity gradients through geological time and their relationship with climatic shifts can help disentangle the different mechanisms that have been used to explain them (e.g., Barnosky et al. 2005, Raia et al. 2011, Romdal et al. 2013). We believe that latitudinal diversity gradients may be a fine research line in evolutionary macroecology, perhaps by applying the same approaches that have been used within the current time frame to deal with fossil assemblages (e.g., Raia et al. 2012, 2013).

Although the integration of phylogenetic and fossil-based macroecology offers several new lines of research and much promise, it also has some limitations. Despite the need for, and growing interest in, combining fossil and phylogenetic data for macroecology, the incompleteness of both will always haunt such attempts. The fossil record is far too limited for most groups and envi-

ronments, particularly for very ancient periods (after the Precambrian) and non-depositional environments, irrespective of how much palaeontologists dig (Paul 2009). Available phylogenies are also too poorly resolved at the species level to allow reconstruction of their entire evolutionary history (except for a few groups; e.g., Bininda-Emonds et al. 2007, Jetz et al. 2012). Most importantly, phylogenies will always be biased towards living species, thus missing important information that fossils cannot necessarily supply (Aze et al. 2011). Nevertheless, the increasing availability of broad-scale, nearly or fully resolved phylogenies, together with extensive palaeoecoinformatics databases (e.g., Brewer et al. 2012) will provide material for satisfying many macroecological analyses coupling fossils and extant taxa.

Concluding Remarks

Incorporating historical components has long been recognised as an important enterprise for macroecology, despite operational difficulties in coupling phylogenetics and palaeontology for the particular interest of macroecological questions. In this regard, evolutionary macroecology can embody a fruitful and prosperous arena to connect phylogenetic and palaeontological research traditions from multiple areas. It is important to highlight that it is still challenging to integrate trait evolutionary models, diversification patterns and climate changes over different time scales within a single macroecological framework. Using both the fossil record and phylogenies to achieve this integration adds, indeed, another level of difficulty to this task. We believe it is possible to extend some of the recently developed approaches in each of the research traditions to better explore the possibility of developing such a framework, hence improving our ability to uncover some historical components underlying general principles related to the structure and function of ecological systems at broad temporal and spatial scales.

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