Can unified theories of biodiversity explain mammalian macroecological patterns?

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The idea of a unifying theory of biodiversity linking the diverse array of macroecological patterns into a common theoretical framework is very appealing. We explore this idea to examine currently proposed unified theories of biodiversity (UTBs) and their predictions. Synthesizing the literature on the macroecological patterns of mammals, we critically evaluate the evidence to support these theories. We find general qualitative support for the UTBs’ predictions within mammals, but rigorous testing is hampered by the types of data typically collected in studies of mammals. In particular, abundance is rarely estimated for entire mammalian communities or of individual species in multiple locations, reflecting the logistical challenges of studying wild mammal populations. By contrast, there are numerous macroecological patterns (especially allometric scaling relationships) that are extremely well characterized for mammals, but which fall outside the scope of current UTBs. We consider how these theories might be extended to explain mammalian biodiversity patterns more generally. Specifically, we suggest that UTBs need to incorporate the dimensions of geographical space, species’ traits and time to reconcile theory with pattern.

Keywords: abundance; body size; distribution; metabolic energy; species richness; species’ traits

1. INTRODUCTION

In science, researchers often tackle the complexity of the world around them by breaking broad subject areas into a plethora of subdisciplines. For example, within biology, ecology traditionally considers how interactions between organisms affect biological processes to determine the distribution and abundance of populations or species within a defined, but usually relatively restricted, area and time period. More recently, ecologists have realized that ecological systems are also profoundly affected by processes occurring at much larger spatial and temporal scales. This has led to the development of the field of macroecology, concerned with understanding the abundance and distribution of species at such large scales [1,2].

Macroeckology has invigorated the field of ecology by stimulating research into the processes underlying a range of large-scale biodiversity patterns. Examples include understanding the frequency distributions of abundance or geographical range size, their interaction, and variation of both distribution and abundance with space, time and life history (see this issue [3–6]). However, while scientists divide and sub-divide nature to aid their understanding of it, these divisions are nevertheless artificial dissections of an underlying whole. It is possible that the diverse range of macroecological patterns actually observed is generated by only a few common underlying mechanisms. The lack of unified theories has long been a shortcoming of ecology [7], and, excitingly, the last decade has seen the publication of at least six unifying hypotheses, unified theories of biodiversity (UTBs; table 1) [9–14]. These theories attempt to explain how a range of different macroecological patterns may be generated from the same underlying processes. More recently, it has been suggested that these unified theories may themselves be unified by a set of underlying processes [8].

The six UTBs are mainly concerned with the broad topics of area, abundance and species richness, i.e. the way individuals are distributed in space and among species. McGill [8] defines a unified theory as one that generates at least two distinct macroecological patterns, such as the species–area relationship (SAR) [15,16] and the species abundance distribution (SAD) [17]. One can argue about the extent to which these patterns are separate and unconnected, or indeed about the minimum number of patterns a theory must explain to qualify as ‘unified’. Nevertheless, McGill’s [8] assessment of what constitutes a
unified theory in this context is reasonable and convenient. The six UTBs are all based on general principles and constraints that should apply to most taxa in most environments [18]. They differ in the set of macroecological patterns predicted (table 1), the precise form of these patterns, the underlying processes hypothesized to explain the patterns and the mathematical context of the theory [8].

In this paper, we first review patterns covered by the UTBs, and the supporting evidence (or otherwise) from mammals for the first time (although see [19] for a plant example). Second, we consider what other biodiversity patterns are known for mammals but are not predicted by UTBs, and consider how UTBs could be extended to cover them. Finally, we conclude with suggestions for future research directions on the basis of the current match (or mismatch) between biodiversity pattern and theory.

2. UNIFIED THEORIES OF BIODIVERSITY AND MAMMALS: RECONCILING PATTERN WITH THEORY
How well do these UTBs explain the macroecological patterns in mammals? Here, we review the support for the different predictions of the UTBs in turn (table 2) and discuss if it is even possible to distinguish between competing UTB explanations for mammalian patterns.

(a) Species–area relationship
There is an extensive literature on the relationship between the size of an area and how many species it contains (the SAR), which has been reviewed many times before [20,25–27]. To summarize, the SAR is a positive power function (linear on log–log axes), with an intercept that varies with overall taxon

Table 1. Unified theories of biodiversity (UTBs) identified by McGill [8], together with a checklist of the macroecological patterns that each is hypothesized to explain using a common mechanism. SAR, species–area relationship; EAR, endemics–area relationship; OAR, occupancy–area relationship; SAD, species abundance distributions; ONR, occupancy–abundance relationship; SDR, similarity–distance relationship.

<table>
<thead>
<tr>
<th>UTB</th>
<th>description</th>
<th>predictions</th>
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<tr>
<td>Continuum [9]</td>
<td>species are randomly distributed with respect to one another. The abundance of each species is described by a Gaussian bell-curve in two-dimensional space</td>
<td>SAR; local SAD; ONR; SDR</td>
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<tr>
<td>Fractal [10]</td>
<td>simulation model of species presence/absence in hierarchically nested patches at multiple scales</td>
<td>SAR; EAR; OAR; local SAD; global SAD</td>
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<tr>
<td>MaxEnt [11]</td>
<td>a Bayesian method taking minimal inputs (total number of species, individuals, total area and total energy)</td>
<td>SAR; EAR; OAR; local SAD; global SAD; ONR</td>
</tr>
<tr>
<td>Neutral [12]</td>
<td>communities are made up of species with equal per capita birth and death rates. Immigration prevents mono-dominance</td>
<td>SAR; local SAD; global SAD; SDR</td>
</tr>
<tr>
<td>Metapopulation [13]</td>
<td>each species has a characteristic population density, which contributes to its rate of migration between patches. Local extinction is a simple function of area</td>
<td>SAR; ONR</td>
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<tr>
<td>Poisson cluster [14]</td>
<td>spatially explicit model in which individuals are positioned in clusters. Species-specific values of the clustering parameters are each drawn from a Poisson distribution</td>
<td>SAR; SDR</td>
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Table 2. Comparison of UTB predictions and mammalian biodiversity patterns. SAR, species–area relationship; EAR, endemics–area relationship; OAR, occupancy–area relationship; SAD, species abundance distributions; ONR, occupancy–abundance relationship; SDR, similarity–distance relationship. Names and acronyms of biodiversity patterns follow McGill [19].

pattern support from macroecological patterns in mammals

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<tr>
<td>SAR</td>
<td>SARs in mammals are widely reported (reviewed in [20]). Mammal SARs tend to have low intercepts and exponents in the typical range (e.g. [4,21]). It seems unclear if currently available empirical data are sufficient to test precise UTB predictions</td>
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<tr>
<td>EAR</td>
<td>mammal EARs have been reported in a couple of studies [4,21]. The form of these EARs does not seem consistent with current predictions but more research is needed</td>
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<tr>
<td>OAR</td>
<td>no available data</td>
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<tr>
<td>SAD</td>
<td>local and global SADs are poorly reported in mammals, but existing studies follow the typical hollow-curve distribution (e.g. [14,22], this study)</td>
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<tr>
<td>ONR</td>
<td>existing studies at a local and a global scale show both positive and negative correlations (e.g. [23,24], this study)</td>
</tr>
<tr>
<td>SDR</td>
<td>decay of similarity with distance is not well documented, but existing studies suggest a weak association in mammals (e.g. [6])</td>
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richness. Exponent values generally fall somewhere in the range 0.1–0.6. These exponent values vary systematically depending on spatial scale (higher at the smallest and largest scales, lower at intermediate scales), are generally found to be higher on islands than for equivalent areas on continents, are lower for nested subsets of habitats than for discrete patches, and vary with the amount of environmental energy available. Mammal SARs have exponents in the typical range, but tend to have low intercepts, because it is not an especially species-rich taxon. For example, exponents range from 0.235 for islands in the Sunda Shelf [28], 0.246 for islands in the Bass Strait [29], 0.429 for montainthrop habitat islands in the Great Basin of North America [30], 0.35 for countries worldwide using mammals globally, 0.55 for island nations and 0.30 for continental nations [21]. Similar results are found across mammals globally using different spatial clustering methods (e.g. hierarchically clustered biotic regions), with slope values reported between 0.24 and 0.47 for 4650 terrestrial mammal species [4].

The SAR is such a fundamental macroecological pattern that any UTB would be quickly discarded if it failed to predict the form of the relationship in exemplar datasets. It is no surprise that the match to real SARs is uniformly high for the UTB models (tables 1 and 2). The wider generality of the models is harder to assess, however, because most of the UTBs require data to produce their predictions that are not typically available with SARs. For example, the slope of the SAR predicted by the Metapopulation UTB is a function of the variance in species abundances and the ratio of colonization to extinction probabilities [13]. Similarly, the MaxEnt UTB requires that the number of individuals be known to predict the SAR [31]. Whether they could accurately predict the range of mammalian SARs found is thus unclear. Indeed, it is doubtful that there are any mammalian datasets of sufficient quality to allow comparative tests of the ability of the various UTBs to predict SARs.

(b) Endemics–area relationship
A related macroecological pattern to the SAR is the relationship between the number of endemic species and area (endemics–area relationship (EAR)). Endemic species are often species of conservation concern, because by definition they occupy only a smaller part of a larger area. Areas rich in endemic species are of interest both to conservationists and to biologists examining diversification processes [32]. The EAR would, therefore, seem likely to be of significant interest to macroecologists, but in fact rather little attention has been paid to it (reviewed in [32]). The notable exception is work by John Harte and co-workers (e.g. [31–34]) in the context of their development of the Fractal and the MaxEnt UTBs. For example, Harte & Kinzig [33] showed that the number of plant species endemic to each of the contiguous 48 states of the USA increased with area with a slope of 3.7 on a log–log plot versus 0.13 for the SAR for these states (see also [34]). There are very few EAR analyses of mammals. One of these, by Ceballos & Brown [21], calculated a range of EARs for all terrestrial mammals using countries as the unit of analysis. The slopes of these relationships lie in the range 0.13–0.67, relative to equivalent SARs in the range 0.12–0.55. Kisel et al. [4] using different spatial clusters found similar values for all mammals (0.14–0.34) but with reduced slopes compared with total and non-endemic species-richness equivalent SARs in their study. They also found the variation in EAR slope values to depend on habitat diversity and the amount of available environmental energy [4].

Both the Fractal and Maxent UTBs produce explicit predictions for the form of EARs. Under the Fractal model as formulated by Harte & Kinzig [33] and Harte [34], the number of endemics in an area is a power function of the area, with the exponent equal to

$$\frac{-\ln(1 - 2^{-z})}{\ln 2},$$

(2.1)

where $z$ is the exponent of the associated SAR. Under the Maxent UTB, the number of endemics in an area is the product of the total species richness of the area, the probability that a species has abundance $n_0$ and the probability that all of these individuals fall in an area of size $A$ (a subset of $A_0$) [31]. Both UTBs produce predictions in broad accordance with empirical EARs as tested by the original authors [31,33,34], but to date no study has compared the relative performance of the models on the same data. Applying equation (2.1) to the $z$ values in Ceballos & Brown [21] produces predictions at substantial variance with their own EAR exponents. Green & Ostling [32] suggest that the form of the EAR will depend on the evenness of the regional SAD, and the degree of intraspecific clustering. The EAR is clearly a relationship that is ripe for more extensive exploration and testing against theory.

(c) Occupancy–area relationship (or scale–area curves)
The occupancy–area relationship (OAR) describes how species’ probability of occurrence increases with the spatial scale, and is based on the observation that species distributions tend to be self-similar, or fractal-like in nature [35]. Specific forms of this relationship are predicted by the Fractal and MaxEnt UTBs. Testing this pattern either requires that the location of each individual is known, or the distribution is mapped at a scale of a few kilometres. The former is difficult for mobile animals (i.e. mammals) and the latter is possible for only a few well-studied species with narrow distributions. The scale–area curve is qualitatively similar to another macroecological pattern, the individual–area relationship (IAR), which describes how abundance increases with area.

(d) Species abundance distribution
The SAD is a description of how many individuals of each species are present in a community. These are among the most common types of data collected in ecology. A universal feature of all SADs is that abundance is distributed extremely unevenly among species. For example, most communities have a lot
of individuals belonging to a few common species and a few individuals of many rare species, leading to the characteristic ‘hollow curve distribution’ when plotted as a histogram. SADs are approximated quite well by a lognormal distribution, although numerous statistical and mechanistic descriptions have been proposed (reviewed in [17]). Hollow-curve SADs are also evident when measured using global or regional population sizes (global SAD) as well as within local communities (local SAD).

Four of the six UTBs predict some form of local SAD (e.g. logseries or lognormal). The most explicit predictions derive from the Neutral UTB, in which the hollow curve SAD arises from the assertion that per capita birth and death rates are constant across species. The form of the SAD under the Neutral UTB is defined by a specific distribution known as the ‘zero-sum multinomial’, which has three parameters [12]. Neutral, MaxEnt and Fractal UTBs all produce global SADs as the sum of local SADs across patches. The Continuum UTB generates a local SAD but takes the global SAD as an input (in common with the Metapopulation and Poisson cluster UTBs, which do not predict a local SAD).

Unfortunately, mammalian SADs are rarely reported, probably because of the scale differences at which large and small-bodied mammals are studied, and the relatively low species richness of most mammalian communities. Among others, examples have been presented for Neotropical bats [22] and desert rodents [14] showing a typical hollow curve distribution at the local community level. At the global scale, both population density and total population size show characteristic hollow curves (figure 1) that superficially resemble a lognormal distribution. However, we suspect that compendium data across many communities such as those presented in figure 1 (data from [36]) are unsuitable for distinguishing rigorously between the various forms of the SAD predicted by the UTBs.

(e) Occupancy–abundance relationship

The tendency for widespread species to be more abundant (occupancy–abundance relationship (ONR)) is a common feature of ecological communities [1,23,26,37]. However, there are exceptions to this pattern [38]. In mammals, existing studies find a positive relationship between species population density and occupancy at a local scale (e.g. [23,24]). However, this pattern does not appear to hold for any mammalian order (that we have data for) at the global scale (figure 2). In fact, the opposite pattern seems to hold: there are many species that either have extremely small distributions but occur at high densities, or the opposite combination. This may be explained by the non-random distribution of species’ geographical ranges: many mammal species have distributions that are parapatric with congeners. However, abundance–size relationships in other taxa have been shown to become progressively weaker as the scale increases over which range size is measured: indeed Cowley et al. [39] reported a significant negative relationship between mean abundance of UK butterfly species and the size of their global distributions. Three UTBs (Continuum, Metapopulation and MaxEnt) can derive the positive correlation between abundance and occupancy (or abundance and range size in the case of the Continuum UTB) [8]. McGill [8] even suggests that the other three UTBs could be extended to predict this relationship as well. However, it is unclear if there is a distinction between local and global ONRs in the UTBs’ predictions.

(f) Similarity–distance relationship (or decay of similarity)

Decay of similarity in community composition with distance (i.e. beta-diversity) is predicted by at least three
UTBs (table 1). The similarity–distance relationship (SDR) is a simple consequence of spatial autocorrelation in the abundance of individual species, combined with the assertion (common to all UTBs) that species are distributed randomly with respect to one another. There is some evidence that the similarity of mammalian communities declines with distance. However, most studies of mammalian beta-diversity have considered only turnover of species composition (e.g. [6]). We are aware of just one SDR for mammalian communities using changes in relative abundance [40].

(g) Underlying assumptions of all unified theories of biodiversity
McGill [8] argues that all the UTBs can be viewed as an attempt to explain the distribution of a set of objects (e.g. individuals or ranges of different species) placed randomly in space. In fact, he suggests that all six theories use the same three assertions to explain this stochastic geometry of biodiversity. These are: (i) individuals are spatially clumped within a species; (ii) abundance between species at a regional and/or global scale varies drastically and is roughly a hollow curve in distribution; and (iii) individuals between species can be treated as independent and placed without regard to others [8]. Although the first two of the assumptions seem reasonable given the documented patterns, the third assumption is more questionable. McGill [8] argues that independence translates into the statistical independence assumed by McGill [8].

3. OTHER MAMMALIAN BIODIVERSITY PATTERNS
We consider mammalian global biodiversity patterns in the context of three axes: space (i.e. geographical patterns), species’ traits (including body size and life-history strategies) and time (e.g. diversification rates and evolutionary history). These axes overlap considerably and are not meant to be exhaustive; however, these are a useful framework for our discussion. As we shall see, at least one of the biodiversity patterns we consider is predicted by one of the six UTBs, raising the possibility that additional constraints or assumptions could extend the existing UTBs to encompass a far wider range of phenomena.

(a) Geographical patterns in biodiversity
The UTBs deal with space in a variety of ways, but most are in some way spatially explicit. However, this spatial component is abstract, and none of the UTBs is capable of reproducing the macroecological patterns that show systematic variation in space. With the construction of global datasets on the distributions of mammals (e.g. [43]), there is a growing body of literature on these geographical patterns of mammalian biodiversity (e.g. [3,21,44–46]). It is evident that mammalian species richness is not randomly distributed across the planet [43,45,47]. While it is certainly true that the areas with highest mammal species richness are tropical (the classic ‘latitudinal gradient’), the relationship between species richness and latitude is more complex than a simple decline [3,48]. Thus, mammals are particularly species rich in the Eastern

Figure 2. Species range–size relationship in 850 mammal species in eight orders. Each point is a species for which geographical range size and average population density have been estimated (data from Jones et al. [36]).
Arc Mountains and tropical Rift Valley of Africa, and in the tropical Andes. A single 100 × 100 km area in the Eastern Arc Mountains can house twice as many species as an identical area at the same latitude just a few 100 km to the west in the Congo basin [43,45,49]. Other species-rich areas for mammals include northern South America, Central America, the African savannah zones and the islands and mainland of tropical southeast Asia. Non-random patterns of species richness are also found across altitudes as well as latitudes. In general, higher elevations are home to fewer species than lower elevations, but the overall relationship between elevation and species richness varies depending on the taxon and location [50]. Non-volant small mammals almost always show a unimodal relationship, with highest richness at intermediate elevations, whereas bats show a roughly even split between unimodal and negative relationships between elevation and species richness [51,52].

Global patterns in functional and phylogenetic richness and beta-diversity also show non-random spatial distributions [5,45,46]. Although high surrogacy has been found between species, functional and phylogenetic richness in mammals, evidence suggests that patterns in relative functional and phylogenetic richness are distinct from the general species-richness patterns [5]. Specifically, Safi et al. [5] found that areas that are characterized by higher variance in temperatures contained higher relative phylogenetic diversity, whereas tropical areas were characterized by a lower relative functional diversity. Beta-diversity, the change in species composition between places, is also non-random in mammals but with striking contrasting patterns to that of species richness [46]. For example, high beta-diversity measured across North and South American continents is found across a wide range of latitudes; and tends to be higher at high altitudes and at biome edges [46]. The spatial pattern in the sizes of geographical ranges is another long-standing macroecological pattern, the classic Rapoport’s rule [53] (reviewed in [54]). Rapoport’s rule suggests that there is a tendency for the geographical ranges of species to increase with latitude and this has been the focus of many studies in mammals (e.g. [55,56]). There is evidence that Rapoport’s rule is applicable to mammals, as patterns within terrestrial species suggest that those with the smallest ranges are mostly restricted to the tropics, and species with the largest ranges are found across high latitudes [44,57]. Using the new mammalian datasets, Davies et al. [3] confirm a Rapoport-like pattern for terrestrial mammals (and most of the separate species-rich orders), where latitudinal range extents are greatest at mid- to high latitudes and narrower at more equatorial latitudes (with the effect more pronounced at higher latitudes).

Geographical patterns in life-history traits are poorly reported in mammals (although there are studies within birds [58]), probably because global mammal trait datasets have only recently been widely available [36,59]. However, spatial patterns in body size have been the focus of many mammalian studies, where analyses have tested the classic ‘Bergmann’s rule’ [60]. Bergmann’s rule suggests that within endothermic species, larger species tend to be found in cooler environments. This pattern has found broad support within mammals, although the relationship varies among taxa and location (e.g. [61–66]). This pattern may also be confounded with the spatial pattern in range size, as larger bodied mammals also have large ranges [67].

Explanations for these non-random spatial patterns in biodiversity are extremely numerous and yet still not definitive. The focus of much attention has been on explaining the latitudinal gradient in species richness, which commonly features in the top unanswered questions in science (reviewed in [68]). Species richness typically correlates strongly with measures of environmental productivity or temperature [69]. However, the precise mechanism underlying these correlations, linking resource availability to species number, remains elusive. There is an increasing recognition that current and historic biogeography, past diversification patterns and life-history traits, as well as the environment, may play interacting roles in determining spatial variation in both species richness [3,4,42,47,70–72] and geographical range size [3,44]. There is also broad congruence in the explanations favoured for altitudinal and latitudinal species-richness gradients, with elevational-richness peaks argued to be in areas with higher productivity [50,51], and increasingly a role posited for historical processes such as phylogenetic niche conservatism (e.g. [73]). Similar environmental explanations have also been suggested for patterns of functional and phylogenetic richness [5] and beta-diversity [46].

None of the UTBs provides an explanation for these geographical patterns in biodiversity. This is because the key parameters of interest are actually inputs into the model, i.e. the number of species, total number of individuals and area available. It is conceivable that these input parameters might be allowed to vary among regions or along an environmental gradient in a way that extends the range of predictions of the UTBs to the patterns listed above. However, such extensions would be of limited insight unless accompanied by a theory for total species richness. Recently, there have been several attempts to build such a theory, starting from spatial–temporal [74], life history [70] and metabolic [75,76] perspectives. A key challenge ahead is to integrate these developments into the framework of the UTBs.

(b) Trait-based patterns in biodiversity

A large volume of macroecological research concerns patterns relating to species’ traits, particularly body size (i.e. allometric scaling relationships) [2,77–79]. Much of the variation in mammalian life-history traits can be related to body size variation [80–83]. The best known of these allometric relationships is Kleiber’s 3/4 scaling law [84], which relates individual energetic requirements (specifically, basal metabolic rate) with body mass. A large part of the metabolic scaling literature has focused on mammals, and the most popular theoretical explanation for 3/4 scaling is designed around the mammalian vascular system [85]. However, there is now clear evidence not only that the exponent in mammals is
significantly shallower than $3/4$ [86,87], but also that it is significantly nonlinear [87–89] and varies substantially among taxa [88]. Modifications to the West et al. [85] model have been proposed to explain these deviations, with mixed results [89,90].

Another prevalent allometric scaling pattern is the tendency for large-bodied organisms to occur at low population densities, known as the size–density relationship [91]. The original size–density relationship was reported in mammals as a power-law with exponent close to $-3/4$ [92,93]. This pattern has been influential in the development of a metabolic theory of ecology (MTE) [94–96], which links biodiversity patterns with individual energetic requirements. For example, MTE could derive the species–abundance relationship if some kind of body size distribution was assumed. However, recent re-analysis of Damuth’s data indicates that size–density exponents are generally much shallower than $-3/4$ [97], illustrating that further work to develop the MTE may be required.

To date, the UTBs have largely treated species as equivalent, such that body size and other traits are irrelevant to the observed patterns of species richness, distribution and abundance. The exception is MaxEnt, which includes a constraint on both the total energy available and the total number of individuals. The model generates size–density relationship consistent with Damuth’s $-3/4$ exponent, using Kleiber’s law as an empirical approximation to convert energy use into body masses for each species [31]. However, this outcome is inevitable if species’ total energy use and abundance are uncorrelated (i.e. energetic equivalence).

In summary, the large body of empirical and theoretical research on allometric relations (and other trait-based patterns) suggest that incorporating these additional dimensions into existing UTBs is conceptually plausible.

(c) Temporal patterns in biodiversity

Diversification rates across mammals have not been equal [41,98], which has led to significant imbalance in the distribution of species at nodes in the mammalian phylogenetic tree over time. This diversification rate variation leads to the distribution of species among higher taxa following a hollow curve, i.e. most species belonging to few taxa and many taxa containing few species [99]. More recently, it has been suggested that the opportunity of accessing new regions of geographical or niche space has influenced the variation in diversification rates [4,42]. Under this model, phylogenies are unbalanced because regions and niches vary in the diversity they can support, because new radiations will probably originate in already diverse clades, and because lineages that are relics are hard to replace. The evidence supporting the importance of historical events and biogeography in explaining current patterns in biodiversity is accumulating rapidly [3,47,71]. It seems reasonable to suggest that a UTB should be able to incorporate this important temporal element of species richness. In fact, the Neutral UTB does include speciation and generates a hollow-curve distribution of species-richness among lineages.

Trait values have also been shown to have a temporal component. For example, evidence suggests that there has been a directed evolution towards large body sizes across North American Cenozoic fossil mammals [100] and in other clades (e.g. dinosaurs [101]). This evolutionary trend, termed Cope’s Rule, is not found consistently in all clades and there are also disadvantages of being large, for example, an increased risk of extinction [102], which may increase extinction rates. However, this is an interesting further temporal pattern which the UTBs could aim to address.

4. CONCLUSIONS

Synthesizing the literature on the macroecological patterns of mammals, we find general qualitative support for the UTBs’ predictions, but we have difficulties in distinguishing between the relative merits of competing theories. As yet none of the six UTBs predicts all the patterns that have been observed. Difficulties in distinguishing between different theories are probably because some of the forms of the UTBs predictions are qualitative and, as McGill [8] suggests, although superficially different, all the UTBs are fundamentally modelling the same phenomena and therefore have similar predictions. Additionally, the type of mammalian data needed for testing of the UTBs is rarely available. For example, mammals (in comparison with birds) are harder to observe directly, and their diverse ecologies and life histories [103] make broad spectrum site-based population databases for entire mammalian communities uncommon. Historically, mammal ecologists have focused on tracking individuals or monitoring populations of single species, where the selection of species is based on personal interests or convenience. More recently, there has been a move towards broader spectrum survey methods for mammals (e.g. camera trapping [104], acoustic surveys [105]), that are capable of producing data for multiple species which are temporally and spatially explicit. These are the kinds of mammalian data that are needed to more explicitly test the specific predictions of the UTBs.

Our examination of other more general mammalian biodiversity patterns that are not currently predicted by UTBs suggests that UTBs need to further consider the dimensions of space, species’ traits and time. Currently, the UTBs are mostly concerned with only two of the major axes of variation (species richness and abundance), although several do have an abstract spatial component. Two UTBs have extended these axes to also consider energy (MaxEnt) and time (Neutral), and these are promising future directions. It is interesting to note that the MTE is approaching many of these problems (the distribution of energy, the mass-dependent energetic needs of different species and the universal dependence of temperature) from a different perspective [75,76,95]. A fruitful area of future research might be to examine whether these two hitherto separate branches of theory could be merged to model biodiversity, including the full pattern of species’ trait variation, in a truly unified fashion.

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