Article (refereed)

1 **Can unified theories of biodiversity explain mammalian**
2 **macroecological patterns?**
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1   **Abstract**

2   The idea of a unifying theory of biodiversity linking the diverse array of macroecological

3   patterns into a common theoretical framework is very appealing. We explore this idea to

4   examine currently proposed unified theories of biodiversity (UTBs) and their predictions.

5   Synthesising the literature on the macroecological patterns of mammals, we critically

6   evaluate the evidence to support these theories. We find general qualitative support for

7   the UTBs' predictions within mammals, but rigorous testing is hampered by the types of

8   data typically collected in studies of mammals. In particular, abundance is rarely

9   estimated for entire mammalian communities or of individual species in multiple

10   locations, reflecting the logistical challenges of studying wild mammal populations. By

11   contrast, there are numerous macroecological patterns (especially allometric scaling

12   relationships) that are extremely well characterised for mammals, but which fall outside

13   the scope of current UTBs. We consider how these theories might be extended to explain

14   mammalian biodiversity patterns more generally. Specifically, we suggest that UTBs

15   need to incorporate the dimensions of geographic space, species' traits and time to

16   reconcile theory with pattern.

17

1   **Introduction**

2   Complexity is often broken down into conceptually manageable chunks. In science,

3   researchers often tackle the complexity of the world around them by breaking broad

4   subject areas into a plethora of sub-disciplines. For example, within biology, ecology

5   traditionally considers how interactions between organisms affect biological processes to

6   determine the distribution and abundance of populations or species within a defined, but

7   usually relatively restricted, area and time period. More recently, ecologists have realised

8   that ecological systems are also profoundly affected by processes occurring at much

9   larger spatial and temporal scales. This has led to the development of the field of

10   macroecology, concerned with understanding the abundance and distribution of species at

11   larger spatial and temporal scales [1-2].

12

13   Macroecology has invigorated the field of ecology by stimulating research into the

14   processes underlying a range of large-scale biodiversity patterns. Examples include

15   understanding the frequency distributions of abundance or geographic range size, their

16   interaction, and variation of both distribution and abundance with space, time, and life

17   history (see this volume [3-6]). However, while scientists divide and sub-divide nature to

18   aid their understanding of it, these divisions are nevertheless artificial dissections of an

19   underlying whole. It is possible that the diverse range of macroecological patterns

20   actually observed is generated by only a few common underlying mechanisms. The lack

21   of unified theories has long been a shortcoming of ecology [7] and excitingly, the last

22   decade has seen the publication of at least six unifying hypotheses, Unified Theories of

23   Biodiversity (UTBs) (Table 1) [8-13]. These theories attempt to explain how a range of

1 different macroecological patterns may be generated from the same underlying processes.

2 More recently, it has been suggested that these unified theories may themselves be

3 unified by a set of underlying processes [14].

4

5 The six UTBs are mainly concerned with the broad topics of area, abundance and species

6 richness, i.e., the way individuals are distributed in space and among species. McGill [14]

7 defines a unified theory as one that generates at least two distinct macroecological

8 patterns, such as the species–area relationship (SAR) [15-16] and the species abundance

9 distribution (SAD) [17]. One can argue about the extent to which these patterns are

10 separate and unconnected, or indeed about the minimum number of patterns a theory

11 must explain to qualify as 'unified'. Nevertheless, McGill's [14] assessment of what

12 constitutes a unified theory in this context is reasonable and convenient. The six UTBs

13 are all based on general principles and constraints that should apply to most taxa in most

14 environments [18]. They differ in the set of macroecological patterns predicted (Table 1),

15 the precise form of these patterns, the underlying processes hypothesised to explain the

16 patterns, and the mathematical context of the theory [14].

17

18 In this paper, we first review patterns covered by the UTBs, and the supporting evidence

19 (or otherwise) from mammals for the first time (although see [19] for a plant example).

20 Second, we consider what other biodiversity patterns are known for mammals but are not

21 predicted by UTBs, and consider how UTBs could be extended to cover them. Finally,

22 we conclude with suggestions for future research directions on the basis of the current

23 match (or mismatch) between biodiversity pattern and theory.

1

2 **UTBs and Mammals: reconciling pattern with theory**

3 How well do these UTBs explain the macroecological patterns in mammals? Here we

4 review the support for the different predictions of the UTBs in turn (Table 2) and discuss

5 if it is even possible to distinguish between competing UTB explanations for mammalian

6 patterns.

7

8 *Species-Area Relationship - SAR*. There is an extensive literature on the relationship

9 between the size of an area and how many species it contains (the species-area

10 relationship, or SAR), which has been reviewed many times before [20-23]. To

11 summarize, the SAR is a positive power function (linear on log-log axes), with an

12 intercept that varies with overall taxon richness. Exponent values generally fall

13 somewhere in the range $0.1 - 0.6$. These exponent values vary systematically depending

14 on spatial scale (higher at the smallest and largest scales, lower at intermediate scales),

15 are generally found to be higher on islands than for equivalent areas on continents, are

16 lower for nested subsets of habitats than for discrete patches, and vary with amount of

17 environmental energy available. Mammal SARs have exponents in the typical range, but

18 tend to have low intercepts, because it is not an especially species rich taxon. For

19 example, exponents range from 0.235 for islands in the Sunda Shelf [24], 0.246 for

20 islands in the Bass Strait [25], 0.429 for mountaintop habitat islands in the Great Basin of

21 North American [26], 0.35 for countries worldwide using mammals globally, 0.55 for

22 island nations, and 0.30 for continental nations [27]. Similar results are found in across

23 mammals globally using different spatial clustering methods (e.g., hierarchically

1 clustered biotic regions), with slope values reported between 0.24 and 0.47 for 4650

2 terrestrial mammal species [4].

3

4 The SAR is such a fundamental macroecological pattern that any UTB would be quickly

5 discarded if it failed to predict the form of the relationship in exemplar datasets. It is no

6 surprise that the match to real SARs is uniformly high for the UTB models (Table 1, 2).

7 The wider generality of the models is harder to assess, however, because most of the

8 UTBs require data to produce their predictions that are not typically available with SARs.

9 For example, the slope of the SAR predicted by the Metapopulation UTB is a function of

10 the variance in species abundances and the ratio of colonization to extinction probabilities

11 [10]. Similarly, the MaxEnt UTB requires that the number of individuals be known to

12 predict the SAR [28]. Whether they could accurately predict the range of mammalian

13 SARs found is thus unclear. Indeed, it is doubtful that there are any mammalian data sets

14 of sufficient quality to allow comparative tests of the ability of the various UTBs to

15 predict SARs.

16

17 ***Endemics-Area Relationship - EAR***. A related macroecological pattern to the SAR is the

18 relationship between the number of endemic species and area (endemics-area

19 relationship, or EAR). Endemics species are often species of conservation concern,

20 because by definition they occupy only a smaller part of a larger area. Areas rich in

21 endemic species are of interest both to conservationists and to biologists examining

22 diversification processes [29]. The EAR would therefore seem likely to be of significant

23 interest to macroecologists but in fact, rather little attention has been paid to it (reviewed

1   in [29]). The notable exception is work by John Harte and colleagues (e.g., [28-31]) in the

2   context of their development of the Fractal and the MaxEnt UTBs. For example, Harte

3   and Kinzig [30] showed that the number of plant species endemic to each of the

4   contiguous 48 states of the US increased with area with a slope of 3.7 on a log-log plot

5   versus 0.13 for the SAR for these states (see also [31]). There are very few EAR analyses

6   of mammals. One of these, Ceballos and Brown [27], calculated a range of EARs for all

7   terrestrial mammals using countries as the unit of analysis. The slopes of these

8   relationships lie in the range 0.13 to 0.67, relative to equivalent SARs in the range 0.12 to

9   0.55. Kisel *et al*.[4] using different spatial clusters find similar values for all mammals

10   (0.14 to 0.34) but with reduced slopes compared to total and non-endemic species

11   richness equivalent SARs in their study. They also found the variation in EAR slope

12   values to depend on habitat diversity and the amount of available environmental energy

13   [4].

14

15   Both the Fractal and Maxent UTBs produce explicit predictions for the form of EARs.

16   Under the Fractal model as formulated by Harte & Kinzig [30] and Harte [31], the

17   number of endemics in an area is a power function of the area, with the exponent equal to

18
$$\frac{-\ln(1-2^{-z})}{\ln 2}$$

19   Equation 1

20

21   where z is the exponent of the associated species-area relationship. Under the Maxent

22   UTB, the number of endemics in an area is the product of the total species richness of the

23   area, the probability that a species has abundance n_0 and the probability that all of these

1   individuals fall in an area of size A (a subset of A_0) [28]. Both UTBs produce predictions

2   in broad accordance with empirical EARs as tested by the original authors [28-30-31],

3   but to date no study has compared the relative performance of the models on the same

4   data. Applying Equation 1 to the z values in Ceballos and Brown [27] produces

5   predictions at substantial variance with their own EAR exponents. Green and Ostling [29]

6   suggest that the form of the EAR will depend on the evenness of the regional species

7   abundance distribution, and the degree of intraspecific clustering. The EAR is clearly a

8   relationship that is ripe for more extensive exploration and testing against theory.

9

10   ***Occupancy Area Relationship – OAR (or Scale-Area curves).*** This describes how

11   species' probability of occurrence increases with the spatial scale, and is based on the

12   observation that species distributions tend to be self-similar, or fractal-like in nature [32].

13   Specific forms of this relationship are predicted by the Fractal and MaxEnt UTBs.

14   Testing this pattern either requires that the location of each individual is known, or the

15   distribution is mapped at a scale of a few kilometres. The former is difficult for mobile

16   animals (i.e., mammals) and the latter is possible for only a few well-studied species with

17   narrow distributions. The scale-area curve is qualitatively similar to another

18   macroecological pattern, the individual-area relationship (IAR), which describes how

19   abundance increases with area.

20

21   ***Species Abundance Distribution - SAD.*** The species abundance distribution (SAD) is a

22   description of how many individuals of each species are present in a community. These

23   are among the most common types of data collected in ecology. A universal feature of all

1 SADs is that abundance is distributed extremely unevenly among species. For example,

2 most communities have a lot of individuals belonging to a few common species and a few

3 individuals of many rare species, leading to the characteristic 'hollow curve distribution'

4 when plotted as a histogram. SADs are approximated quite well by a log-normal

5 distribution, although numerous statistical and mechanistic descriptions have been

6 proposed (reviewed in [17]). Hollow-curve SADs are also evident when measured using

7 global or regional population sizes (Global SAD) as well as within local communities

8 (Local SAD).

9

10 Four of the six UTBs predict some form of local SAD (e.g., logseries or lognormal). The

11 most explicit predictions derive from the Neutral UTB, in which the hollow curve SAD

12 arises from the assertion that per-capita birth and death rates are constant across species.

13 The form of the SAD under the Neutral UTB is defined by a specific distribution known

14 as the 'zero-sum multinomial', which has three parameters [9]. Neutral, MaxEnt and

15 Fractal UTBs all produce Global SADs as the sum Local SADs across patches. The

16 Continuum UTB generates a Local SAD but takes the Global SAD as an input (in

17 common with the Metapopulation and Poisson cluster UTBs, which do not predict a

18 Local SAD). Are SADs present in mammalian communities? Unfortunately, mammalian

19 SADs are rarely reported, probably because of the scale differences at which large and

20 small-bodied mammals are studied, and the relatively low species richness of most

21 mammalian communities. Amongst others, examples have been presented for Neotropical

22 bats [33] and desert rodents [11], showing a typical hollow curve distribution at the local

23 community level. At the global scale, both population density and total population size

1   show characteristic hollow-curves (Figure 1) that superficially resemble a lognormal

2   distribution. However, we suspect that compendium data across many communities such

3   as those presented in Figure 1 (data from [34]) are unsuitable for distinguishing

4   rigorously between the various forms of the SAD predicted by the UTBs.

5

6   ***Occupancy Abundance Relationship – ONR.*** The tendency for widespread species to be

7   more abundant (Occupancy Abundance Relationship) is a common feature of ecological

8   communities [1-21-35-36]. However, there are exceptions to this pattern [37]. In

9   mammals, existing studies find a positive relationship between species population density

10   and occupancy at a local scale (e.g., [36-38]). However, this pattern does not appear to

11   hold for any mammalian order (that we have data for) at the global scale (Figure 2). In

12   fact, the opposite pattern seems to hold: there are many species that either have extremely

13   small distributions but occur at high densities, or the opposite combination. This may be

14   explained by the non-random distribution of species geographic ranges: many mammal

15   species have distributions that are parapatric with congeners. However, abundance-size

16   relationships in other taxa have been shown to become progressively weaker as the scale

17   increases over which range size is measured: indeed Cowley *et al*. [39] reported a

18   significant negative relationship between mean abundance of UK butterfly species and

19   the size of their global distributions. Three UTBs (Continuum, Metapopulation and

20   MaxEnt) can derive the positive correlation between abundance and occupancy (or

21   abundance and range size in the case of the Continuum UTB) [14]. McGill [14] even

22   suggests that the other three UTBs could be extended to predict this relationship as well.

23   UTB predictions are only qualitative so it is difficult to test quantitatively with

1 mammalian patterns. It is also unclear if there is a distinction between local and global

2 abundance occupancy relationships in the UTBs' predictions, but the abundance

3 occupancy relationship in mammals is present at both scales (Figure 2).

4

5 ***Similarity Distance Relationship (SDR) (or Decay of similarity).*** Decay of similarity of

6 communities with distance (i.e., beta diversity – the change in species composition

7 between places) is predicted by at least three UTBs (Table 1). Decay of similarity with

8 distance is a simple consequence of spatial autocorrelation in the abundance of individual

9 species, combined with the assertion (common to all UTBs) that species are distributed

10 randomly with respect to one another. There is some evidence that the similarity of

11 mammalian communities declines with distance. For example, Cardillo [6] found that the

12 degree of similarity weakly declines with the size of ecoregion area in an analysis of the

13 phylogenetic community structure of carnivores. However, this study considered only

14 turnover of species composition, not changes in relative species abundance.

15

16 ***Underlying Assumptions of all UTBs***. McGill [14] argues that all the UTBs can be

17 viewed as an attempt to explain the distribution of a set of objects (e.g., individuals or

18 ranges of different species) placed randomly in space. In fact, he suggests that all six

19 theories use the same three assertions to explain this stochastic geometry of biodiversity

20 and can be unified. These are: (1) individuals are spatially clumped within a species; (2)

21 abundance between species at a regional and/or global scale varies drastically and is

22 roughly a hollow curve in distribution; and (3) individuals between species can be treated

23 as independent and placed without regard to others [14]. Although the first two of the

1 assumptions seem reasonable given the documented patterns, the third assumption is

2 more questionable. McGill [14] argues that independence among species distributions is

3 approximated accurately (in a statistical sense), because most species interact directly

4 with only a few others (e.g., through competition or predation). At a global scale, it is

5 clear that evolutionary biogeography places strong constraints on regional abundance and

6 species richness [40-41], but it is not clear whether this kind of non-independence

7 translates into statistical independence assumed by McGill [14].

8

9 **Other Mammalian Biodiversity Patterns**

10 We consider mammalian global biodiversity patterns in the context of three axes: space

11 (i.e., geographic patterns), species' traits (including body size and life history strategies),

12 and time (e.g., diversification rates, evolutionary history). These axes overlap

13 considerably and are not meant to be exhaustive; however these are a useful framework

14 for our discussion. As we shall see, at least one of the biodiversity patterns we consider

15 are predicted by one of the six UTBs, raising the possibility that additional constraints or

16 assumptions could extend the existing UTBs to encompass a far wider range of

17 phenomena.

18

19 *Geographical patterns in biodiversity*. The UTBs deal with space in a variety of ways,

20 but most are in some way spatially explicit. However, this spatial component is abstract,

21 and none of the UTBs are capable of reproducing the macroecological patterns that show

22 systematic variation in space. With the construction of global datasets on the distributions

23 of mammals (e.g., [42]), there is a growing body of literature on these geographical

1   patterns of mammalian biodiversity (e.g, [3-27-43-45]). It is evident that mammalian

2   species richness is not randomly distributed across the planet [42-44-46]. While it is

3   certainly true that the areas with highest mammal species richness are tropical (the classic

4   'latitudinal gradient'), the relationship between species richness and latitude is more

5   complex than a simple decline [3-47]. Thus, mammals are particularly species rich in the

6   Eastern Arc Mountains and tropical Rift Valley of Africa, and in the tropical Andes. A

7   single 100 x 100 km area in the Eastern Arc Mountains can house twice as many species

8   as an identical area at the same latitude just a few 100 km to the west in the Congo basin

9   [42-44-48]. Other species-rich areas for mammals include northern South America,

10 Central America, the African savannah zones, and the islands and mainland of tropical

11 South-East Asia.

12

13 Non-random patterns of species richness are also found across altitudes as well as

14 latitudes. In general, higher elevations are home to fewer species than lower elevations,

15 but the overall relationship between elevation and species richness varies depending on

16 the taxon and location [49]. Non-volant small mammals almost always show a unimodal

17 relationship, with highest richness at intermediate elevations, whereas bats show a

18 roughly even split between unimodal and negative relationships between elevation and

19 species richness [50-51].

20

21 Global patterns in functional and phylogenetic richness and beta-diversity also show non-

22 random spatial distributions [5-44-45]. Although high surrogacy has been found between

23 species, functional and phylogenetic richness in mammals, evidence suggests that

1 patterns in relative functional and phylogenetic richness are distinct from the general

2 species richness patterns [5]. Specifically, Safi *et al*. [5] find that areas that are

3 characterised by higher variance in temperatures contained higher relative phylogenetic

4 diversity, whereas tropical areas were characterised by a lower relative functional

5 diversity. Beta-diversity, the change in species composition between places, is also non-

6 random in mammals but with striking contrasting patterns to that of species richness [45].

7 For example, high beta-diversity measured across North and South American continents

8 is found across a wide range of latitudes; and tends to be higher at high altitudes and at

9 biome edges [45].

10

11 The spatial pattern in the sizes of geographic ranges is another long-standing

12 macroecological pattern, the classic Rapoport's rule [52] (reviewed in [53]). Rapoport's

13 rule suggests that there is a tendency for the geographic ranges of species to increase with

14 latitude and this has been the focus of many studies in mammals (e.g., [54-55]). There is

15 evidence that Rapoport's rule is applicable to mammals, as patterns within terrestrial

16 species suggest that those with the smallest ranges are mostly restricted to the tropics, and

17 species with largest ranges are found across high latitudes [43-56]. Using the new

18 mammalian data sets, Davies *et al*. [3] confirm a Rapoport-like pattern for terrestrial

19 mammals (and most of the separate species-rich orders), where latitudinal range extents

20 are greatest at mid- to high latitudes and narrower at more equatorial latitudes (with the

21 effect more pronounced at higher latitudes).

22

1   Geographical patterns in life-history traits are poorly reported in mammals (although

2   there are studies within birds [57]), probably because global mammal trait data sets have

3   only recently been widely available [34-58]. However, spatial patterns in body size have

4   been the focus of many mammalian studies, where analyses have tested the classic

5   'Bergmann's rule' [59]. Bergmann's rule suggests that within endothermic species, larger

6   species tend to be found in cooler environments. This pattern has found broad support

7   within mammals, although the relationship varies among taxa and location (e.g., [60-65]).

8   This pattern may also be confounded with the spatial pattern in range size, as larger

9   bodied mammals also have large ranges [66].

10

11   Explanations for these non-random spatial patterns in biodiversity are extremely

12   numerous and yet still not definitive. The focus of much attention has been on explaining

13   the latitudinal gradient in species richness and commonly features in the top unanswered

14   questions in science (reviewed in [67]). Species richness typically correlates strongly

15   with measures of environmental productivity or temperature [68]. However, the precise

16   mechanism underlying these correlations, linking resource availability to species number,

17   remains elusive. There is an increasing recognition that current and historic

18   biogeography, past diversification patterns and life-history traits, as well as the

19   environment, may play interacting roles in determining species richness [3-4-41-46-69-

20   71] as well as spatial variation in geographic range size [3-43]. There is also broad

21   congruence in the explanations favoured for altitudinal as for latitudinal species richness

22   gradients, with elevational richness peaks argued to be in areas with higher productivity

23   [49-50], and increasingly a role posited for historical processes such as phylogenetic

1 niche conservatism (e.g., [72]). Similar environmental explanations have also been

2 suggested for patterns of functional and phylogenetic richness [5] and beta-diversity [45

3].

4

5 None of the UTBs provides an explanation for these geographical patterns in biodiversity.

6 This is because the key parameters of interest are actually inputs into the model, i.e., the

7 number of species, total number of individuals and area available. It is conceivable that

8 these input parameters might be allowed to vary amongst regions or along an

9 environmental gradient in a way that extends the range of predictions of the UTBs to the

10 patterns listed above. However, such extensions would be of limited insight unless

11 accompanied by a theory for total species richness. Recently, there have been several

12 attempts to build such a theory, starting from spatial-temporal [73], life-history [69] and

13 metabolic [74-75] perspectives. A key challenge ahead is to integrate these developments

14 into the framework of the UTBs.

15

16 ***Trait-based patterns in biodiversity***. A large volume of macroecological research

17 concerns patterns relating to species' traits, particularly body size (i.e., allometric scaling

18 relationships) [2-76-78]. Much of the variation in mammalian life-history traits can be

19 attributed to body size variation [79-82]. The best known of these allometric relationships

20 is Kleiber's 3/4 scaling law [83], which relates individual energetic requirements

21 (specifically, basal metabolic rate) with body mass. A large part of the metabolic scaling

22 literature has focussed on mammals, and the most popular theoretical explanation for 3/4

23 scaling is designed around the mammalian vascular system [84]. However, there is now

1   clear evidence not only that the exponent in mammals is significantly shallower than 3/4

2   [85-86], but also that it is significantly nonlinear [86-88] and varies substantially among

3   taxa [87]. Modifications to the West *et al.'s* [84] model have been proposed to explain

4   these deviations, with mixed results [88-89].

5

6   Another prevalent allometric scaling pattern is the tendency for large-bodied organisms to

7   occur at low population densities, known as the size-density relationship [90]. The

8   original size-density relationship was reported in mammals as a power-law with exponent

9   close to -3/4 [91-92]. This pattern has been influential in the development of a metabolic

10   theory of ecology (MTE) [93-95], which links biodiversity patterns with individual

11   energetic requirements. For example, MTE could derive the species abundance

12   relationship if some kind of body size distribution was assumed. However, recent

13   reanalysis of Damuth's data indicates that size-density exponents are generally much

14   shallower than -3/4 [96], illustrating that further work to develop the MTE may be

15   required.

16

17   To date, the UTBs have largely treated species as equivalent, such that body size and

18   other traits are irrelevant to the observed patterns of species richness, distribution and

19   abundance. The exception is MaxEnt, which includes a constraint on both the total energy

20   available and the total number of individuals. The model generates size-density

21   relationship consistent with Damuth's -3/4 exponent, using Kleiber's law as an empirical

22   approximation to convert energy use into body masses for each species [28]. However,

23   this outcome is inevitable if species' total energy use and abundance are uncorrelated

1 (i.e., energetic equivalence). In summary, the large body of empirical and theoretical

2 research on allometric relations (and other trait-based patterns) suggest that incorporating

3 these additional dimensions into existing UTBs is conceptually straightforward.

4

5 ***Temporal patterns in biodiversity***. Diversification rates across mammals have not been

6 equal [41-97], which has led to significant imbalance in the distribution of species at

7 nodes in the mammalian phylogenetic tree over time. This diversification rate variation

8 leads to the distribution of species among higher taxa following a hollow curve, i.e., most

9 species belonging to few taxa and many taxa containing few species [98]. More recently,

10 it has been suggested that the opportunity of accessing new regions of geographic or

11 niche space has influenced the variation in diversification rates [4-41]. Under this model,

12 phylogenies are unbalanced because regions and niches vary in the diversity they can

13 support, because new radiations will probably originate in already diverse clades, and

14 because lineages that are relics are hard to replace. The evidence supporting the

15 importance of historical events and biogeography in explaining current patterns in

16 biodiversity is accumulating rapidly [3-46-70]. It seems reasonable to suggest that a UTB

17 should be able to incorporate this important temporal element of species richness in their

18 models. In fact, the Neutral UTB does include speciation and generates a hollow-curve

19 distribution of species-richness among lineages.

20

21 Trait values have also been shown to have a temporal component. For example, evidence

22 suggests that there has been a directed evolution towards large body sizes across North

23 American Cenozoic fossil mammals [99] and in other clades (e.g., dinosaurs [100]). This

1   evolutionary trend termed Cope's Rule is not found consistently in all clades and there

2   are also disadvantages of being large, for example an increased risk of extinction [101],

3   which may increase extinction rates. However, this is an interesting further temporal

4   pattern which the UTBs could aim to address.

5

6   **Conclusions**

7   Synthesising the literature on the macroecological patterns of mammals, we find general

8   qualitative support for the UTBs' predictions, but we have difficulties in distinguishing

9   between the relative merits of competing theories. As yet none of the six UTBs predicts

10   all the patterns that have been observed. Difficulties in distinguishing between different

11   theories are probably because some of the forms of the UTBs predictions are qualitative

12   and, as McGill [14] suggests, although superficially different, all the UTBs are

13   fundamentally modelling the same phenomena and therefore have similar predictions.

14   Additionally, the type of mammalian data needed for testing of the UTBs is rarely

15   available. For example, mammals (in comparison to birds) are harder to observe directly,

16   and their diverse ecologies and life-histories [102] make broad spectrum site-based

17   population databases for entire mammalian communities uncommon. Historically,

18   mammal ecologists have focused on tracking individuals or monitoring populations of

19   single species, where the selection of species is based on personal interests or

20   convenience. More recently, there has been a move towards broader spectrum survey

21   methods for mammals (e.g., camera trapping [103], acoustic surveys [104]), that are

22   capable of producing data for multiple species which are temporary and spatially explicit.

1   These are the kinds of mammalian data which are needed to more explicitly test the

2   specific predictions of the UTBs.

3

4   Our examination of other more general mammalian biodiversity patterns that are not

5   currently predicted by UTBs suggest that UTBs need to further consider the dimensions

6   of space, species' traits and time. Currently, the UTBs are mostly concerned with only

7   two of the major axes of variation: species richness and abundance, although several do

8   have an abstract spatial component. Two UTBs have extended these axes to also consider

9   energy (MaxEnt UTB) and time (Neutral UTB), and these are promising future

10   directions. It is interesting to note that the Metabolic Theory of Ecology is approaching

11   many of these problems (the distribution of energy, the mass-dependent energetic needs

12   of different species and the universal dependence of temperature) from a different

13   perspective [74-75-94]. A fruitful area of future research might be to examine whether

14   these two hitherto separate branches of theory could be merged to model biodiversity,

15   including the full pattern of species' trait variation in a truly unified fashion.

16

23
24   **References**

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10

11

1 **Figure legends**
2
3 **Figure 1**. Mammalian Species Abundance Distributions. Panels show histograms for
4 average population density (950 species) and total population size (887 species, estimated
5 as the product of geographic range and average population density). In each case, six
6 hyper-abundant species have been omitted. Data from Jones *et al*. [34].
7
8 **Figure 2**. Species Range-size Relationship in 850 mammal species in eight orders. Each
9 point is a species for which geographic range size and average population density have
10 been estimated (data from [34]).

Table 1. Unified theories of biodiversity (UTBs) identified by McGill [14], 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.

UTB	Description	Predictions
Continuum [8]	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.	SAR; Local SAD; ONR; SDR
Fractal [12]	Simulation model of species presence/absence in hierarchically-nested patches at multiple scales.	SAR; EAR; OAR; Local SAD; Global SAD
MaxEnt [13]	A Bayesian method taking minimal inputs (total number of species, individuals, total area and total energy).	SAR; EAR; OAR; Local SAD; Global SAD; ONR;
Neutral [9]	Communities are made up of species with equal per-capita birth and death rates. Immigration prevents mono-dominance.	SAR; Local SAD; Global SAD; SDR
Metapopulation [10]	Each species has a characteristic population density, which contributes to its rate of migration between patches. Local extinction is a simple function of area.	SAR; ONR
Poisson cluster [11]	Spatially-explicit model in which individuals are positioned in clusters. Species-specific values of the clustering parameters are each drawn from a Poisson distribution.	SAR; SDR

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.

UTB Prediction	Support from macroecological patterns in mammals
SAR	SARs in mammals are widely reported (reviewed in [23]). Mammal SARs tend to have low intercepts and exponents in the typical range (e.g., [4-27]). It seems unclear if currently available empirical data is sufficient to test precise UTB predictions.
EAR	Mammal EARs have been reported in a couple of studies [4-27].The form of these EARs does not seem consistent with current predictions but more research is needed.
OAR	No available data.
SAD	Local and Global SADs are poorly reported in mammals, but existing studies follow the typical hollow-curve distribution (e.g., [11-33], this study).
ONR	Existing studies at a local and a global scale show both positive and negative correlations (e.g., [36-38], this study).
SDR	Decay of similarity with distance is not well documented, but existing studies suggest a weak association in mammals (e.g.,[6])