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Speciation gradients and the distribution of biodiversity

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Global patterns of biodiversity are influenced by spatial and environmental variations in the rate at which new species form. We relate variations in speciation rates to six key patterns of biodiversity worldwide, including the species–area relationship, latitudinal gradients in species and genetic diversity, and between-habitat differences in species richness. Although they sometimes mirror biodiversity patterns, recent rates of speciation, at the tip of the tree of life, are often highest where species richness is low. Speciation gradients therefore shape, but are also shaped by, biodiversity gradients and are often more useful for predicting future patterns of biodiversity than for interpreting the past.

Speciation is the ultimate source of species diversity but speciation events are unevenly distributed across Earth. This variation is now being quantified, and its causes and consequences are being explored. Of particular interest is the relationship between the variation in speciation in space and across various environments and the distribution of biodiversity. Gradients in species richness along spatial and environmental axes have fascinated ecologists, biogeographers, evolutionary biologists and natural historians for centuries. Ecological explanations for these gradients in biodiversity focus on the effects of environmental variables, including productivity, temperature, precipitation and ecological disturbance regimes (the pattern of perturbations in environmental conditions), on species coexistence, whereas evolutionary processes are acknowledged mainly through a historical effect on regional pools of species[1–4]. The role of variations in speciation rate on biodiversity gradients has been considered occasionally, for example, to explain the greater numbers of species in the tropics compared with temperate regions (the latitudinal biodiversity gradient)[5–7]. However, the wider role of such variation in speciation, its environmental causes and its consequences for the slopes of biodiversity gradients — how steeply biodiversity changes between points along the gradient — remain largely unexplored[3,4,8,9]. The number of species in an area is also determined by levels of immigration (colonization) and extinction and the age of the habitat. However, in this Review, we focus on speciation because it is less well integrated into ecological models of species richness than these other processes.

We define a speciation gradient as the spatial or environmental variation in the per species rate of species origination per unit of time. We treat the rate of speciation per species (hereafter described as the speciation rate) as synonymous with per lineage branching rates that are estimated from species-level phylogenies[10] and as distinct from the per individual speciation rate that is used in the neutral theory, a model of biodiversity that ignores functional differences between species[11]. Speciation is the evolution of reproductive isolation (genetically based barriers to gene exchange), which is an evolutionary process, but the speciation rate is determined by demographic processes and metapopulation dynamics as well. The speciation rate might be higher in a given lineage at certain points along an environmental gradient than at others if reproductive isolation evolves more quickly there, or if a greater number of descendent populations are established that survive long enough to evolve reproductive isolation. Even if the rate of evolution of reproductive isolation is unchanged, other processes can also yield higher speciation rates, including a higher establishment rate of new populations, longer population persistence times (reduced population extinction rates) and the faster establishment of sympatry after reproductive isolation is complete[12–14]. Sympatry refers to overlap in the geographic ranges of species derived from a common ancestor, and is included here because it leads to higher community diversity and restarts the speciation cycle.

We use available data to address the links between speciation processes and several well known biodiversity gradients. We focus mainly on patterns of variation in current speciation rates, which are those measured at the ‘tips’ of the tree of life. In practice, this includes speciation events that occurred in the relatively recent past, between 10–20 million years (Myr) ago and the present, a period that roughly spans the ages of species belonging to the same genus. The distinction between current speciation rates and those of the more distant past is crucial because these rates might not be the same — for example, speciation rates within clades are known to change through time[15]. The current speciation rate is the most relevant measure for understanding the maintenance of biodiversity gradients and recent changes in gradient slope, and for predicting future biodiversity. We also focus on speciation gradients that are repeatable, which means that they are relatively consistent in space or across several taxa. Therefore, we exclude variation in speciation that might be the result of the idiosyncrasies of particular locations or clades rather than spatial and environmental differences.

There are a number of different views on how speciation gradients might affect the slopes of biodiversity gradients at the local or regional scale. (Here, we define region as the area in which speciation becomes an important source of new species, which differs between taxa[16].) One view is that speciation leads only to species turnover, with species losses balancing gains; numbers of species in this scenario are determined by regional carrying capacities — diversity ceilings set by environmental conditions[17]. In this case, variation in the speciation rate has minimal impact on biodiversity gradients if all ecological communities are saturated with species. However, evidence for ubiquitous saturation is elusive[18,19]. More realistically, the number of species in a region is the net result of inputs from colonization and speciation and losses by extinction[20–22], with local diversity changing to some extent with regional diversity[23]. Under this ‘net rates’ view, differences in speciation rate along a gradient lead to differences in species richness.

Why do speciation rates vary in space and across environments? The answer lies in the effects that physical and biotic environments have on

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the evolution of reproductive isolation and on the rates of population establishment, persistence and sympatry. Natural and sexual selection are probably the main drivers of evolution that lead to reproductive isolation between populations[24,25], with the rate of evolution and the diversity of phenotypes influenced by amounts of standing genetic variation[26,27]. Opportunities for the geographical separation of populations can also cause variation in speciation rates. Spatial separation is typically a prerequisite for speciation because it reduces gene flow that can slow divergence. Alternative mechanisms of speciation (for example, whether selection is divergent or uniform) are differentially prone to the effects of gene flow[24,25]. Environmental factors, including productivity, temperature, niche availability and interactions between species, can contribute to the speciation rate in two ways. First, they can affect the strength of selection. Second, they are likely to affect the rates of population establishment, persistence and sympatry[14,28]. Therefore, it would be surprising if environmental gradients were not associated with variations in speciation rates[29]. Variation in species richness along an environmental gradient might feed back to affect contemporary speciation rates, although how it does so is the subject of debate. Speciation might slow as species diversity builds and resources become depleted (the ecological controls model[14,22]), or it might speed up if species themselves are resources that promote further speciation (the 'diversity begets diversity' model[30,31]).

Unfortunately, speciation gradients cannot be estimated using field observations or experimental data. Such gradients are, however, becoming well documented through the use of first occurrences of species in the fossil record or, more often, increasingly reliable phylogenetic data and statistical models of diversification[32]. Our ability to estimate speciation rates from phylogenetic data is nevertheless hampered by considerable uncertainty. The inference of speciation gradients requires that we disentangle speciation from extinction, which is challenging[33]. Methods for inferring temporal-, spatial- or clade-level differences in speciation, extinction and diversification rates from phylogenetic trees are unreliable under realistic scenarios[34,35]. Many large-scale phylogenies also remain under-resolved and under-sampled, particularly near the tips[36,37], and may also be prone to sampling biases that subsequently influence rate estimates. We recognize that current estimates are therefore provisional and that future work may be better able to identify robust signals of speciation in phylogenies. The prospects for recent speciation rates, our focus here, are likely to be better than those for estimates from deep time. Unless there has been a recent elevation in extinction rates, the rate of accumulation of species at the tips of the tree of life primarily reflects the speciation rate[10,37]. For now, we take available estimates at face value to enable us to develop a framework for evaluating the role of speciation gradients in shaping patterns of biodiversity.

Our goal in this Review is to explore the causes of speciation gradients and to investigate their relationship with, and consequences for, the slopes of biodiversity gradients. In some cases, such as the relationship between numbers of species and geographical area (the species–area relationship), theory exists to predict spatial variation in speciation rates as well as how such variation should cause the slope of the biodiversity gradient to differ from that seen without variation in the speciation rate. In other cases, the theory is lacking but long-standing hypotheses propose that speciation rates are highest where species richness peaks — for example, in the tropics. And in further cases, although repeatable speciation gradients across habitats can be seen, we lack a good understanding of the reasons for such gradients. A future goal is to explicitly incorporate variation in speciation processes in general theories of patterns of biodiversity. Neutral models of community diversity incorporate speciation, but niche-based models have yet to do so[11]. However, niche differences are thought to be an important source of divergent selection that drive many speciation events[15,25,38] and influence rates of population establishment, persistence and sympatry. We therefore work towards such a theory by highlighting what is known or uncertain about the relationships between speciation gradients and six familiar types of biodiversity gradients.

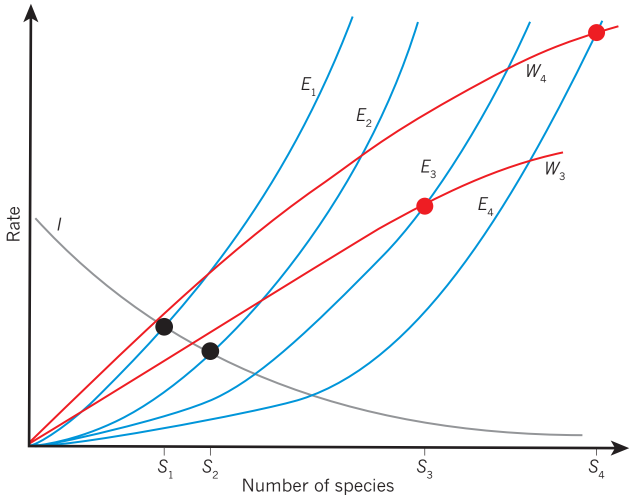

Figure 1 | The relationship between rates of immigration, extinction and species origination and species number on islands of increasing size. Immigration (I) is the main source of species on small islands (1 and 2), whereas within-island species origination (W) becomes more important on large islands (3 and 4). (W_1 and W_2 are 0 and therefore not shown.) The speciation rate (per species) is the slope of the relationship between W and S (the number of species present). Hypothetically, W is described by a curve instead of a straight line, which represents the possibility that the speciation rate on a large island declines as the number of species rises. Black circles indicate the numbers of species on small islands at which immigration and extinction (E) are balanced (S_1 and S_2). Red circles indicate species numbers on large islands where speciation and extinction are balanced (S_3 and S_4), ignoring immigration. S increases with island size, but the increments are greater between large islands than between small islands because of speciation.

Speciation and area

We begin with islands because they provide a clear example of a case in which a speciation gradient affects the slope of a biodiversity gradient. They also explain some of the most important challenges that are faced in efforts to link speciation rates with biodiversity gradients in general. We define an island as a spatially isolated unit of habitat surrounded by inhospitable environments that limit colonization — a definition that includes oceanic islands and isolated lakes.

The processes that determine variation in species numbers on relatively small islands — colonization and extinction — are well described by the theory of island biogeography[39]. These processes produce the familiar relationship between species number and island area. Speciation between a mainland ancestor and its island descendants, as well as the speciation of populations on different islands within archipelagos, can raise the number of species that are available to colonize, and therefore lift species richness beyond the level predicted from colonization and extinction alone[39,40].

Area further increases within-island speciation rates on sufficiently large islands (Fig. 1). A greater area provides more opportunities for geographical isolation, which raises the rate of establishment of spatially separated populations. It also increases population sizes and, consequently, persistence times. The increase in speciation rate with area therefore probably stems from the effects of area on the demographic processes that affect speciation: more populations form and more are given sufficient time to evolve reproductive isolation. The rate of evolution of reproductive isolation might also increase with area if a greater diversity of habitats and resources strengthens selection, or if larger populations experience increased inputs of adaptive mutations[41].

Within-island speciation is predicted to steepen the slope of the species–area relationship[42–45]. This is because, unlike the colonization rate (immigration, I), the rate of species origination within islands (the total number of new species produced per unit time, W) rises with island area (Fig. 1). Also, unlike *I*, which declines with *S* (the number of species present), *W* increases with species richness, which magnifies the positive effects of area. The predicted increase in the slope of the species–area curve with island size has been observed in lizards of the genus *Anolis* on large islands of the Greater Antilles[43]. Similarly, cichlid fish in lakes in Africa show a steepening in the slope of the species–area relationship in large lakes compared with small lakes (Fig. 2). This transition in slope is linked to the increasing importance of speciation events between spatially separated populations in larger lakes. (African cichlid speciation can occur without spatial separation even in the smallest lakes.) The threshold island size that marks the transition between moderate and steep slopes increases as the dispersal capabilities of the taxon being investigated increases[16]. This suggests that highly dispersive taxa require more area for speciation within islands than do less dispersive taxa, and it also supports the conclusion that the opportunity for the establishment and persistence of spatially separated populations with reduced gene flow underlies the effects of island area on speciation.

The speciation gradient that is associated with area might change as the biodiversity gradient develops. In Fig. 1, we draw a curvilinear relationship between *W* and *S* to indicate such a possibility. If it is true, then a decline in the speciation rate with increasing species richness will weaken the association between current speciation rates — those that are measured at the values of *S* achieved — and island area[22]. It is probable that *W* will curve downwards as *S* increases if the extinction rate curves upwards. This is because a higher rate of species extinction (*E*) implies that there will be a higher rate of population extinction with increasing *S*, which also reduces the number of populations that survive to complete the evolution of reproductive isolation. Slower speciation rates can therefore result from changes in the demographic processes that underlie speciation. The rate of the evolution of reproductive isolation might also decline as species richness increases[46]. Apparent diversity-dependent declines in speciation rate have been detected in species of *Anolis* in the Caribbean, especially those found on the smaller of the large islands[47], although a positive relationship between island area and speciation rate still exists. It is debatable whether equilibrium is ever attained in large areas, but within-region speciation should steepen the species–area slope well before this occurs because larger areas accumulate species more rapidly than smaller areas.

These findings indicate that *in situ* speciation is a rate-limiting step in the development of species–area relationships on islands. This has implications for other biodiversity gradients, for example, if the extent of the regional area varies between habitats along the gradient[48].

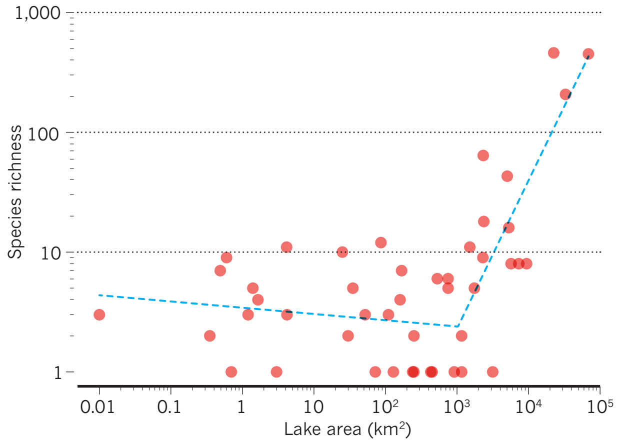

Figure 2 | The species–area relationship for cichlid fish in African lakes. The number of cichlid species changes little with increasing lake area until the area reaches about 1,000 square kilometres. Species richness rises steeply with lake area thereafter, an effect that is caused by higher speciation in larger lakes. Modified from ref. 44.

The latitudinal gradient in species diversity

The latitudinal gradient in species richness — an increase in the number of species from the poles to the Equator — is Earth's most impressive biodiversity gradient. Numerous potential explanations have been put forward to explain why the tropics have more species than the temperate zone[1,5,49]. Here, we focus on evolutionary hypotheses that propose that the diversity gradient is caused by a latitudinal gradient in per lineage speciation rates that decreases from the Equator to higher latitudes. One class of such hypotheses states that speciation is faster in the tropics because higher temperatures lead to higher metabolic rates (in ectotherms), shorter generation times and more rapid genetic divergence between populations[50,51]. A second class of hypotheses attributes higher speciation rates in the tropics to greater ecological opportunities that stem from the greater heterogeneity of resources and species interactions that are made possible by greater amounts of solar energy, higher annual productivity (on land, at least), reduced temperature seasonality and stronger biotic interactions[5,6,31]. Both classes of hypothesis predict that higher speciation rates in the tropics are the result of the faster evolution of reproductive isolation, although greater ecological opportunities can also increase the rates of population establishment, persistence and sympatry. We address this prediction by comparing speciation in the tropics (latitudes of about 0–30°) and the temperate zone (latitudes of 30–60°), which have relatively similar total numbers of individual organisms[52].

Evidence is scant, but so far does not support consistently higher recent speciation rates in the tropics than in the temperate zone. In birds and mammals, sister species (species that are each other's closest relatives) and phylogenetically distinct populations within species are youngest, on average, in the temperate zone[53] (Fig. 3 shows these patterns for mammals), which is unexpected if speciation rates are highest in the tropics. In mammals (but not in birds), the molecular clock runs slightly faster in the tropics than it does in the temperate zone, but this effect is too small to account for a roughly twofold difference in molecular divergence times[54,55]. Data from birds indirectly suggest that the greater age of sister species in the tropics is linked to the slower evolution of reproductive isolation in the region. The rates of divergence between sister taxa in plumage, song and body size, which are often cues in assortative mating (the tendency of individuals to prefer mates from their own population or species), are fastest in the temperate zone[6,56]. Secondary sympatry is also established more rapidly in the temperate zone than in the tropics[46], which suggests that demographic processes might also contribute to higher rates of recent speciation in birds of the temperate zone. By contrast, *Drosophila* shows equal rates of evolution of assortative mating in tropical and extra-tropical sister species[57]. Hybrid sterility, which accumulates more slowly than assortative mating, evolves more than twice as rapidly in the tropics as in non-tropical regions.

Estimates of latitudinal speciation gradients are few but variable, and include examples of both positive and inverse relationships between the speciation rate and latitude[6,58]. Rates of current speciation, which are estimated on the basis of data at or near the tips of the tree of life, tend to be equal or higher in the temperate zone than in the tropics. By contrast, lower estimates are often obtained for the temperate zone than the tropics when they are made using data that integrate the recent and distant past for large clades. An example is shown in Fig. 4, which compares the results of two analyses of New World birds (found in continental areas of and on islands near to the Americas) that were carried out over these two time frames. Clades of mainly South American birds, which are predominantly tropical, have higher numbers of species than do North American clades of birds, most of which come from the temperate zone, when averaged over the last 30 Myr (Fig. 4a). This difference leads to both a higher estimated speciation rate and a higher diversification rate in the New World tropics[59,60] than in the temperate zone. Yet, species-level metrics of speciation and diversification rates find no latitudinal gradient[37,61] (Fig. 4b). One explanation for this could be that speciation (and diversification) rates in the temperate zone relative to those in the tropics have changed from the past to the present[6].

Why are recent rates of speciation in the temperate zone as high as, and sometimes higher than, those of the tropics? High speciation rates at higher latitudes might be a response to the greater ecological opportunities created by the relatively recent expansion of the seasonal temperate zone as Earth cooled over the past 30 Myr, and again following deglaciation[6]. If so, the modern speciation gradient is partly a response to — and not simply the cause of — the latitudinal biodiversity gradient. The recent speciation gradient is therefore flattening, rather than augmenting, the latitudinal biodiversity gradient. This conclusion only refers to the per species speciation rate. The total species production rate, which is the product of the speciation rate and the number of species, remains highest in the tropics because that is where most species are found.

Altitudinal gradients

Mountains of the tropics might provide another case in which the direction of the slopes of recent speciation gradients are opposite to those of the biodiversity gradient. Data are few and must be inferred from diversification rates: we must assume that high rates of species accumulation in the recent past reflect high rates of speciation. Whereas species richness in tropical mountains generally peaks at low to mid elevations[62], the speciation rates of such regions seem to peak at high elevations[63,64]. This is especially true in the Andes mountains of South America, where estimates of the per species production of new plant species include some of the highest rates ever recorded[65]. Lineages that speciate at high elevation are derived from lowland ancestors or from lineages that are found elsewhere in the temperate zone[63,65]. Rapid recent accumulations of species have also been observed high in the eastern Himalayas and in other mountain ranges[64].

In the Andes, the high mountain grasslands above the tree line (known as the páramo) were formed during the final phase of mountain building about 2–3 Myr ago. Similarly to the temperate zone, high elevations in the tropics were glaciated during the Pleistocene era. The rapid recent speciation probably therefore reflects the high levels of ecological opportunity that are associated with the opening up of new habitats and space at high elevations, despite a relatively small total area in comparison to lowland habitats. This also suggests that high rates of recent speciation can result when lineages colonize new habitats that harbour low species richness for a time. Opportunities for the spatial separation of populations might also be common at high elevations, which promote speciation.

The latitudinal gradient in genetic diversity

Although gradients in species richness attract most attention, gradients in the amount of variation within species are also coming to light. Latitudinal gradients in the genetic diversity of species tend to be similar to the latitudinal gradient in species richness, which raises the tantalizing possibility of a causal link. Cases of higher genetic diversity in the tropics than in the temperate zone are usually interpreted as being indicative of higher rates of evolution at warmer temperatures, which portends more rapid speciation through the faster evolution of reproductive isolation. However, the association between genetic diversity and speciation rates is not straightforward and has other possible explanations.

Vertebrates, which have been studied most frequently, show latitudinal patterns of both α (within population) genetic diversity and β (between populations) genetic diversity. In birds and mammals, the overall levels of genetic divergence between populations of individual species are greater in the tropics than in the temperate zone[66,67] (Fig. 3b). This pattern can be explained most simply by the greater age of tropical species[53] or by there being a longer period of reduced gene flow between populations in tropical species, as the molecular clock is relatively similar between latitudes in such endothermic taxa. A tropical peak in genetic diversity between populations within species is expected if reproductive isolation evolves most rapidly in the temperate zone. This is because the completion of reproductive isolation converts genetic differences between populations into genetic differences between species, which depletes a major component of intraspecific genetic diversity. Variation in the amounts of gene flow between populations and in rates of molecular divergence (especially in ectotherms) at different latitudes will also contribute to the gradient in intraspecific molecular divergence.

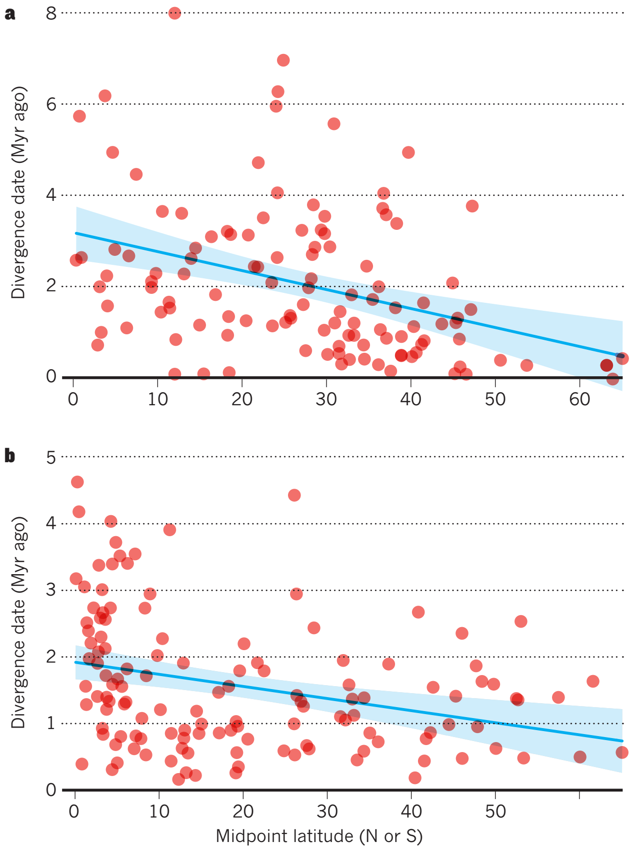

Figure 3 | Variation in ages of New World mammal species with latitude. **a**, The age of sister-species pairs of New World mammals is shown, together with the average absolute midpoint of their latitudinal distribution (blue line). Sister species are younger, on average, at higher latitudes. **b**, The maximum coalescent times (estimated ages of common ancestors for the oldest intraspecific haplotype variation) within New World mammal species. Blue shading indicates 95% confidence bands, which highlight the uncertainties of the linear fits. Adapted from ref. 53.

Within species of both endothermic and ectothermic vertebrates and plants, greater molecular divergence is seen between populations at lower latitudes than between those at higher latitudes[68–71]. Higher rates of molecular evolution at higher temperatures might contribute to this pattern, because faster rates of molecular evolution in putatively neutral markers have been observed for plants and ectotherms at lower latitudes[72]. However, the pattern is seen even in some tropical species that experience little variation in temperature across their latitudinal range[69,70]. Higher-latitude populations are often younger than lower-latitude populations within species and may have experienced genetic bottlenecks at the edge of their high-latitude range, given that so many species in both glaciated and unglaciated regions expanded their ranges towards the poles after the end of the last ice age[73].

These patterns describe latitudinal patterns of β genetic diversity, which can be calculated using the spatial turnover in the frequencies of nucleotides between populations of the same species. The α genetic diversity within single populations of mammals and amphibians has been approximated by the nucleotide diversity (π) present in a 386 kilometre × 386 kilometre cell of an equal-area grid on a map of the continents[74]. No consistent latitudinal gradient in mean α genetic diversity is evident among species of terrestrial continental mammals and amphibians when the genetic diversity of a species is calculated as the weighted average of nucleotide diversity values in grid cells (Supplementary

Methods). However, as with β genetic diversity within species, α genetic diversity within species is higher in lower-latitude populations than in higher-latitude populations (Supplementary Methods).

The relationship of these gradients in genetic diversity to speciation is not yet clear. Recent speciation rates seem to be largely decoupled from rates of (putatively neutral) molecular evolution and the distribution of α and β genetic diversity. Higher β genetic diversity in lower-latitude populations is seen even in the species of vertebrate clades that do not have higher species richness in the tropics[70], as well as in groups of species in which recent speciation rates are similar or higher in the temperate zone compared with the tropics[6]. One possible explanation for the decoupling is that variation in demographic processes is more important for determining differences in the speciation rate than differences in the rates of evolution[75]. However, in birds, faster divergence of phenotypic traits that are involved in assortative mating, including plumage and song, between populations and species suggests that rates of evolution are faster in the temperate zone than in the tropics, although the rate of evolution of assortative mating has not been measured directly. Another possibility is that we are not measuring genetic diversity in the correct genes. When phenotypic variation between populations of particular species is greatest in the temperate zone[76], then divergence is presumably also faster at the underlying genes, in contrast to divergence at neutral loci. If this is true, the strength of selection may be more important than the overall levels of genetic variation for determining rates of the evolution of reproductive isolation.

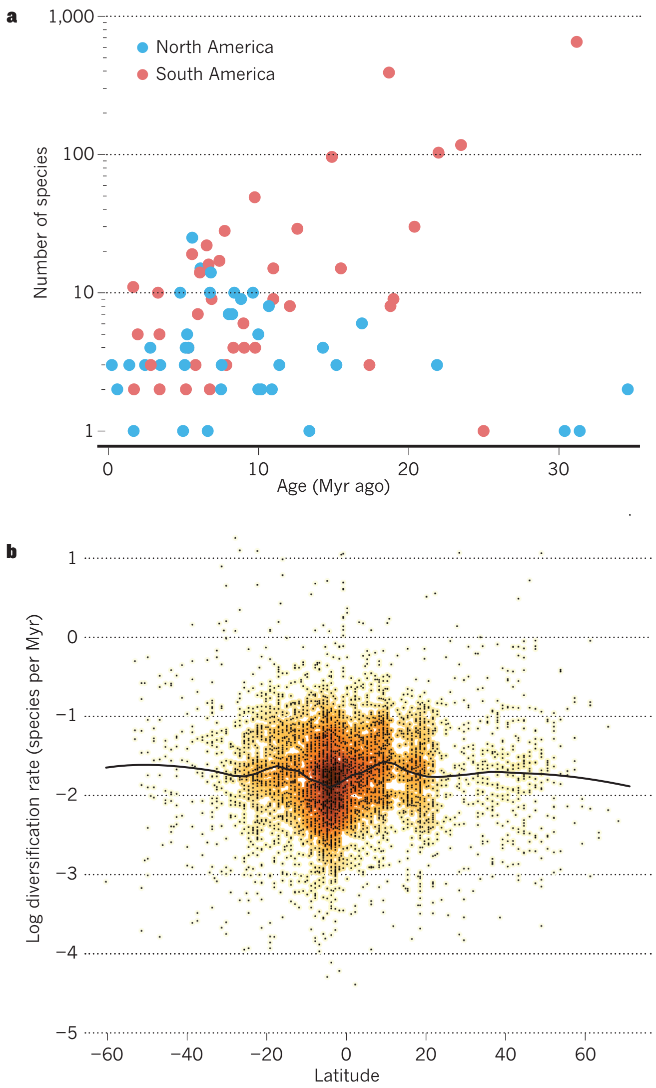

Figure 4 | The relationship between diversification, speciation and latitude in birds. **a**, Using the approach presented in ref. 59, the numbers of species in avian clades that are predominantly from South America (a mainly tropical environment) and North America (a mainly temperate environment) were plotted, on the basis of the phylogenetic tree of birds published in ref. 37. South American clades have more species, on average, than do North American clades of a similar age, which suggests that diversification rates in the tropics are higher than those in the temperate zone when averaged over the last 30 Myr. The difference in species number between tropical and temperate zones is most apparent in the older clades. **b**, Recent species-level diversification rates in New World birds (black line; data from ref. 37, kindly redrawn by W. Jetz). The speciation gradient calculated from the same data (not shown) is also flat across latitudes[61].

Habitat gradients

Species richness often varies greatly between environments and habitats in close proximity in continental regions. Adjacent habitats also often differ in their levels of productivity and the types and amounts of resources that they offer, and the differences in species richness of such habitats are typically interpreted in terms of the limits that the resources place on colonization and coexistence. However, within-habitat speciation rates, and speciation events that are initiated by colonization between habitats, can also contribute to differences in species richness. Differences in the regional areal extent of habitats that result in changes in speciation rates might help to explain why some habitats have more species than others in their local communities[3]. Differences in the rates of colonization to some habitats in comparison to others can similarly affect speciation rates through changes in the rate of secondary sympatry[28,77].

For example, Mediterranean-climate ecosystems contain almost 20% of known plant species despite covering only 5% of land worldwide[78]. Most notably, the fynbos evergreen shrublands of the Cape floristic region of South Africa contain more than 8,000 species of plant in an area of about 90,000 square kilometres, which makes it one of Earth's biodiversity hotspots. Most fynbos species are endemic, having accumulated in the last 7–8 Myr, which suggests that there is a very high rate of *in situ* speciation[79,80] and possibly also a steep speciation gradient between the fynbos and adjacent habitats. Such a steep biodiversity gradient might be attributed to historical or biogeographical features that are peculiar to the South African Cape region were it not for the fact that the gradient is repeated in phylogenetically unrelated shrub lineages of the kwongan habitat of Australia — the Mediterranean habitat most similar overall to the fynbos, with features that include infertile soils, a high frequency of fires and the dominance of fire-adapted sclerophyllous vegetation[78]. Similar shrublands in the Mediterranean-climate ecosystems of Chile, California in the United States and even the Mediterranean itself burn less frequently and have a diversity mainly of short-lived herbs and smaller shrubs[78]. The environmental causes of the shared high rates of speciation in these Mediterranean habitats have been the subject of speculation[81]. For example, the evolution of low seed-dispersal distances and high rates of population persistence may contribute. This case therefore represents an example in which a repeatable speciation gradient is suggested by the data — and is concordant with a steep biodiversity gradient — but for which the causes remain uncertain.

As a further example, the increase in diversity of bird species and foliage height in temperate forests is a textbook case of a biodiversity gradient and is frequently regarded as evidence that structural heterogeneity promotes species coexistence. The pattern was brought to prominence more than 50 years ago by Robert MacArthur and John MacArthur[82], who demonstrated the relationship for the birds of eastern North America. Subsequently, a similar relationship was seen in the birds of the temperate zone of Australia[83], which seemed to confirm that the number of bird species that can coexist in the same environment is positively related to the number of niches. A comprehensive review published in 2004 showed that a relationship between animal biodiversity and plant-habitat heterogeneity is common but not universal[84]. An evolutionary interpretation is also possible, whereby the numbers of species that are found at sites along the gradient are the resolution of inputs from colonization and speciation, and outputs of extinction. This alternative interpretation receives support from a similar survey that was conducted in temperate Patagonia, South America, which found that the diversity of bird species is negatively related to the diversity of foliage height[85]. This pattern can be explained by taking into account the relative spatial extent of different habitats: temperate forests are relatively rare. Because *in situ* speciation rates increase with area, it is possible that a speciation–area gradient is affecting the slope of the gradients of species richness and habitat heterogeneity[3]. Speciation may also be affected by the structural diversity of foliage through its effects on the evolution of ecological specialization and divergence, as well as on population establishment, persistence and sympatry. To our knowledge, only one study has attempted to estimate speciation, extinction and colonization in (neotropical) forest habitats compared with adjacent open habitats using phylogenetic comparative methods[86]. The forest habitat contains more species of ovenbird (Furnariidae) than the surrounding open habitats, but the speciation gradient is estimated to be in the opposite direction: new species tend to be produced in open habitats and subsequently colonize forests. Such findings need to be replicated in other groups of species, but the initial result suggests that speciation gradients do indeed influence one of the canonical biodiversity gradients in ecology — and in the opposite way to the one that was predicted.

Anthropogenic gradients

The activity of humans now influences almost all ecosystems on Earth and has led the current epoch, the Anthropocene, to be literally defined by our impacts. It is well known that people have engendered a wave of extinction, at least in some taxonomic groups. Researchers estimate that current rates of species loss worldwide may be much higher than background rates[87]. However, this does not imply that species richness has decreased uniformly everywhere. What will be the effect of human activity on future speciation and how will this change biodiversity gradients?

Species richness in many local communities has not changed detectably in the past several decades[88,89] (but see ref. 90, which argues that declines may be widespread). Local extirpations are often compensated for by human-assisted introductions of species into the community or by range shifts caused by climate change or other environmental factors. However, the spatial distribution of human impacts will probably soon influence many of the biodiversity gradients we have discussed. Numerous species are expanding their ranges towards the poles and to higher elevations, as well as retracting their ranges from lower latitudes. For some groups, human-induced extinction rates are higher in the tropics than in the temperate regions[91]. If this is a general trend, in 100–1,000 years' time the latitudinal species richness gradient may be substantially shallower.

At the same time, human impacts might be generating new speciation gradients between environments that are highly affected and those that are more pristine. The direction of those gradients is basically unknown. Using biogeographical models, Michael Rosenzweig[92] postulated that if speciation rate is positively related to area, as we describe in this Review, a reduction in the natural habitats that are available to species will cause a reduction in the per species rates of speciation. This means that not only are we depleting biodiversity now, but we are also robbing future Earth of wild species that have yet to originate. However, such an analysis assumes that speciation happens only in pristine habitats.

By creating new environments and selection pressures, people are also setting the stage for ecological speciation in the future. By moving species around Earth, we have also opened up fresh possibilities for hybrid speciation, which may be an important generator of new species, particularly in plants. Unfortunately, there are few data on speciation processes in altered landscapes but it seems plausible that current rates of speciation are higher than ever before. For example, a 2015 study of the flora of Great Britain estimated speciation rates to be at least an order of magnitude higher than background rates[93]. Similarly, there is a dearth of studies on adaptation to urban environments[94], which undoubtedly exerts unique selection pressures[95] that may drive divergence and speciation.

Artificial speciation will probably also speed up in the future, and the case could be made that speciation rates in crops are already very high. For example, broccoli and cauliflower are variants of the same ancestral species (*Brassica oleracea*) and have evolved numerous phenotypic and genetic differences in the hands of people. These differences can be thought of as reducing interbreeding (because humans intervene to prevent it). It could be argued that in the Anthropocene era this counts as reproductive isolation, as long as the prevention of interbreeding is a consequence of the evolved differences between the forms and is consistent across their range. Advances in biotechnology have enabled researchers to create synthetic genotypes (again, particularly in crops), which has been accompanied by efforts to engineer intrinsic genetic barriers to prevent 'transgene flow'[96] between synthetic and wild populations. This may also have the side effect of constructing intrinsic barriers to gene flow between independently synthesized transgenic lines that originate from the same ancestral forms. Biodiversity scientists and conservation biologists have yet to fully reckon with the implications of this synthetic speciation[97]. The species that result may not be as majestic as those that evolve in nature, and few will probably manage to escape into the outdoors at all, even to depauperate urban environments. These new species may not persist long enough to be recorded by phylogenetic biologists and palaeontologists of the future[98] — indeed, this is the reason that we focus on phylogenetic rather than experimental or field data in this Review. However, we think it is at least possible that synthetic speciation gradients along an ecological axis that runs from 'wild' to 'altered by humans' will help to shape biodiversity gradients in the future, and we suggest that this possibility is worth investigating more seriously than it has been so far.

Future prospects

Biodiversity gradients are one of the most striking biological features of our planet and to explain how they arise and are maintained is one of the main challenges of biodiversity science. In the broadest terms, the number of species that are present in a given environment is determined by the balance of local extinction, immigration from other environments and *in situ* speciation[20,21]. All of these rates are probably determined, at least in part, by the conditions of the ecological environment, but we may also expect species diversity to feed back to and affect the rates of these processes.

In this Review, we have focused on how differences in speciation rates in space and between environments contribute to biodiversity gradients. With a flurry of new phylogenetic methods[20,32], we are poised to receive better estimates of speciation gradients (as well as estimates of the other rates that affect present species numbers at points along gradients). Intuitively, we might predict that species richness is higher at locations in which speciation rates are higher. This view underlies the expectation that speciation rates should be highest in the tropics, where species diversity is usually higher. However, in a number of our examples, we found speciation rates to be highest where biodiversity is low, which suggests that the biodiversity gradient was causing a gradient in speciation rates rather than vice versa. Such feedback will make it more challenging to assess the role of speciation in the origin of biodiversity gradients.

We anticipate that further methodological improvements will facilitate more process-based inferences about speciation rates, for example, through the explicit incorporation of the population dynamics of speciation in phylogenetic models. However, even with improvements in methods, the amount of extractable information in phylogenetic data is likely to be limited. For example, we can probably only infer speciation gradients reliably in the relatively recent past. And, as we have already discussed, a number of existing approaches have been called into question[34,35]; we hope that in the future we will better understand when estimates are reliable and repeatable. Furthermore, to infer ancient gradients, we are likely to be restricted to groups of organisms with a good fossil record[21].

Beyond the methodological issues and the small sample size of speciation gradients that have been estimated so far, we also wanted to draw attention to the paucity of theory with which to predict the slopes of speciation gradients and how they influence the slopes of biodiversity gradients. Although we do not think that speciation rates are always the most important factor in determining biodiversity gradients, in general, they have been overlooked in biogeographical and ecological models of species richness, with the notable exception of the neutral theory of biodiversity. For the most straightforward case (the species–area relationship), a number of theoretical models that include speciation have been proposed[42,44,45,99]. However, little speciation-explicit theory is available for many of the other biodiversity gradients that we have discussed. Identifying repeatable patterns of variation in the speciation rate along biodiversity gradients will aid in the development of such theories. We have hardly begun to explore how human activities might shape speciation gradients or the way in which these potential changes will affect the distribution of biodiversity over spatial and environmental gradients in the future. Our hope is that this Review inspires other researchers to take on these challenges. ■

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