Introduction

Ecology and evolution of mammalian biodiversity

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Mammals have incredible biological diversity, showing extreme flexibility in eco-morphology, physiology, life history and behaviour across their evolutionary history. Undoubtedly, mammals play an important role in ecosystems by providing essential services such as regulating insect populations, seed dispersal and pollination and act as indicators of general ecosystem health. However, the macroecological and macroevolutionary processes underpinning past and present biodiversity patterns are only beginning to be explored on a global scale. It is also particularly important, in the face of the global extinction crisis, to understand these processes in order to be able to use this knowledge to prevent future biodiversity loss and loss of ecosystem services. Unfortunately, efforts to understand mammalian biodiversity have been hampered by a lack of data. New data compilations on current species’ distributions, ecologies and evolutionary histories now allow an integrated approach to understand this biodiversity. We review and synthesize these new studies, exploring the past and present ecology and evolution of mammalian biodiversity, and use these findings to speculate about the mammals of our future.

Keywords: biogeography; conservation; diversification; phylogeny; life-history traits; species richness

1. INTRODUCTION

Mammals (class Mammalia) are an extraordinary group, showing an amazing diversity of species, forms, ecologies, physiologies, life histories and behaviours. Their taxonomic diversity of 5416 extant or recently extinct species [1] increases every year with the discovery of new ones [2], even in well-known groups such as primates (e.g. [3]). The greatest numbers of extant species (99%) are in the subclass Theria which consists of 5136 eutherian mammal species (i.e. placental species such as rodents, bats, carnivores, primates, cows, whales and elephants), and a smaller proportion (346 species) of metatherian species (i.e. marsupial mammals such as kangaroos and opossums). However, where the rest of the known mammalian diversity fit taxonomically is more controversial. Traditionally, the rest of the class Mammalia has been classified into the subclass ‘Prototheria’, which is wholly extinct apart from five species of egg-laying mammals—the platypus and echidnas (Monotremata) [4]. However, the validity of Prototheria has been questioned and other arrangements have been proposed, for example, grouping monotremes with recently discovered fossil forms into a new clade Australosphenida [5].

Equally important for understanding mammal ecology and evolution is that the extant diversity of mammals hides an even more interesting past, where the number of extinct genera known outnumbers those now present [4]. Mammals split from mammal-like reptiles in the Mesozoic (Late Triassic) around 210 Ma and are thought to have evolved in successive waves of diversification, involving many dead-end lineages, short-lived clades and convergent ecological specializations [6]. For example, most of the now extinct Cretaceous placental and marsupial species are phylogenetically distant from the later Cenozoic marsupial and placental forms [7,8], as both groups underwent independent waves of diversification. Even the extant mammalian diversity is a subset of the original Late Quaternary ‘pre-human impact’ fauna, where a number of mostly large-bodied species underwent prehistoric and historical-era human-mediated extinctions [9].

Mammals show extreme morphological diversity, for example, ranging in size from one of the smallest extant species, the bumble-bee bat (Craseonycteris thonglongyai) at under 2 g to the largest known to have ever lived, the blue whale (Balaenoptera musculus) at over 154 000 kg [10]. Tongues, teeth, fingers, faces and feet (among many other body parts) show similar extremes of adaptions. For example, the tube-lipped nectar bat (Anoura fistulata) has a tongue so long that this species has evolved a special chest cavity to store it when not feeding on nectar [11]. Fingers have been
modified to type this, fly (the bats) and to form the mammal analogue of woodpecker’s beak to find and locate insects from under tree bark (the aye-aye, Daubentonia madagascariensis), among many other adaptations. Large morphological diversity is present even in very closely related groups. For example, the feet of Cetartiodactyla (cows, pigs, whales and dolphins) have been modified into the extremes of hooves and flippers in a relatively short evolutionary time span [12]. Although diversification of mammal eco-morphologies is thought to have accelerated with the vacation of niches occupied by the non-avian dinosaurs at the end of the Cretaceous, there is evidence that even the earliest mammals were highly specialized [6]; for example, species with a beaver-like tail for swimming (Castorocauda [13]) and wings for gliding (Volaticotherium [14]). This suggests many independent convergent evolutionary adaptations and extreme flexibility in mammals over the course of their evolutionary history.

Ecologically, mammals have colonized all continents including the most inhospitable environments on earth. For example, jerboas (small rodents belonging to the family Dipodidae) inhabiting harsh desert environments, polar bears (Ursus maritimus) adapting to polar ice caps [15], some carnivores and Cetartiodactyla living successfully in both marine and freshwater ecosystems, and bats sharing the air with the birds and insects. Physiologically and neurologically, mammals have also evolved remarkably diverse adaptations. For example, the use of electro-receptors for orientation, electrolocation (e.g. the platypus, Ornithorhynchus anatinus) [16] and repeated evolution of echolocation as a means to orient in the absence of visual cues (many bats and cetaceans, some shrews and rodents) [17]. Mammals also show extremes of life histories and behaviours along a fast–slow continuum, where some groups live faster and die much younger (e.g. rabbits and hares, rodents) than others (e.g. elephants, primates, whales, bats) [18,19]. Mammals undoubtedly play an important role in ecosystems by providing essential services such as seed dispersal, pollination and regulating insect populations, and reducing disease transmission [20–22] and there is some evidence that some groups act as indicators of general ecosystem health [23].

The macroecological and macroevolutionary processes underpinning past and present mammal biodiversity patterns are only beginning to be explored on a global scale. For example, studies in diversification rates [24,25], extinction risk [15,26,27], spatial species–richness patterns [15,28], body-size evolution [29–31], and life-history evolution [32,33]. It is also particularly important, in the face of the global extinction crisis [34], to understand these processes in order to be able to use this knowledge to prevent future biodiversity loss and loss of ecosystem services. Unfortunately, efforts to understand mammalian biodiversity have been hampered by a lack of data, for example, global datasets on species’ distributions, life histories, ecologies and evolutionary histories. Recent advances in collating these data for all mammals [10,15,24,28] (www.utheria.org) mean that there is now a unique and exciting opportunity to explore factors determining mammalian biodiversity. Here, we review recent studies in this volume [35–44] that are among the first to integrate these new ecological, evolutionary and spatial datasets. We conclude by synthesizing these investigations of the ecology and evolution of mammalian biodiversity to understand the mammals of our future.

2. MAMMALS IN THE PAST
Understanding the past evolutionary history of mammals is challenging. Palaeontological approaches have been used successfully to investigate mammalian origins and the processes of subsequent diversification, extinction and biogeographic spread (e.g. [45,46]). However, relying solely on fossil evidence can be problematic as fossils may be unevenly distributed and sampled taxonomically, temporally and spatially [4,47]. Another approach to understanding the past can be gained by also examining the relationships among living species and using these phylogenetic trees to test hypotheses about divergence and morphological, ecological and behavioural diversification [48]. The past few decades have seen a revolution in our understanding of mammalian evolutionary histories with the development and analysis of comprehensive molecular datasets (reviewed in [49]). For example, the consensus of recent studies recognizes four major clades of placentals: Afrotheria (e.g. golden moles, tenrecs, elephant shrews, elephants, dugongs), Xenarthra (e.g. armadillos, anteaters), and the sister taxa of Laurasiatheria (e.g. shrews, hedgehogs, whales, cows, dogs, bats) and Euarchontoglires (e.g. tree shrews, flying lemurs, primates, rodents) [50,51]. With the exception of Xenarthra, these groupings were never suspected on the basis of morphology. These re-arrangements have fundamentally changed our understanding of mammalian evolution, where more surprising examples include grouping whales Cetacea (whales and dolphins) within Artiodactyla (cows and sheep) to form Cetartiodactyla [52].

Many phylogenetic methods that investigate the past require complete or near-complete trees of all the taxa under consideration [53]. Complete phylogenies only started to appear for individual large clades of mammals in the last decade, at first using now-controversial techniques [54,55] to combine previously published phylogenies into one meta-analysis or ‘supertree’ (e.g. [56–58]). More recently with an increase in the availability of data, other methods which analyse original data in the phylogenetic studies are starting to be used for some mammalian clades (e.g. [59–61]). Our understanding of the ecology and evolution of these groups has seen a huge leap forward with the analysis of these complete trees. For example, the first supertree of nearly all extant mammals was published in 2007 [24] investigating evidence for shifts in diversification rates over the course of mammalian evolution. Controversially, this was the first to suggest that diversification rates of present-day mammals did not change at the Cretaceous–Tertiary boundary (as traditionally thought) but around 10 Myr after. However, which clades in particular were responsible for changes in diversification...
rates, and why diversification rates change is little understood.

In this volume, Purvis et al. [35] re-examine the mammalian supertree to demonstrate significant imbalance (i.e. that diversification rates are not equal across contemporaneous groups) and identify 15 points in the tree where diversification rate has increased (radiations) and 12 clades that may be downshifts. For example, a significant radiation was found in the clade containing the Laurasiathea and Euarchontoglires compared to the other mammals. Purvis et al. [35] also compare multiple lines of evidence (similarity of the imbalance of real phylogenies to simulated ones, relationship of spatial scale to phylogenetic imbalance) to hypothesize that the opportunity of accessing new regions of geographical or niche space has more influence on diversification rates than trait variation (e.g. a single key innovation).

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. Different clades radiate in different places so the global phylogeny will tend to be less unbalanced than for the phylogeny of species within a smaller region.

Purvis et al.’s [35] innovative idea is consistent with a number of independent lines of evidence, e.g. dispersal ability has been found to be the most important predictor of diversification rate in birds [62], and yet other trait variations are not strong predictors of diversification rates across different taxa [63]. Importantly, the model sets up testable predictions to explain global diversification rate asymmetries and highlights the importance of spatial processes in determining mammalian biodiversity. Springer et al. [36] in this volume, turn this approach on its head, and review how phylogenetic information, timing of divergences, and present day and fossil distributions can be used to reconstruct the ancestral distributions of mammals to test the importance of dispersal and vicariance in shaping biodiversity. Reconstructing ancestral states is problematic [64–66] and reconstructing geographical ranges even more so, because of the lack of a robust hypothesis about how ranges might evolve [67]. However, new more suitable methods are becoming available (e.g. [68–70]) and our growing understanding of mammalian phylogenetics is changing our views on mammalian palaeobiogeography.

To illustrate these new methods and this approach, Springer et al. [36] review and use nine different geographical reconstruction methods and an order-level phylogeny for 43 placental mammals [71]. They conclude that ambiguous reconstructions are a problem for all of the current methods and that important differences result from coding areas based on extant ranges versus fossil lineages. Using these new methods, Springer et al. [36] show that out of the four major clades of placental mammals, Africa was reconstructed as the ancestral area for Afrotheria, while South America was more probable for Xenartha. Most methods reconstructed Eurasia as the ancestral area for Laurasiathea and Euarchontoglires. Springer et al. [36] also propose that the coincidence of molecular dates for the separation of Afrotheria and Xenartha at approximately 100 Ma with the plate tectonic sundering of Africa and South America hints at the importance of vicariance in the early history of placental mammals. The importance of dispersal events in addition to vicariance is nicely shown for Madagascar through the co-occurrence of the four lineages of terrestrial mammals (tenrecs, lemurs, carnivores and rodents) as well as for South America (platyrrhines and caviomorphs) [36]. As Springer et al.’s [36] review concludes, it is clearly an exciting time for mammalian palaeobiogeography, with the rapid development and application of new methodologies to our increasing knowledge and completeness of mammalian phylogenies.

3. MAMMALS IN THE PRESENT

Spatial variation in species, phylogenetic and functional richness, ecological community composition, species–area relationships (SARs), geographical range size, diversification rates, and rates of molecular evolution are all components of biodiversity that are somehow inextricably linked together. Here, we review studies that take an integrated ecological and evolutionary approach to explore these linkages to determine common factors underlying present-day mammalian biodiversity patterns [37–42].

Spatial variation in species richness is one of the most studied macroecological patterns in nature [72]. Consistent with many other taxa, the highest species richness of mammals is found in the tropics [15,28]. Many hypotheses have been suggested to explain this latitudinal gradient found across many different organisms; these include the effects of speciation, extinction, colonization and dispersal, as well as more subtle processes such as range shifts and associations with primary productivity, environmental seasonality, and habitat complexity (e.g. [73–79]). Investigating the spatial variation in species richness is therefore a complex multifaceted problem.

In this issue, Bromham [37] starts dissecting this problem with a review of the factors influencing the variation in the rates of molecular evolution. Molecular evolution rate may influence speciation rates and therefore, indirectly, the spatial variation in species richness. Body size is the most notable correlate, where small-bodied species generally have faster molecular rates than large-bodied relatives [80], but the mechanism behind this pattern continues to be debated. Many life-history traits covary with body size and there is evidence that factors such as generation time, fecundity, longevity, population size, metabolic rate and environmental energy also influence rate of molecular evolution [37]. Bromham’s [37] review concludes that although it is still unclear as to how different mechanisms determine the rate of molecular evolution, it is evident that a significant part of this rate variation is connected to the species’ life history. This has important implications on the estimates of divergence times on molecular phylogenies. This suggests that further research is needed to investigate any systematic bias on the dates obtained by not accounting for life history of the species under...
study, for example, dates obtained for mammal divergence times (e.g. [24]). It has been demonstrated over different spatial scales and in many taxa that the number of species in an area increases as the size of the region increases [81–84]. This SAR might also help to explain the puzzle of the spatial variation in species richness. SARs have mostly been treated from an ecological perspective focusing on immigration, local extinction and resource-based limits to species co-existence [81, 82]. However, over large spatial scales, rates of speciation and extinction could also contribute to these patterns of biodiversity [83, 85]. In this issue, Kisiel et al. [38] take a new look at the SAR, and present a framework for understanding how evolutionary processes could contribute to the creation of large-scale SARs based on a density-dependent model of clade diversification. They suggest that SARs result from the direct and positive effects of area on diversification (increasing the probability of allopatic speciation and decreasing the probability of global extinction). Kisiel et al. [38] use the new mammal datasets to show that these hypothesized effects are apparent in the histories of mammal diversification—clades occupying larger areas had higher initial diversification rates and lower rates of decline in diversification. They propose that SARs also result from the indirect effects of area through population size, habitat diversity and fragmentation. Again using the mammal data they found that energy availability and environmental heterogeneity had the effect of increasing species richness, and increased the slopes and intercepts of the species–area relationships. Kisiel et al. [38] also highlight the importance of historical contingency in SARs and use the mammal datasets to show that clades able to colonize new, competitor-free regions are more diverse than their stay-at-home sister clades. Interestingly, this is predicted from Purvis et al.’s [35] model of clade diversification presented earlier in this volume, and is consistent with Springer et al.’s [36] suggestion that vicariance was an important driver of early placental mammal evolution.

Although, as Kisiel et al. [38] show, current environmental variation influences the spatial variation of mammalian species richness, Davies et al. [39], in this volume, highlight the importance of past as well as present climatic conditions on determining both range size and species richness. Geographical range sizes of mammals are highly non-random, where terrestrial mammals with the smallest ranges are mostly restricted to the tropics, and species with the largest ranges are found across high latitudes [77, 86]. Using the new mammalian datasets, Davies et al. [39] confirm a Rapoport-like pattern [87] 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). Their analysis reveals that range size at high latitudes correlates strongly with the magnitude of Quaternary temperature oscillations, indicating that Rapoport’s rule may be a product of long-term climate cycles rather than seasonal variability. Davies et al. [39] also show that species richness is similarly influenced by past climate. For example, the relationship between species richness and present environmental conditions is quite different in areas where Quaternary temperatures fluctuated. The authors suggest that the Quaternary climatic oscillations in the high northern-latitude areas directly limited diversity below carrying capacity through repeated extinctions and range contractions. On the other hand, the climatic stability of the tropical areas during the same time allowed for the persistence of small-ranged specialist species by a tight packing of species in ecological niche space allowing for the evolution of high local species richness [39].

Safi et al. [40], in this issue, also explore correlates of the spatial variation in mammalian richness but they focus on the linkages between species, functional and phylogenetic richness at a global scale. Functional diversity may represent the amount of trait similarity in an ecological community and phylogenetic diversity, the amount of shared evolutionary time. The authors suggest that by comparing the relationship between functional and phylogenetic diversity, the relative importance of historical and evolutionary processes shaping present richness patterns can be teased apart. Using the new mammal datasets, Safi et al. [40] find that all richness measures follow the classic latitudinal gradient. Although there is a high surrogacy between all the measures, climatic conditions impact relative phylogenetic and relative function richness differently. They find that tropical areas are characterized by a lower functional diversity suggesting that under stable environmental conditions, niche space can be more tightly packed and higher species richness levels achieved. It would be interesting to see if the influence of past climate was similarly heterogeneous across the different measures of richness as predicted by Davies et al. [39].

Cardillo [41], in this issue, explores further how species can be packed into niches (or community assembly) by reviewing some of the ecological and macroecological processes that are suggested to play a role. The attributes of a set of species in a particular region can give clues to the processes determining community assembly. For example, if competition between species for resources occurs in an area, then less adapted species will be excluded. Species that are closely related are often more ecologically similar so may compete more strongly. So if competition is important in determining species composition, then we would expect to see fewer closely related species co-existing [88]. Cardillo [41] notes that this rapidly growing research area mostly focuses on testing the phylogenetic community composition of local-scale assemblages [89]. Macroecology, also a field of research interested in understanding the structure of assemblages but at large scales, has historically not taken a phylogenetic perspective on this problem. Cardillo [41] takes a new look at this to merge the two approaches and ask whether we would expect large-scale assemblages to show significant structure. Using an example exploring the phylogenetic structure of carnivore assemblages within Africa he finds that many assemblages at these large scales are phylogenetically non-random (either clustered or over
dispersed. Cardillo [41] suggests that one explanation of this is that many clades underwent rapid biome-filling radiation, followed by diversification slowdown and competitive sorting as niche space became saturated. This is consistent with Kisel et al.'s [38] finding that clades able to colonize new, competitor-free regions are more diverse than their stay-at-home sister clades and Cardillo's [41] theory of diversification has the best predictive power in explaining the asymmetry of mammal phylogenies [35].

The underlying communalities in the findings of all these recent studies are consistent with the idea of a unifying theory of biodiversity (UTB) [90]. Jones et al. [42] explore this idea with a synthetic review of the mammalian macroecological literature, firstly reviewing the processes underlying the UTBs and their predictions, and then reviewing the evidence to support them. They also assess what other macroecological patterns are known for mammals but are not predicted by UTBs, and consider how UTBs might need to be extended to cover them. Their conclusions point to where our future research should be focused to reconcile the pattern and the theory.

4. LESSONS FROM THE PAST AND PRESENT
Mammalian biodiversity is rapidly declining [15], along with the other measured biodiversity on this planet, as anthropogenic activity monopolizes more of the earth’s ecosystems and natural resources [34,91]. Perhaps these new integrated approaches to understanding the processes determining mammalian biodiversity can help us to prevent future biodiversity loss and the loss of ecosystem services that mammals provide? Previous work using this approach and these datasets (and others) have examined species-level patterns and processes determining current global mammalian extinction [15,26,27,77,92–96]. These studies have suggested that extinction risk in mammals (among other things) is phylogenetically and spatially non-random, that the trait correlates of extinction risk depend on the taxonomic group, past extinction filters, type of extinction threat and that these trait/extinction risk relationships interact with body size. Here we review two new studies furthering our understanding of the extinction process, first from the recent past [43] and the second examining which factors influence populations to decline and whether these are the same as those factors that are important at the species level [44].

It is often difficult to draw parallels between studies of extinction risk in current taxa and those already extinct. These two types of studies are often done at very different taxonomic and time scales, cover different taxa which are differently sampled, use different methods and definitions of extinction (actual versus risk of extinction) [93]. In this issue, Turvey & Fritz [43] do just this by comparing present day extinction risk patterns to the spatial, taxonomic and phylogenetic pattern of 241 mammal species known to have gone extinct from the Holocene (11 500 years ago) up to the present day. Adding this Holocene data [97] into the new mammal databases, Turvey & Fritz [43] find that, as with extinction risk in current taxa, Holocene extinctions show a phylogenetic and spatially non-random pattern. However, there are important differences in these patterns; specifically, regional faunas from which susceptible species have gone extinct now appear less threatened. This is consistent with the ‘extinction-filter’ hypothesis, originally conceived to explain the patterns in regional faunas of extant taxa [98]. Turvey & Fritz’s [43] study highlights the importance of incorporating patterns of extinction over longer time periods when examining current extinction risk analyses. However, they also caution against uncritical use of past extinction data without considering the sampling biases inherent in these kinds of data.

Rates of decline in populations across the world have provided convincing evidence that biodiversity is rapidly declining [34]. However, how declining populations translate to global species-level extinction events is poorly understood. Collen et al. [44], in this issue, examine for the first time, the relationship between the well-documented correlates of extinction risk (e.g. [92]) and those of population trends. Studies of extinction risk typically use a measure of risk from the International Union for Conservation of Nature (IUCN) [99] which is a composite measure for each species consisting of population size, trends in different populations and geographical range size. However, this composite measure is uninformative for estimating trends in local populations. Collen et al. [44] collated three measures of population change from 292 mammal species of 1384 different populations from the living planet index (LPI) database [100], the largest repository of wildlife population abundance trends in the world. Combining this with the new mammal datasets of traits and evolutionary history, they found that significant traits were similar to studies of extinction risk, but environmental conditions were generally better determinants of population declines than intrinsic biological traits. Specifically, areas of high temperature and evapotranspiration (tropical areas) were associated with declining species. Collen et al. [44] suggest that the intensity of the decline may mask a correlation with intrinsic biological traits, i.e. if pressures are of a high intensity, then species biology ceases to matter. Although these are interesting patterns, the authors conclude that further research is needed to tease apart these trends with a more even sample of taxa and geographical coverage than is currently available in the LPI database.

5. MAMMALS IN OUR FUTURE
So what of the future? With the increasing availability of global datasets we are learning more about the rules that determine mammalian biodiversity and beginning to appreciate that the past plays a central role in our understanding of the present. However, our ability to make predictions of future mammalian biodiversity and the effect any biodiversity change will have on ecosystem function is only beginning. Examples of this approach include studies that examine the patterns of biodiversity, such as areas of high richness (measured taxonomically, functionally or phylogenetically), threat or endemicity, and apply current threat
drivers or models of future changes to these areas to predict future biodiversity (e.g. [101–104]). Only a few of these studies have focused explicitly on mammals. Niche modelling is another pattern-based approach which models the environmental conditions for species presence and/or absence data to predict possible geographical ranges. These can then be used to predict changes in distributions under different climate change scenarios [105]. However, these studies do not often account for competition between species, species life histories or ability to disperse to new niches predicted by the models, although research is progressing in this area [106].

Other studies have tried to apply our understanding of the processes shaping biodiversity more explicitly using extinction risk models [27] to identify species that were currently at lower risk than predicted from the model—species at ‘latent risk’ [107]. This study proposed 20 regions which were currently intact but contained these hotspots of latent risk species, assuming that extinction drivers would intensify linearly. More realistic scenarios of global change need to be incorporated into such analyses to be more policy relevant, which is challenging [77]. Davies et al. [77] present some examples of how this approach could be attempted and this is clearly an important and timely area of future research. More studies are needed that incorporate our knowledge of biodiversity processes into understanding our future. For example, based on the consensus of the evidence in this volume, opening of new ecological or spatial niche space seems to have played a major role in patterns of mammalian diversification. We would argue that as a substantial amount of new niches are unlikely to become available in the near future (given the rate of human population growth and consumption), mammalian diversification may be in a phase of stabilization or decline. Additionally, evidence suggests that environmental stability and available energy are important determinants of species composition and richness which is rapidly changing with anthropogenic global change. Predicting the future for mammals needs a more process-based approach.

Finally, we point out that any predictive approach to understand mammals of our future must attempt to include the mammalian biodiversity that is currently poorly known or completely unknown. In 1993, 4629 extant or recently extinct species were recognized [108], 5416 in 2005 [1], which in 3 years had increased to 5488 for IUCN’s global mammal assessment [15]. In fact, based on the current discovery rate of 200–300 species per decade, Reeder et al. [2] suggest that over 7000 mammalian species will be recognized by 2050. Using a species-accumulation curve and assuming a linear relationship between total cumulative number of species and time by decade (figure 1), Reeder et al. [2] estimated an additional 300 species would be discovered in the decade following 2000.

Extending this approach, we used the year of discovery for species in IUCN’s global mammal assessment [15] to estimate how many mammals we would expect to have discovered in the next decade from 2008 until 2018. We used a generalized additive model (GAM) to provide greater precision than a linear model (figure 1). The GAM was built with the smooth term being the years since 1785 fitted to the cumulative number of species. The degrees of freedom and thus the number of knots determining the smoothness of the fit were chosen using a restricted estimated maximum likelihood approach [109] (smooth term statistics: estimated d.f. = 8.978 [109], d.f. = 9, F = 74 648, p < 2e−16). For the next decade, the GAM predicts an additional discovery of 97 species in 2018 and a total of 336 additional species in the next 25 years (up until 2033; figure 1). Our models tend to underestimate the number of species in the future subset, but the mean difference between the actual value and the 10 and 25 year predictions are quite small (figure 1; 10 year mean difference ± standard deviation = −8 ± 175 species; 25 year difference ± standard deviation = −10 ± 432). In these predictions, we assume that discovery effort will remain more or less constant. However, the application of new efficient molecular identification methods may shift the intercept of the line upwards (a grade-shift), which may result in perhaps thousands more species.

These new species are likely to be biased both taxonomically, ecologically and spatially, as is the case...
for the most recently discovered species [2,110]. Following these patterns, we could predict that most species to be described will probably be found among the most species-rich clades (e.g. rodents and bats) and will be small with a restricted range. Spatial biases in the 341 species of mammals discovered since 1992, show associations with islands and the tropics [2]. We also show this for the most recently discovered 1000 species of mammals using data in IUCN’s global mammal assessment [15], where most species have been discovered in the lowland Amazonian forests, East African tropical forests, Indo-Malayan forests, Papua New Guinea highlands and Australia (figure 2). The expectation is therefore that future discoveries would be also within these regions, although currently species-rich areas are likely to be important sources of new discoveries. Worryingly, most recently discovered mammals and most threatened mammal species occur in the tropical belt indicating that some species may go extinct before even being discovered (figure 2).

What of poorly known species? How can these be included into predictive models? The threat status of 836 out of 5488 species is unassessed by IUCN because they are too poorly known, and classified as data deficient [99] (figure 3). It is unclear whether the proportion of threat categories among these data-deficient species is the same as among the assessed species. Often data-deficient species have restricted ranges, so may be more likely to be threatened. Finding ways of assessing the status of these species seems important for understanding future mammalian biodiversity. Here, we provide an example of such an approach using methodology developed to assess the phylogenetic and spatial signal of extinction risk in carnivores [111]. We used a combination of spatial eigenvector estimation and phylogenetic eigenvectors as described in Safi & Pettorelli [111] and modelled a binary response (threatened/not threatened) for data-deficient species for each mammalian order separately. Due to the size of some of the mammalian orders we used a forward selection procedure minimizing the Akaike’s information criterion of the alternative models, instead of the step-wise forward selection/backward elimination procedure based on model deviance originally proposed in Safi & Pettorelli [111]. The performance of the models was assessed using a cross-validation among bats. In the validation, we compared modelled and known threat status by running 100 models where we removed an assessed species randomly and compared its probability of being threatened with its known IUCN rank. The cross-validation revealed that the procedure was reliable and consistently modelled threatened species to have significantly higher probabilities of threat than non-threatened species (median and interquartile range of modelled threat probability for non-threatened species: 0.04 [0.001, 0.1] and for threatened species: 0.52 [0.24, 0.75], Wilcoxon signed-rank test \( W = 129, p < 0.0001 \)).

Out of 481 data-deficient species with distribution and phylogenetic information, we estimated a proportion of 35 per cent to be threatened (figure 3). The proportion of threatened species among the data-deficient species is significantly higher than among the assessed species (difference in proportions \( \hat{\pi} = -0.09, z = -3.14, p = 0.002 \)). This suggests that data-deficient species are of greater conservation concern. Of a total of 836 data-deficient species, 355 species did not have distribution and/or phylogenetic data. If we assume the same modelled ratio of threatened versus non-threatened species for the entire set of 836 data-deficient species, and then add the total number of threatened species in all of the assessed species, then 28 per cent (1513 species) are in more or less immediate risk of going extinct. Approaches such as these seem a promising start on including poorly known species in any predictive modelling of future mammalian biodiversity.

6. CONCLUSIONS

This issue brings together biodiversity experts to use new compilations of global data on mammal species’ distributions, life histories, ecologies and evolutionary histories to understand the pattern and processes

Figure 2. Species richness of all threatened and the most recently discovered 1000 mammals globally, data from [15]. The values on both axes have been standardized between 0 and 1 and binned in 10 equal-sized categories.
underlying mammalian biodiversity. The consensus of evidence suggests that current mammalian biodiversity is the result of a strong signature of past events and also the present environmental and ecological conditions. For example, opening of new ecological or spatial niche space seems to have played a major role in patterns of mammalian diversification whose signature can be seen in the current patterns of biodiversity. There is a pressing need to understand this complex pattern to allow us to predict mammals most at risk of extinction to preserve some of their fascination for our future generations.

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