insight review articles

Global patterns in biodiversity

Kevin J. Gaston

*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
(e-mail: k.j.gaston@sheffield.ac.uk)*

To a first approximation, the distribution of biodiversity across the Earth can be described in terms of a relatively small number of broad-scale spatial patterns. Although these patterns are increasingly well documented, understanding why they exist constitutes one of the most significant intellectual challenges to ecologists and biogeographers. Theory is, however, developing rapidly, improving in its internal consistency, and more readily subjected to empirical challenge.

Biodiversity, the variety of life, is distributed heterogeneously across the Earth. Some areas teem with biological variation (for example, some moist tropical forests and coral reefs), others are virtually devoid of life (for example, some deserts and polar regions), and most fall somewhere in between. Determining why these differences occur has long been a core objective for ecologists and biogeographers. It constitutes a continuing, an important, and to many an enthralling, challenge. Indeed, the past decade has seen a veritable explosion of studies documenting broad-scale (geographical) spatial patterns in biodiversity, seeking to explain them, and exploring their implications. The reasons for this interest are twofold. First, it reflects increased opportunity provided by improvements in available data and analytical tools, the former resulting mostly from extensive collation of existing specimen and species occurrence records, the establishment of dedicated distribution-mapping schemes, and the use of remote-sensing technology (to measure vegetation and other environmental variables). Second, it reflects concern over the future of biodiversity, and the resultant need to determine its current status, to predict its likely response to global environmental change, and to identify the most effective schemes for *in situ* conservation and sustainable use. Many of these issues can be addressed satisfactorily only by resolving the historical mismatch between the fine resolution of study plots in ecological field work (typically a few square metres) and, by comparison, the poor resolution of land-use planning and models of environmental change.

A host of global patterns of spatial variation in biodiversity has been explored (Fig. 1). This includes patterns in hotspots and coldspots (highs and lows) of diversity (including comparisons between biological realms and between biogeographical regions), variation with spatial scale (for example, species–area relationships and relationships between local and regional richness) and along gradients across space or environmental conditions (for example, latitude, longitude, altitude, depth, peninsulas, bays, isolation, productivity/energy and aridity[1,2]). Although several different levels of organization (genes to

ecosystems) of biological variation can be distinguished, most analyses of spatial variation concern biodiversity as measured by the number of species observed or estimated to occur in an area (species richness). This results from widespread recognition of the significance of the species as a biological unit, and from the practical issues of the ease and magnitude of data acquisition. Consideration of spatial variation in other measures of biodiversity, particularly those concerning the difference between entities rather than simply their numbers, has been remarkably sparse (with the possible exception of patterns in body size and morphology). Thus, although much attention has been paid to latitudinal variation in species richness, little is known about variation in the diversity of genes, individuals or populations along latitudinal gradients.

The growth of interest in broad-scale spatial variation in biodiversity has been particularly striking with regard to four areas of enquiry: latitudinal gradients in species richness, species–energy relationships, relationships between local and regional richness, and taxonomic covariance in species richness. In this review, the progress being made in each of these areas will be used to substantiate four broader cross-cutting observations about global patterns of biodiversity: respectively, that no single mechanism adequately explains all examples of a given pattern, that the patterns observed may vary with spatial scale, that processes operating at regional scales influence patterns observed at local ones, and that the relative balance of causal mechanisms means that there will invariably be variations in and exceptions to any given pattern.

Latitudinal gradients in species richness

High proportions of terrestrial and freshwater species occur in the tropics. Moving from high to low latitudes the average species richness within a sampling area of a given size increases, as has been documented for a wide spectrum of taxonomic groups (including groups as different as protists, trees, ants, woodpeckers and primates) for data across a range of spatial resolutions[3,4]. Such gradients in species richness may be steep (for a given area, tropical assemblages are often several times more speciose than temperate ones), and have been a persistent feature of the
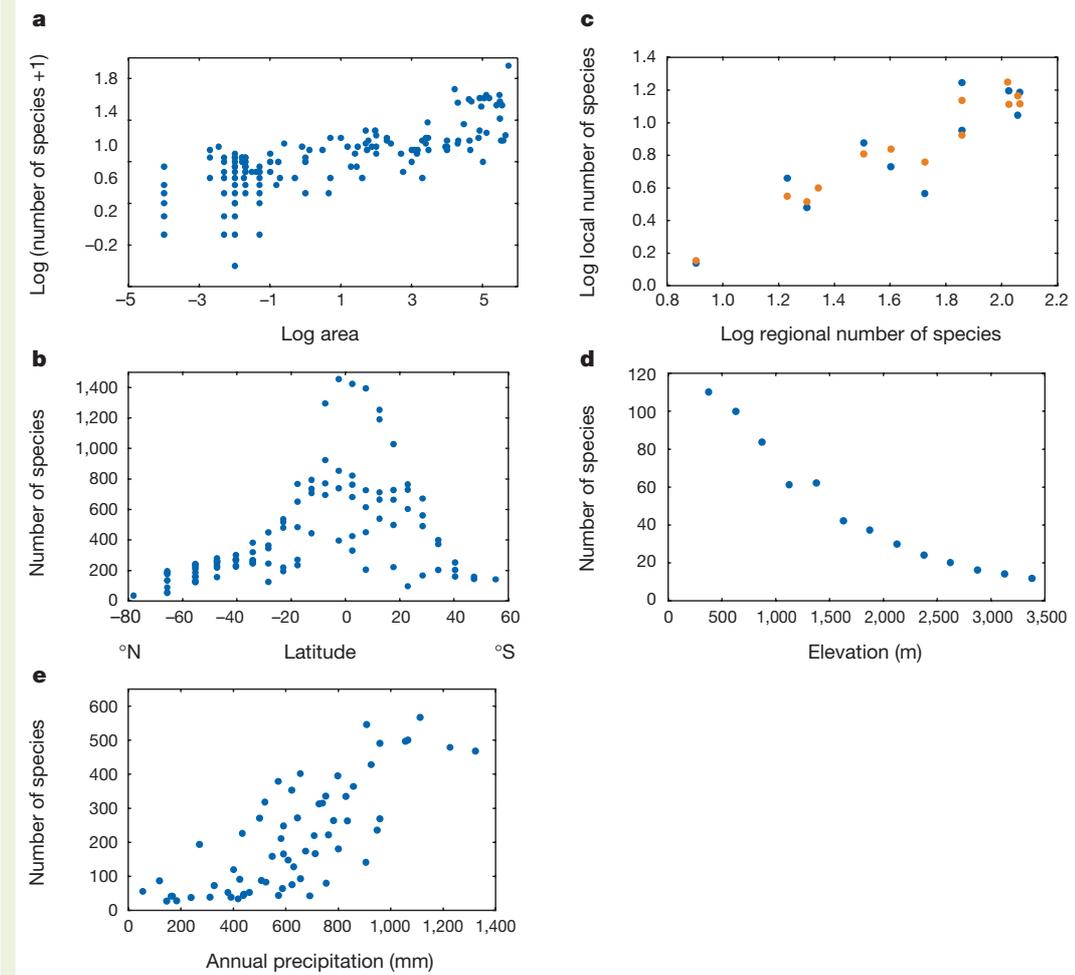
Figure 1 Spatial patterns in species richness.
a, Species–area relationship: earthworms in areas ranging from 100 m^2 to >500,000 km^2 across Europe[76]. **b**, Species–latitude relationship: birds in grid cells (~ 611,000 km^2) across the New World[44]. **c**, Relationship between local and regional richness: lacustrine fish in North America (orange circles, large lakes; blue circles, small lakes)[61]. **d**, Species–elevation relationship: bats in Manu National Park & Biosphere Reserve, Peru[77].
e, Species–precipitation relationship: woody plants in grid cells (20,000 km^2) in southern Africa[78].

history of biodiversity[5,6]. In the marine environment, open-ocean pelagic and deep-sea taxa also show broad latitudinal gradients in species richness, but some debate continues to surround evidence for shallow-water systems, particularly for non-calcareous taxa[7].

The growing number of increasingly refined analyses of latitudinal gradients in species richness has begun to suggest some important nuances to this pattern, although the extent of their generality remains uncertain. Thus, it seems that declines in richness with latitude may be faster in the Northern than in the Southern Hemisphere[8,9], and that peaks in richness may not lie actually at the Equator itself but some distance away[10,11]. Although poorly documented, such latitudinal asymmetries would be unsurprising given that these exist also in contemporary climate, in historical climatic events, and in the latitudinal complexities of the geometry and area of land and ocean.

Indeed, the latitudinal gradient in species richness is a gross abstraction. Any underlying pattern is disrupted, sometimes markedly, by variation in species richness with other positional variables (for example, longitude, elevation and depth), and environmental ones (for example, topography and aridity). Thus, the detailed pattern of change with latitude depends on where one looks, reflecting the generally complex patterns of spatial variation in species richness. This indicates that consideration of latitudinal gradients in richness in isolation from other gradients might not be the most profitable way forward. In as much as latitude *per se* (and likewise other positional variables) cannot be a determinant of species richness, but only a correlate of numbers of potentially causal environmental factors, this is doubtless correct. Nonetheless, more than any other pattern the latitudinal gradient in species richness has

held an enduring fascination for biologists, particularly because of the obviously striking diversity of many tropical floras and faunas when contrasted with their counterparts at high latitudes.

The latitudinal gradient in species richness, however complex it might be, is a consequence of systematic spatial variation in the balance of speciation and the immigration of species, which add species to an area, and of the extinction and emigration of species, which take them away. For very large areas, the effects of speciation and regional or global extinction will predominate, and immigration and emigration will be less important. More than 25 different mechanisms have been suggested for generating systematic latitudinal variation in these processes[2], commonly emphasizing reasons as to why the tropics are highly speciose (although there is no *a priori* expectation that either tropical or temperate zones in any sense represent an 'unusual' condition[12]). These include explanations based on chance, historical perturbation, environmental stability, habitat heterogeneity, productivity and interspecific interactions.

Many of these mechanisms are not mutually exclusive, and others merely offer different levels of explanation. Nonetheless, to some, *en masse* they have been perceived to constitute a gordian knot. Two recent attempts to cut it concern the importance of the physical structure of the Earth. First, null models that assume no environmental gradients, but merely a random latitudinal association between the size and placement (midpoint) of the geographical ranges of species, predict a peak of species richness at tropical latitudes[13]. This occurs because when the latitudinal extents of species in a given taxonomic group are bounded to north and south — perhaps by a physical constraint such as a continental edge or perhaps by a climatic constraint such as a critical temperature or precipitation threshold — then the

number of ways in which ranges can be distributed changes systematically between the bounds. Thus, whereas species with latitudinal midpoints midway between the bounds can extend a little or a long way before those bounds are encountered, those with midpoints close to the bounds can extend only a little way before this occurs. A null model has been wanting from discussions of latitudinal gradients in species richness. The 'mid-domain' model is thus likely to stimulate much interest. It is also likely to be most applicable for groups whose distributions are genuinely limited by a physical boundary (for example, those of large islands such as Madagascar), although its extension to two spatial dimensions is problematic, given the longitudinal variation in land and ocean area. The application of the model to other kinds of constraints is more questionable, as the position of those constraints that are recognized will be dependent on the inclusiveness of the set of species considered.

The second attempt to explain latitudinal gradients in species richness based on the physical structure of the Earth concerns the role of area (its importance has long been entertained[14,15] and recently brought to prominence[16,17]). The tropics have a larger climatically similar total surface area than any other ecoclimatic zone. This is because: (1) the surface area of latitudinal bands decreases towards the poles; (2) the temperature gradient between the Equator and the poles is nonlinear (the mean being relatively constant between approximately 20° N and 20° S); and (3) the regions of similar climate immediately north and south of the Equator abut. It has been contended that, for a given species richness, larger mean geographical-range sizes of species in the tropics result from the large area (which is not to be confused with any observed pattern in mean range sizes at different levels of richness), and that these translate into higher speciation rates (presuming larger ranges have higher probabilities of speciation) and lower extinction probabilities (presuming larger ranges have lower probabilities of extinction)[16,17]. As a consequence, tropical regions have greater numbers of species than extratropical ones.

Area is almost certainly an important contributor to latitudinal gradients in species richness (indeed, area effects have a pervasive influence on patterns of biodiversity). However, tests of the 'area model' have been limited (and often tangential), and have seldom sought the signal of the influence of area on latitudinal gradients when other factors have been controlled for. Moreover, as a sole explanation the area model is insufficient. To account fully for a latitudinal gradient in species richness (rather than simply for the greater richness of the tropics) the model requires that ecoclimatic zones decline systematically in area moving from the Equator towards the poles. However, they do not do so (ecoclimatic zones at high latitudes tend to be large[10,17]). Three possible explanations have been advanced for why a latitudinal gradient in species richness might nonetheless be expressed: (1) low productivity/energy availability at high latitudes reduces the species richness they would gain as a result of area alone[10,17]; (2) zonal bleeding of tropical species into extratropical regions smoothes out species-richness gradients[18,19]; and (3) high

local climatic variability at high latitudes effectively increases the area of ecoclimatic zones that species can actually occupy, because it requires that individuals have broad environmental tolerances[3].

The observation that area alone is insufficient as a determinant of latitudinal gradients in species richness could equally be made about almost any other factor that has been proposed as being important (although critical tests are typically lacking). This highlights an issue that has been central to much of the debate about the cause of this and other global patterns in biodiversity, namely the assumption that where a pattern is common to many taxa it must result from the same single mechanism — "wherever there is a widespread pattern, there is likely to be a general explanation which applies to the whole pattern"[20]. To argue for a single primary cause may be to expect from ecological interactions a simplicity for which there is little evidence. There is no necessary reason why latitudinal gradients exhibited by taxa as distinct as protozoa and mammals, and in environments as structurally different as the deep sea and tropical forests, need be generated in the same way, whatever the attractions of Occam's razor. Increasingly it seems that patterns in biodiversity are likely to be generated by several contributory mechanisms[12,21]. The strongest and most general may be those where all the different mechanisms pull in the same direction[22]. It is instructive that although numerous mechanisms for latitudinal gradients in species richness have been identified, and rather few processes that would oppose such a trend, no single mechanism has of itself proven sufficient.

Species–energy relationships

One factor thought to be important in modulating any effect of the physical structure of the Earth in determining latitudinal gradients in species richness is the relationship between the number of species in an area and ambient available ('usable') environmental energy. (This energy is usually estimated from models or indirectly from other variables, and often used interchangeably with 'net primary productivity'.) The form and cause of this relationship are some of the most hotly debated topics in the study of global patterns in biodiversity, with many fundamental issues as yet unresolved. Much of the discussion centres on the influence of spatial scale on observed relationships.

At a relatively local scale (spatial resolution and extent), there is a marked tendency for a general hump-shaped relationship between species richness and available energy, with species richness increasing from low to moderate levels of energy and then declining again towards high levels of energy when a sufficient range of energy values is sampled[16,17,23]. At least across temperate to polar areas, at geographical scales there is substantial evidence for a broadly positive monotonic relationship between species richness and energy availability to be common[10,24–33] (Fig. 2). The best correlates for plants tend to be measures of both heat and water (such as actual evapotranspiration and net primary productivity), whereas for terrestrial, and perhaps marine, animals the best correlates are measures of heat (such as mean annual temperature and potential evapotranspiration)[28,29,34]. For example, whereas the species richness of trees in temperate Europe, eastern North America and East Asia increases with primary productivity[27], the richness of butterflies and birds in areas of Britain increases with the temperature during the appropriate season[25,26], and the species richness of amphibians, reptiles, birds and mammals in areas of North America increases with annual potential evapotranspiration (estimated as a measure of the net atmospheric energy balance, independent of water availability[28]). The form taken by species–energy relationships at geographical scales, when extended to include subtropical and tropical areas, or at least to include the fullest range of variation in available energy (which may not be the same thing), remains unclear. There is evidence to suggest that they remain broadly positive and monotonic, that they become mildly or strongly hump-shaped, and that they begin to break down altogether[10,32,35–37]; the answer may depend critically on the measure of energy used and the taxon concerned.
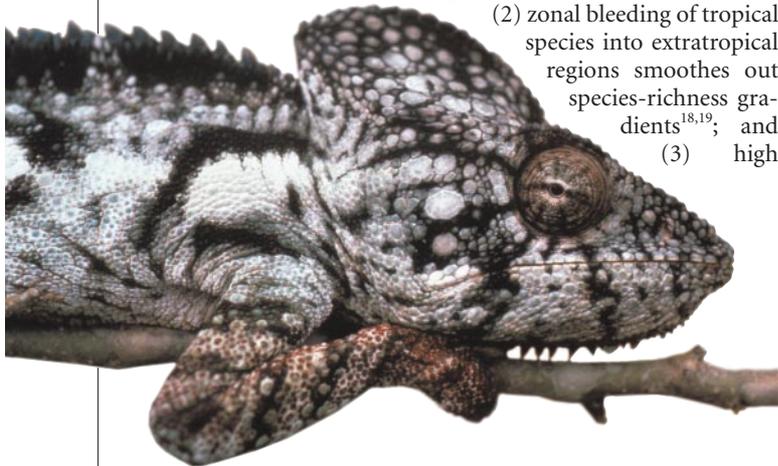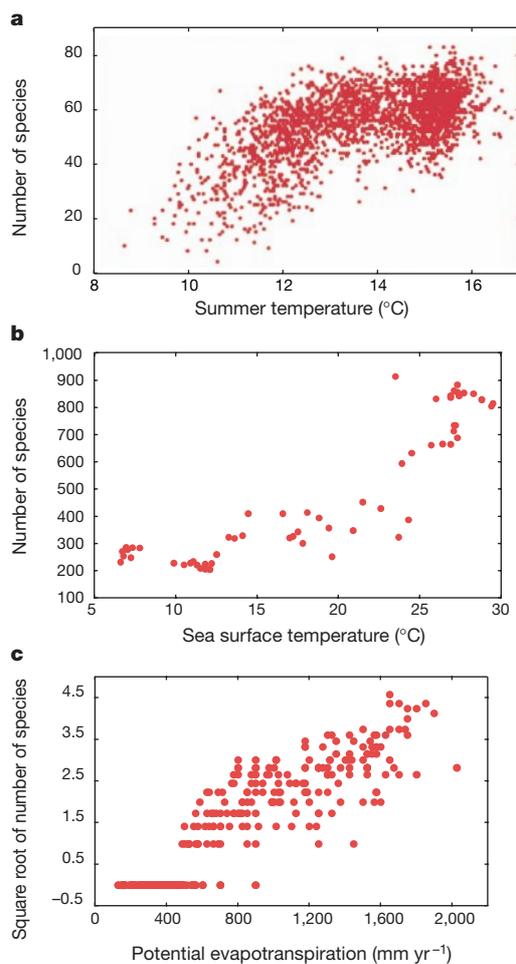
Figure 2 Species–energy relationships. **a**, Mean monthly summer temperature (°C) and richness of breeding birds in Britain (grid cells of 10 km × 10 km)[33]. **b**, Mean annual sea surface temperature and richness of eastern Pacific marine gastropods (bands of 1° latitude)[10]. **c**, Potential evapotranspiration (mm yr^{-1}) and richness of *Epicauta* beetles (Meloidae) in North America (grid cells of 2.5° × 2.5° south of 50° N, 2.5° × 5° north of 50° N)[31].

Any contingency of the gross or more detailed form of patterns in biodiversity on the spatial extent and dispersion of sampling units is not restricted to species–energy relationships. Indeed, the almost ubiquitous positive relationship between the numbers of species in an area and the size of that area (the species–area relationship) may itself vary in form with the absolute sizes of areas, their spatial relationships (for example, isolation), and their latitudinal position[38,39]; this is often forgotten when attempting to control for differences in area in analyses of global patterns of biodiversity. Reconciliation of the patterns in biodiversity that are observed at different scales may provide significant insights into their determinants. If this is to be achieved, it is important to ensure that the scale of sampling and the scale of processes that are postulated to explain patterns in species richness are closely matched. One criticism of some discussion of species–energy relationships at broad scales has been that this has not been done; curiously, this has been interpreted, by different parties, as yielding species–energy relationships that may be misleadingly strong or misleadingly weak[40–42]. Matching scales of sampling and processes is more readily achievable at local scales, and constitutes one of the most significant obstacles to testing mechanisms over broader areas.

Although other explanations have been offered, the processes resulting in a broadly positive relationship between species richness and energy availability at geographical scales (and at low-to-moderate energy levels at more local scales) are believed to be reasonably straightforward. Greater energy availability is assumed to enable a greater biomass to be supported in an area. In turn, this enables more individual organisms to coexist, and thus more species at abundances that enable them to maintain viable populations. The result is an increase in species richness with energy availability. This assumes a basic equivalence between species in their energetic requirements at different levels of energy availability[43]. Although there is some evidence in animal systems that average densities and body sizes of species in an area decrease as energy availability increases (that is, energy is divided more finely[44]), this will tend to enhance the species–energy relationship provided these trends are sufficiently marked compared with the scaling of metabolic rate to body mass.

There are important similarities between this 'more-individuals model'[45] and the area model as explanations of variation in species richness[44]. First, both to some degree concern variation in solar energy (and water availability), with the level and availability of this energy source being important in the former case, and the spatial extent of a given level (as reflected in an ecoclimatic zone) in the latter. If ecoclimatic zones vary in available energy, then observed species–energy relationships (and those between richness and latitude) may reflect the joint effects of their area and this availability[37]. Second, the area model assumes that area influences richness through its effect on geographical-range size, and the more-individuals hypothesis that energy influences richness through its effect on population size. There is a general, positive, interspecific relationship between total population size (or local density) and size of geographical range[46]. Any factor that increases one of these variables will also be likely to increase the other. Both mechanisms therefore depend, in effect, on some factor that is posited to influence the biomass available to be worked on by the processes of speciation and extinction, which will be a product of both area and available energy per unit area[29,47]. Presumably, it is for this reason that small areas tend to be species poor however high their energy input, whereas large areas tend to be species poor if there is low energy input.

Assuming that species–energy relations are causal and that a more-individuals model is operating, then it is unlikely that the path of causality is simple. Levels of available energy may constrain the amount of biomass that is achieved in an area, but characteristics of the biosphere, and particularly those of vegetation, are themselves known to be key influences on climate, including temperature and precipitation[48]. For example, the coupling of an atmospheric model and a simple land-surface scheme has indicated that coastal deforestation in West Africa has been a significant contributor to the observed drought in the region[49]; this deforestation has resulted in a number of species being threatened with extinction[50]. Complex patterns of causality suggest an important connection between species–energy theory and debates over the ecosystem function of biodiversity[51,52].

Even accepting that paths of causality may be complex, there are some potentially significant difficulties with a more-individuals model.

1. The assumption that the number of individual organisms increases with available energy and total biomass may not apply to plants, for which there is evidence that as standing crop increases the numbers of adult individuals per unit area actually declines (and their size increases), which should tend to reduce species richness rather than increase it[35]. However, this argument is based in large part on findings from monospecific stands of species differing substantially in their architecture, and it is unclear to what extent it generalizes to multispecies stands and systems that are structurally more similar (for example, temperate compared with tropical forests). Evidence as to how overall biomass and numbers of individuals change with species richness in animal systems is scant, even for well-known groups such as birds, and is plagued by a paucity

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of strictly comparable studies from areas differing markedly in species richness.

2. Many taxa use such a small proportion of the total energy available in an area, or at least of the energy that is being measured, that it seems unlikely that detectable relationships with species richness would arise (especially given the likely magnitude of measurement errors). Thus, although species richness of birds tends to increase with available energy, avian assemblages may, directly and indirectly, commonly exploit only a small proportion of the primary production in a locality. (The avian community of the forested watersheds of the Hubbard Brook Experimental Forest has an average ingestion rate which represents 0.17% of ecosystem net annual productivity[53].)

3. In its simplest form, the more-individuals model ignores the likely effects of temporal variance in energy levels on species richness. High average levels of energy may not result in large numbers of species if they are accompanied by high temporal variability in those levels. The relationship between levels of available energy and their variance may be broadly different between some terrestrial and marine systems (negative in the former, positive in the latter), perhaps explaining why even at very broad spatial scales high richness may not be associated with high productivity in marine systems[37].

4. At regional scales, levels of species richness have not been produced directly by present environmental conditions, as processes of speciation and extinction do not operate on these timescales. If the more-individuals model is to apply this must mean that present environmental conditions are a good proxy for past ones, or at least of relative differences in the conditions in different areas.

Alternatives to the more-individuals model have been advanced to explain positive species–energy relationships. These have been based particularly on variation with energy in levels of constraints on geographical ranges, specialization, population growth rates and number of trophic levels[45]. Foremost is the idea that the relationships may reflect physiological constraints on the distribution of species, with energy availability capturing factors that limit distributions as a result of metabolic considerations[30].

In the absence of strong support for any of these alternative explanations, difficulties with the more-individuals model fuel growing speculation that at least some species–energy relationships may not be causal, and that energy availability may often be only a covariate of some other factor that is actually driving species richness. Bird richness may, for example, be responding to a second-order effect of greater vegetational complexity with increased available environmental energy. Likewise, recent work has shown that whereas sea surface temperature explained nearly 90% of geographical variation in planktonic foraminiferal diversity throughout the Atlantic Ocean, this temperature was also correlated with temperatures at different depths. This indicates that the diversity may be controlled by the physical structure of the near-surface ocean and not directly by available energy[32].

Continuing with this theme, there has been debate as to the respective roles of contemporary levels of energy and of historical factors in generating global patterns of tree species richness in moist forests. The debate has centred on the extent to which differences in richness between continents and between latitudes result from variation in annual actual evapotranspiration (a good, but not universal, predictor of primary productivity) or from long-term evolutionary and geographical processes[40–42]. The practical constraints on conducting experiments at relevant scales mean that differentiating between hypotheses necessarily requires that they make divergent testable predictions, and even then may not enable the relative roles of different factors to be quantified. Historical factors have doubtless had a substantial role in shaping contemporary spatial patterns of biodiversity, but deriving such *a priori* predictions and quantifying the part played by history can often prove difficult. Molecular phylogenies, with estimated dates of diversification events, provide
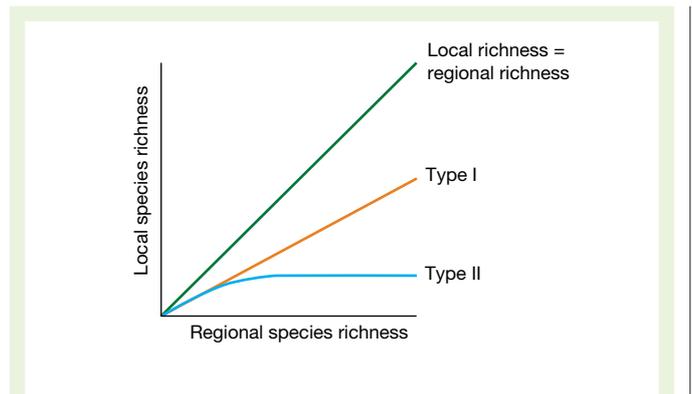
one rich source of data for testing hypotheses about the significance of history.

Relationships between local and regional richness

In exploring global variation in biodiversity, we need to understand not only the importance of differences in spatial scale for the patterns that are observed (for example, hump-shaped species–energy relationships at local scales and positive relationships at regional ones), but also how diversity at one scale might relate to that at another. Indeed, it is increasingly apparent that knowledge of the roles of pattern and process at different scales is at the very heart of an understanding of global variation in biodiversity.

Two theoretical types of relationship have been contrasted between the local richness an assemblage might attain and the species richness of the region in which that assemblage resides[54] (Fig. 3). Local richness may be directly proportional to, but less than, regional richness, following a proportional-sampling model (type I). Alternatively, as regional richness increases, local richness might attain a ceiling above which it does not rise despite continued increases in regional richness (type II).

Acknowledging a number of technical concerns[55–57], most real systems seem to exhibit an underlying type I relationship[54,56,58]; not uncommonly, regional richness explains a large proportion (>75%) of variance in local richness, and local richness constitutes a marked proportion (>50%) of regional richness. For example, type I relationships have been documented for fig wasps and their parasitoids in southern and central Africa[59], tiger beetles in North America and in India[60], lacustrine fish in North America[61] (Fig. 1c), and primates in Africa and in South America[62]. The predominance of type I relationships is supported by the observation that some spatial gradients in species richness are documented both for localities and regions across those gradients (with obvious implications for the interpretation of regional collations of fossil records).

A recurrent problem in studies of spatial patterns in biodiversity has been the conflation of pattern with mechanism. Nonetheless, the preponderance of examples of type I relationships, particularly where habitat type has been kept constant, backed up with other evidence (for example, the limited support for community convergence, density compensation and invasion resistance), indicates that there are not hard limits to levels of local richness[63]. That is, local assemblages do not seem to be saturated, in the way one might have expected if ecological interactions (for example, competition, predation and parasitism) limited local richness. Three potential anomalies arise if this conclusion is correct. First, it suggests that although ecological interactions are known to be strong in some circumstances, they may typically not be sufficient to have a marked effect on species richness. Second, it may be at odds with the more-individuals
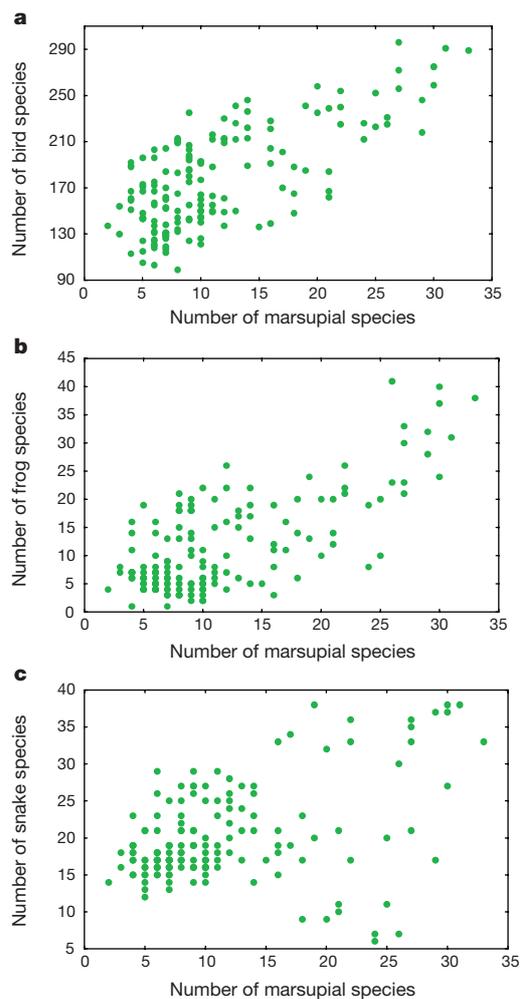

Figure 3 Relations between local and regional species richness, illustrating the form of type I and type II relationships and the limiting condition where local richness equals regional richness.

Figure 4 Relationships between species richness of different vertebrate groups (in grid cells of 240 km × 240 km) across Australia. **a**, Birds; **b**, frogs; and **c**, snakes, with marsupials (from data in ref. 79).

the region (its age, geology, size and climate), and broad-scale ecological or evolutionary processes, such as species migrations, invasions, speciation and regional extinction[55]. They set the species composition and the abundance, body size and trophic structure of the pool from which local communities draw. Indeed, a core issue in ecology is the extent to which local assemblages can be modelled accurately as random draws from regional species pools, or conversely the extent to which local factors modify the similarity of real assemblages to randomly simulated ones[66]. Almost invariably such models can explain some, often much, and occasionally most of the basic structure of local assemblages[44,66]. Local assemblage structure and the regional context are inseparable.

Recognition of the importance of regional-scale processes and the structure of the regional species pool to local community structure has led to the emergence of macroecology, which is concerned with understanding the abundance and distribution of species at large spatial and temporal scales[44,67]. However, although regional pools doubtless are important in structuring local assemblages, they are perhaps best seen as contributing to, rather than determining, local assemblage structure — local processes remain important. Resolving the relative contributions of local and regional processes may provide a key to understanding global patterns of biodiversity[55], but this issue once again emphasizes that patterns in biodiversity are unlikely to have a single primary cause.

Taxonomic covariance in species richness

Most major terrestrial and freshwater groups are more speciose in tropical than temperate regions, at low elevations than at high, and in forests than in deserts. One might therefore expect that the regional richness of different groups of organisms would covary positively and, because of the positive relationship between local and regional richness, local richness would do likewise. This would be important because it would simplify the development of an understanding of global patterns in biodiversity.

In practice, mismatches between the spatial occurrence of peaks in the richness of different groups have often been observed. For example, among trees, tiger beetles, amphibians, reptiles, birds and mammals, the 5% of land area across the United States and southern Canada in which the highest levels of species richness are attained overlap between some pairs of taxa, but this pattern is not a general one[68]. Likewise, although the numbers of species in different, large and similar-sized areas for two groups are often significantly correlated, and may enable a very general impression of the patterns in richness of one group to be obtained from those of another, these correlations are frequently weak, of rather limited predictive value, and in some cases explained by latitudinal gradients in diversity[68] (Fig. 4). These conclusions seem to hold at finer resolutions over more constrained areas. Thus, at a scale of 10 km × 10 km squares, species-rich areas for different taxa in Britain frequently do not coincide[69]. These areas are not distributed randomly, overlapping more often than expected by chance, but still at a rather low level. Likewise, different taxa are species poor or species rich in different areas of the northern region of South Africa[70].

Where positive relationships are found between the species richness of two or more groups, this may reflect patterns of sampling effort (a complication plaguing many biodiversity studies), rather than any underlying covariance. If real, then this does not necessarily imply any direct linkage between the richness of those groups. Covariance can occur because of trophic or other relations, but might also result from random effects, because groups share common determinants of richness, or even because groups differ in determinants of richness but these determinants themselves exhibit spatial covariance[71].

The lack of strong positive covariance in the species richness of higher taxa is significant in that it constrains the extent to which observed patterns in biodiversity can be extrapolated from one group to another, and from exemplar groups to biodiversity at large (with implications for the planning and likely success of networks of

hypothesis as an explanation for positive species–energy relationships based on local site data, because this requires that energy levels limit the number of species that can co-occur (through limitation on the number of individuals). And third, it seems at odds with the existence of marked regional (for example, latitudinal) variation in beta diversity, although this variation may be confounded by differences in habitat composition. (Defining beta diversity as $(S/\alpha) - 1$ (where S is regional and α is local richness[64]), regions having the same ratio of local-to-regional richness should have the same beta diversity[57].) The marked growth in studies of global patterns in biodiversity is steadily resolving such apparent anomalies by examining multiple patterns for the same assemblage, and thus generating a more coherent picture of the inter-relations between them. But high-quality data sets documenting at high resolution the occurrence of large numbers of species over extensive areas are desperately required.

If most systems exhibit type I relationships between local and regional richness, then a prime driver of local richness seems to be regional richness. The importance of regional-scale phenomena for local-scale assemblage structure is a general one[65]. A local community is assembled from a regional pool of species (this has variously been defined as the total pool of species in a region, or the pool of species in the region that is actually capable of colonizing a given site). The size and structure of this pool are influenced by regional processes, including the effects of the geophysical properties and history of

protected areas). The latter is particularly important given that only ~15% of the total number of species estimated to be extant has been formally described taxonomically, that the distributions of most of these remain largely unknown (a high proportion are known from only a single locality[72,73]), and that species whose distributions are well documented are strongly biased with respect to their higher taxonomic affinities. But such outcomes are inevitable, because of the multiple forces at work in structuring global patterns of biodiversity, and because the particular outcomes observed rest fundamentally on the balance of those forces. Indeed, even where two groups exhibit similar spatial gradients in biodiversity there is substantial variation around those trends, and the details are seldom similar. In the extreme, some groups exhibit patterns of biodiversity that are entirely contrary to the norm. For example, several major taxonomic groups exhibit peaks of species richness at high or mid-latitudes (for example, aphids, sawflies, ichneumonids, braconids, bees, various groups of freshwater invertebrates, marine amphipods, and procellariiforms[1,74]); exceptions to patterns of biodiversity tend to be observed more frequently at lower taxonomic levels than at higher levels. Which particular patterns are and are not expressed by a given taxon rest on contingencies (for example, physiology, dispersal ability, resource requirements and evolutionary history[56]).

In conclusion

Development of a markedly improved understanding of the global distribution of biodiversity is one of the most significant objectives for ecologists and biogeographers. Spatial heterogeneity in species richness, in particular, is an obvious feature of the natural world. An understanding of its determinants will impinge on applied issues of major concern to humankind, including the role of biodiversity in ecosystem processes, the spread of alien invasive species, the control of diseases and their vectors, and the likely effects of global environmental change on the maintenance of biodiversity.

A substantial proportion of regional variation in species richness can be explained statistically in terms of a few environmental variables[1]. This is, however, far from a predictive theory of species richness. It is the need to identify the contingencies involved in the expression of patterns in biodiversity, and to weigh their significance, that constitutes the real challenge to developing such a theory. The number of species is determined by the birth, death, immigration and emigration rates of species in an area. These rates in turn are determined by the effects of abiotic and biotic factors (the latter may be intrinsic or extrinsic to the organisms of concern) acting at local and regional scales. Although multiple factors doubtless contribute, if a factor influences biodiversity on one spatial axis (for example, latitude) then it seems reasonable to presume that all else being equal it will do so along others where the factor also varies (for example, elevation). Thus, relationships between species richness and environmental energy have been found to be associated with latitudinal, elevational and depth gradients[75]. If this were the whole story, patterns in richness would seem reasonably straightforward, if not easy, to predict. However, it is not simply the current states of these factors that are important but also their historical dynamics. These have shaped variations in the distribution of different groups of organisms, in their diversification, and hence the availability of species with different attributes to exploit opportunities provided by prevailing conditions. As such, the study of global patterns in biodiversity demands insights from geneticists through to ecosystem ecologists. All concerned will need to remember that no single mechanism need adequately explain a given pattern, that observed patterns may vary with spatial scale, that processes at regional scales influence patterns observed at local ones, and that no pattern is without variations and exceptions. □

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