



SPECIAL
PAPER



Why are there so many species in the tropics?

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ABSTRACT

Known for centuries, the geographical pattern of increasing biodiversity from the poles to the equator is one of the most pervasive features of life on Earth. A long-standing goal of biogeographers has been to understand the primary factors that generate and maintain high diversity in the tropics. Many ‘historical’ and ‘ecological’ hypotheses have been proposed and debated, but there is still little consensus. Recent discussions have centred around two main phenomena: phylogenetic niche conservatism and ecological productivity. These two factors play important roles, but accumulating theoretical and empirical studies suggest that the single most important factor is kinetics: the temperature dependence of ecological and evolutionary rates. The relatively high temperatures in the tropics generate and maintain high diversity because ‘the Red Queen runs faster when she is hot’.

Keywords

Ecological interactions, evolutionary rates, Janzen–Connell dynamics, latitudinal diversity gradient, metabolic theory, Red Queen, species diversity, tropics.

There is, however, one natural feature of this country, the interest and grandeur of which may be fully appreciated in a single walk: it is the ‘virgin forest’. Here no one who has any feeling of the magnificent and the sublime can be disappointed; the sombre shade, scarce illuminated by a single direct ray even of the tropical sun, the enormous size and height of the trees, most of which rise like huge columns a hundred feet or more without throwing out a single branch, the strange buttresses around the base of some, the spiny or furrowed stems of others, the curious and even extraordinary creepers and climbers which wind around them, hanging in long festoons from branch to branch, sometimes curling and twisting on the ground like great serpents, then mounting to the very tops of the trees, thence throwing down roots and fibres which hang waving in the air, or twisting round each other form ropes and cables of every variety of size and often of the most perfect regularity. These, and many other novel features – the parasitic plants growing on the trunks and branches, the wonderful variety of the foliage, the strange fruits and seeds that lie rotting on the ground – taken altogether surpass description, and produce feelings in the beholder of admiration and awe. It is here, too, that the rarest birds, the most lovely insects, and the most interesting mammals and reptiles are to be found. Here lurk the jaguar and the boa-constrictor, and here amid the densest shade the bell-bird tolls his peal.

Alfred Russel Wallace on tropical forest in Brazil in his 1849 letter to the members of the Mechanics’ Institution, published in Wallace, 1905 (p. 270).

INTRODUCTION

For more than three centuries Western science has known that biodiversity is greatest in the tropics. European explorers and traders returned from Africa, Asia and the Americas with thousands of specimens of previously unknown kinds of animals and plants. Many were sent to Carl Linnaeus, who by his last edition of *Systema Naturae* in 1758, had catalogued 7700 species of plants and 4400 species of animals, including 17 species of hummingbirds from South America and the Caribbean (Linnaeus, 1758). Explorer-naturalists who accompanied voyages to the tropics were awed by the variety of species, form and function, and wrote accounts comparable to Wallace’s letter from Brazil (above). Many giants of 19th century natural science, including Joseph Banks, Thomas Belt, Alexander von Humboldt, Joseph Dalton Hooker, Charles Darwin, Henry Walter Bates and Alfred Russel Wallace, were indelibly influenced by their exposure to tropical biodiversity.

In the mid-20th century, most of the great synthesizers who laid the foundations of modern evolution, systematics, biogeography and ecology commented on the pattern of increasing biodiversity from the poles to the equator (e.g. Theodosius Dobzhansky, Ernst Mayr, Charles Elton, Evelyn Hutchinson, Philip Darlington, Alfred Fischer, George Gaylord Simpson, Robert MacArthur and Edward O. Wilson).

But the data were still sketchy and there was little consensus as to the causal processes. Within the last few decades, biogeographers have taken advantage of new biological inventories of previously poorly studied taxa and regions and of technological advances in computers, electronic databases and geographical information systems to quantify and clarify the empirical patterns. It is now clear that the tropics harbour not only the most species of plants and animals, but also the most diverse genomes, clades of higher taxa (e.g. Willig *et al.*, 2003; Lomolino *et al.*, 2010), and even languages and cultures of subsistence human societies (Collard & Foley, 2002; Pagel & Mace, 2004; Gavin *et al.*, 2013). And the pattern is ancient, apparent in the fossil record dating back hundreds of millions of years (e.g. Stehli *et al.*, 1969; Crane & Lidgard, 1989; Crame, 2001). Even as the patterns have become clearer, however, the explanations have remained elusive and controversial.

So why is life most diverse in the tropics? The number of hypotheses to explain the latitudinal diversity gradient (LDG) has only increased in recent decades. Pianka (1966) listed 6, Brown (1988) 8, Rohde (1992) 23, Willig *et al.* (2003) 27, and Lomolino *et al.* (2010) 32. These proliferating hypotheses are a mixed bag, ranging from specific ideas for restricted taxonomic or functional groups to general phenomena potentially applicable to all organisms. They invoke different kinds and levels of explanation from proximate to ultimate, random to deterministic, historical to ecological, abiotic to biotic. Most importantly, many are not alternatives in the sense that they offer mutually exclusive explanations. There are too many for me to review and evaluate all of them here.

Instead, I offer a personal overview: highlighting some theoretical and empirical advances, evaluating the present state of the art, and offering a unifying, but admittedly incomplete, synthesis. I focus my treatment on the LDG of species richness across spatial scales from local communities to regional biotas.

BACKGROUND

Patterns: diversity of species, clades and cultures

The LDG is pervasive. It occurs in nearly all kinds of organisms – plants, animals and microbes – and environments – terrestrial, freshwater and marine. It occurs at all levels of evolutionary differentiation, not only at the species level, but also for intraspecific genetic and phenotypic differentiation and for lineages and higher taxa of multiple species. Many examples are shown in Lomolino *et al.* (2010; see also Willig *et al.*, 2003; Hawkins *et al.*, 2012).

Although the LDG is pervasive, it is definitely not universal. There are many clear exceptions. For example, species of conifers, amphipods, crayfish, ichneumonid wasps, voles and penguins are most diverse at mid- or high latitudes and greatly reduced or absent in the tropics (e.g. Willig *et al.*, 2003; Lomolino *et al.*, 2010). These exceptions are among

the ‘natural experiments’ that offer potentially powerful insights into the mechanisms that generate the more general pattern.

Processes: historical and ecological

Efforts to explain both the cases that exhibit LDGs and the cases that are exceptions have typically focused on effects of either ‘history’ or ‘ecology’. The historical hypotheses suggest that the LDGs are legacies of past geological, climatic and evolutionary events, most of which occurred thousands to millions of years ago. Some historical hypotheses are non-equilibrial in the sense that they propose that diversity is still changing in a lagged response to past perturbations. An example is the idea that the LDG in at least some groups in North America and Eurasia is a legacy of past glaciations: the high latitudes were uninhabitable or inhospitable during the glacial epochs, and there has not been sufficient time for animals and plants to disperse and adapt to the habitats that became available during the interglacial periods, including the current one (e.g. Fischer, 1960; Hortal *et al.*, 2011). Other historical hypotheses suggest that many LDGs reflect a longstanding, approximately steady-state relationship between the abiotic template of the Earth and the evolutionary processes that have shaped biodiversity. An example is the out of the tropics hypothesis which is discussed in more detail below.

In contrast to historical hypotheses, ecological hypotheses assume that, regardless of their evolutionary origin, most LDGs were originally caused and are now maintained by biological responses to the Earth’s abiotic template, especially variables that are due to solar radiation. The poles-to-equator gradients of temperature and seasonality and the corresponding gradient of biodiversity have existed for hundreds of millions of years, although the details of the patterns have fluctuated over time in response to tectonic events, Milankovich orbital cycles and other factors. One class of ecological hypotheses invokes productivity: there is a latitudinal gradient of primary production, and the more productive tropics support more individuals apportioned among more species. A second class invokes niche relationships: adaptations to some combination of abiotic conditions and biotic interactions allow tropical species to be more specialized, dividing resources more finely among more species.

THE ROLE OF HISTORY

Out of the tropics

Both fossil and phylogenetic reconstructions provide compelling evidence that most lineages originated in the tropics. The relevant dynamics are perhaps most simply and cogently presented in the ‘out of the tropics’ model (Jablonski *et al.*, 2006; Roy *et al.*, 2009; Cavender-Bares *et al.*, 2011; Bowen *et al.*, 2013) and supporting empirical evidence, mostly from the fossil record. Here is my depiction: (1) rates of

origination of new species are highest in the tropics; (2) higher rates of speciation than extinction generate high diversity of species and clades within the tropics; (3) most species and clades of tropical origin remain confined to low latitudes, because abiotic environmental constraints inhibit colonization and range expansion out of the tropics; (4) a minority of tropical species overcome these constraints and expand their ranges to colonize and sometimes diversify secondarily at higher latitudes; and (5) at these latitudes high rates of extinction result in lower standing stocks of species and clades. According to this model the tropics are both a 'cradle', because most lineages originate there, and a 'museum', because some of these lineages survive for long periods. Progressively higher latitudes tend to contain progressively younger species and clades, because of the higher extinction rates. The predicted patterns appear to be well supported by the fossil record, especially when sampling effort and other complications are taken into account (Jablonski *et al.*, 2006).

Niche conservatism

A complementary historical hypothesis invokes 'phylogenetic niche conservatism' (Wiens & Graham, 2005; Hawkins *et al.*, 2007, 2012; Donoghue, 2008; Wiens *et al.*, 2010; Buckley *et al.*, 2010; Cavender-Bares *et al.*, 2011). My interpretation is as follows: (1) closely related species tend to share similar traits inherited from their common ancestors; (2) among these phylogenetically conservative traits are niche attributes, requirements and tolerances for environmental conditions; (3) tropical environments with relatively warm, aseasonal climatic regimes have been present throughout most of Earth's history, whereas more extreme conditions, including periods of continental glaciation, have been more intermittent; (4) because of a long evolutionary history in relatively equable environments, most tropical species and lineages cannot tolerate the abiotic stresses at higher latitudes – especially cold temperature, low water (in terrestrial environments), and extreme seasonality – and so they are restricted to the tropics; (5) novel adaptive traits are required to tolerate stressful abiotic conditions and expand ranges to higher latitudes; and (6) the increasing severity of stress acts as a filter, resulting in a decreasing number of species and lineages with increasing latitude. The predicted patterns appear to be generally supported by phylogenetic analyses of trait evolution, climatic niche models, palaeoclimatic conditions and geographical range limits of naturalized exotic species. Tropical species experience and are adapted to only a narrow and equable range of abiotic conditions (e.g. Janzen, 1967; Terborgh, 1973; Gaston & Chown, 1999; Colwell, 2011). So, niche conservatism offers historical, ecological and evolutionary mechanisms to explain why only a minority of species and lineages have expanded out of the tropics to colonize and sometimes diversify in the more variable and stressful environments at higher latitudes.

Together, the out of the tropics and niche conservatism hypotheses provide a compelling account of the historical

dynamics of the LDG. I do not question most parts of this explanation. In my judgement, however, several issues still need to be addressed. Why are rates of speciation highest in the tropics? How does variation in speciation and extinction rates and the severity of abiotic conditions across latitudes generate and maintain the standing stocks of species richness seen in the LDGs? What are the implications of the exceptions, such as the diversification in tropical South America of lineages of placental mammals and cultures of aboriginal humans that colonized the New World relatively recently via the cold, seasonal environment of the Bering land bridge?

THE ROLE OF ECOLOGY

It is apparent that the above 'historical' hypotheses ultimately rely, implicitly and explicitly, on 'ecology'. G.E. Hutchinson (1959, p. 347) perceptively addressed these issues in his famous Homage to Santa Rosalia:

If we can have one or two species of a large family adapted to the rigors of Arctic existence, why can we not have more? It is reasonable to suppose that the total biomass may be involved. If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favorable conditions, then the rarer species in a community may be so rare that they do not exist. It is also probable that certain absolute limitations on growth-forms of plants, such as those that make the development of forest impossible above a certain latitude, may in so acting, severely limit the number of niches.

Here Hutchinson, in just a few elegantly worded sentences, addresses the role of ecology in generating and maintaining the LDG: (1) how productivity ultimately limits the total biomass of living matter; (2) how that biomass is apportioned among the 'number of niches' and hence among species; and (3) how rare species with specialized niches persist in the face of extinction.

Productivity

For the last few decades, the main ecological explanation for the LDG has been that regions of high productivity have higher biodiversity because more species can obtain sufficient resources to maintain viable populations. This explanation is based on the well-documented pattern that terrestrial net primary production, which is controlled largely by temperature and seasonality, increases from effectively zero at the poles to a maximum in the lowland wet tropics. Consequently, resources to support organisms of all trophic levels and most lifestyles are most abundant in the tropics, so these resources can be divided among more species with each getting 'a large-enough piece of the pie' to persist in the face of stochastic extinction. The productivity hypothesis has been advanced in several forms by multiple investigators (e.g. Hutchinson, 1959; Connell & Orias, 1964; MacArthur, 1965, 1972; Pianka, 1966; Brown, 1981; Wright, 1983; Currie, 1991; O'Brien *et al.*, 1998).

There can be no doubt that the LDG is ultimately due, at least in part, to productivity. The poles and driest deserts are

nearly devoid of life because they are simply too cold or too dry for organisms to survive and reproduce there. Fundamental physical, chemical and biological constraints limit the capacities of organisms to convert energy and nutrients into biomass (e.g. O'Brien *et al.*, 1998). In contrast, the tropics teem with life because the warm moist environment offers relatively benign abiotic conditions and abundant resources. Recently, the metabolic theory of ecology (MTE; Brown *et al.*, 2004; Sibly *et al.*, 2012) and empirical research in ecosystem ecology have made progress in synthesizing our understanding of the linkages between physiochemical limits on biological metabolism and the major environmental variables that affect photosynthesis and respiration. Nearly all of the energy that supports life comes from the sun, and the rate of photosynthesis or net primary production (NPP) is limited primarily by temperature and water in terrestrial environments and by nutrients and solar radiation in marine environments. NPP sets absolute limits on total resource use, biomass and number of individuals in an ecosystem, although there are tradeoffs, largely due to body size, in how energy and biomass are apportioned among individuals.

Strong correlations between species richness and NPP in terrestrial environments led many ecologists, myself included, to infer that productivity affects biodiversity in the way that Hutchinson suggested, by limiting the number of individuals per species that could persist in the face of extinction (e.g. Brown, 1981; Wright, 1983; Currie, 1991; Wright *et al.*, 1993; Fraser & Currie, 1996; Francis & Currie, 1998; Kaspari *et al.*, 2000; Kilpatrick *et al.*, 2006). Now, however, several lines of evidence suggest that this mechanism, by itself, is inadequate to explain the ubiquity and magnitude of LDGs in different organisms and habitats.

Kinetics

In 1992 Klaus Rohde (see also Fischer, 1960) reviewed the hypotheses and supporting evidence for the LDG, and proposed a relatively novel mechanism: 'It is concluded that greater species diversity is due to greater "effective" evolutionary time (evolutionary speed) in the tropics, probably as the result of shorter generation times, faster mutation rates, and faster selection at greater temperatures' (Rohde, 1992, p. 514). Rohde suggested that the effect of temperature on physiological processes causes faster rates of evolution and more rapid responses to selection in the tropics. Empirical studies have provided strong support for the idea that biotic interactions are 'more important' in the tropics, and that the density-dependent relationships play a major role in generating and maintaining the LDG (e.g. Janzen, 1970; Connell, 1971; MacArthur, 1972; Sax, 2001; Mittelbach *et al.*, 2007; Schemske *et al.*, 2009; Comita *et al.*, 2010; Ricklefs, 2010; Swamy & Terborgh, 2010; Johnson *et al.*, 2012; Terborgh, 2012). But it is not clear how temperature or other abiotic factors that vary with latitude affect the rates and outcomes of interactions so that 'diversity begets diversity'.

The MTE has modelled explicitly and quantitatively the linkages between temperature, metabolic biochemistry, and physiological, ecological and evolutionary rates (e.g. Allen *et al.*, 2002, 2006; Brown *et al.*, 2004; Savage *et al.*, 2004; Gillooly *et al.*, 2005; Gillooly & Allen, 2007; Sibly *et al.*, 2012). The theory assumes that over a biologically realistic range of temperatures, biological rates increase exponentially with temperature: $R \propto e^{-E/kT}$, where R is the rate of some process such as metabolism, population growth or speciation, e is the root of the natural logarithm, E is an 'activation energy' that gives the temperature dependence, k is Boltzmann's constant ($8.62 \times 10^{-5} \text{ eVK}^{-1}$), and T is temperature in Kelvin (Gillooly *et al.*, 2001; Brown *et al.*, 2004; Sibly *et al.*, 2012). The theory is still incomplete, but it provides a framework for analysing temperature dependence of phenomena related to biodiversity. I show an example, using preliminary data on forests from our National Science Foundation (NSF)-supported Macrosystems research project (Table 1). The upper panel of Fig. 1 shows productivity as a function of average annual temperature in an 'Arrhenius plot', where the logarithm of NPP is plotted as a function of inverse temperature, $1/kT$. The relationship is highly significant, with $E = 0.46$, which is intermediate between empirical values for rates of photosynthesis and secondary succession ($E \approx 0.33$) and respiration ($E \approx 0.65$; Allen *et al.*, 2005; Anderson *et al.*, 2006). The lower panel of Fig. 1 shows the temperature dependence of tree abundance and species richness. Both relationships are significant, but the relationship is much stronger for species than for individuals ($E = 0.80$ and 0.16 , respectively). Similar relationships for species richness have been published elsewhere (e.g. Allen *et al.*, 2002, 2006; Allen & Gillooly, 2006; Wang *et al.*, 2009).

The important point to be made here, however, is that species diversity increases with increasing temperature much more rapidly than the number of individuals and NPP. This implies that productivity alone is not a sufficient explanation for the LDG. Instead, it suggests that the LDG is due in large part to relatively direct effects of kinetics. The higher temperatures in the tropics cause higher rates of metabolism, ecological dynamics and coevolutionary processes, which generate and maintain higher biodiversity.

SYNTHESIS

I offer the synthetic framework outlined in Fig. 2 and fleshed out below.

Productivity

The flow of energy through an ecosystem determines its capacity to support life. Net primary production (NPP) gives the whole-ecosystem rate of energy supply. NPP sets powerful constraints on total abundance and biomass of all organisms. Given a fixed NPP, an ecosystem can support either a high biomass composed of a relatively few large individuals or a low biomass composed of many small individuals (e.g.

Table 1 Preliminary data for mean annual temperature, annual net primary productivity (NPP), number of individual trees and number of tree species at six forest sites of our Macrosystems project (five Long-Term Ecological Research sites and the Smithsonian's Barro Colorado Island). NPP data are from Kaspari *et al.* (2000) except for Luquillo, which is from http://daac.ornl.gov/NPP/guides/npp_doc.html. Data for number of individual trees > 0.25 cm d.b.h. and number of tree species in standardized modified 'Gentry plots' totalling 5000 m² in area were collected by V. Buzzard, C. Sides, A. Henderson and B.J. Enquist.

Site	Latitude	Longitude	Temperature (°C)	NPP (g C/m ² /yr)	Number of individuals	Number of species
Niwot Ridge (Colorado, USA)	40° 3' 34" N	105° 37' 1" W	-4	180	2031	6
H.J. Andrews Forest (Oregon, USA)	44° 13' 59" N	122° 10' 34" W	9	200	2322	17
Harvard Forest (Massachusetts, USA)	42° 31' 53" N	72° 11' 23" W	7	450	1384	25
Coweeta Forest (Georgia, USA)	35° 3' 38" N	83° 24' 59" W	13	550	1730	52
Luquillo Forest (Puerto Rico)	18° 16' 52" N	65° 47' 58" W	23	1033	2128	96
Barro Colorado Island (Panama)	9° 9' 7" N	79° 50' 47" W	27	1310	4971	263

trees in a forest compared to planktonic algae in the ocean). The rate of photosynthesis increases with increasing temperature in both terrestrial plants and aquatic algae (Allen *et al.*, 2005; Yvon-Durocher *et al.*, 2010; Anderson-Teixeira & Vitousek, 2012). However, geographical variation in NPP is complicated by water limitation in terrestrial ecosystems (e.g. Lieth, 1975; O'Brien *et al.*, 1998) and nutrient limitation in marine and freshwater ecosystems (e.g. Bunt, 1975; Smith, 1979; Moore *et al.*, 2013).

The effect of productivity on diversity is positive, but modest: too small to account for the magnitude of the LDG. The number of species increases much more rapidly with decreasing latitude and increasing temperature than the increase in total ecosystem energy supply (NPP), biomass or abundance (Fig. 1; see also Enquist & Niklas, 2001; Currie *et al.*, 2004). The effect of productivity on biodiversity is addressed by species–energy theory and its extensions and empirical tests (Wright, 1983; Wright *et al.*, 1993; Currie *et al.*, 2004; Hurlbert, 2006). Species–energy relationships are conceptually similar to species–area relationships in island biogeography. The empirical patterns are comparable to other species–energy and species–area relationships (MacArthur & Wilson, 1967; Wright, 1983; Wright *et al.*, 1993; Currie *et al.*, 2004; Hurlbert, 2006), where a typical *z*-value of 0.25 would require four orders of magnitude increase in NPP to increase species richness by one order of magnitude (i.e. a 10,000-fold increase in productivity for a 10-fold increase in diversity). I conclude that there is a latitudinal gradient of productivity due to the temperature dependence of NPP (see below), and it plays a small but significant role in the LDG.

Niches

The LDG in alpha diversity depends, therefore, not so much on the rate of resource supply as on how these resources are apportioned among individuals and species. Indeed, it has long been known that tropical communities typically contain disproportionately more specialized and rare species than assemblages at higher latitudes (Klopfer & MacArthur, 1961; Hubbell, 1979, 2008). This is perhaps best depicted by com-

paring the shapes of ranked species-abundance distributions (SADs): when the number of individuals is scaled logarithmically, high latitude communities are typically steep and approximately linear, whereas tropical communities are much flatter and strongly curvilinear (Fig. 2, top).

The temperature dependence of alpha diversity and the shape of SADs imply that local species richness is regulated by temperature-dependent ecological and evolutionary processes, mediated through the kinetics of metabolism as Rohde suggested in 1992. The kinetics of ecological interactions and coevolutionary adaptation result in species occupying more specialized niches in the tropics. Local species richness is indeed strongly temperature-dependent. Arrhenius plots of diversity as a function of inverse temperature typically have negative slopes, with $E = 0.6\text{--}0.8$ (e.g. Allen *et al.*, 2002, 2006; Wang *et al.*, 2009; Fig. 1).

Metabolic theory has the potential to model and account for these relationships. There have been attempts to do so (e.g. Allen *et al.*, 2002; Brown *et al.*, 2004; Allen & Gillooly, 2006; Wang *et al.*, 2009), but I agree with David Storch (2012) that 'a metabolic theory of biodiversity is a work in progress'. The obvious questions are: what are the temperature-dependent processes, and how do they generate and maintain standing stocks of local species richness? I believe that the answer lies primarily in the effect of temperature on interspecific ecological interactions and Red Queen coevolution. 'Diversity begets diversity' to generate the LDG, because ecological and evolutionary rates increase exponentially with temperature and are highest in the tropics. But we need theoretical and simulation models and relevant empirical studies to show how this occurs.

To go from typical log–linear temperate to curvilinear tropical SADs requires species-specific density-dependent processes that (1) suppress broad-niched dominant species, freeing up resources, and (2) facilitate the persistence of specialized species, allowing them to increase when rare, colonize from the metacommunity, and speciate. One phenomenon that has this effect is the Janzen–Connell process (Janzen, 1970; Connell, 1971). The idea is that 'enemies', some combination of predators, herbivores, parasites and diseases, have negative density-dependent impacts on their

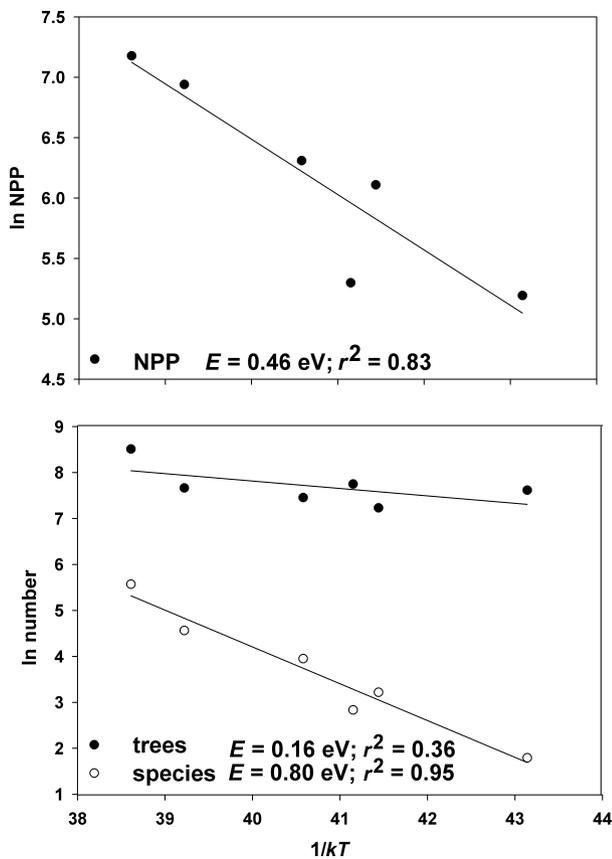


Figure 1 Temperature dependence of productivity, number of trees and number of tree species on the six forest study sites of our Macrosystems project (Table 1). Data are presented as Arrhenius plots, with the natural logarithm of rate as a function of inverse temperature, $1/kT$ (so colder temperatures are to the right). Data were fitted by ordinary least squares regression: values of E give the slopes, the measure of temperature dependence, and values of r^2 give the proportion of variation explained. Above: rate of net primary production (NPP); below: number of individual trees and number of tree species: data from V. Buzzard, C. Sides, A. Henderson and B.J. Enquist. Note that the temperature dependence for species richness was substantially higher than for NPP, which was substantially higher than for the number of individuals.

prey or hosts through both short-term ecological interactions and longer-term coevolutionary adaptations. The Janzen–Connell process has increasingly gained empirical support (e.g. MacArthur, 1972; Clark & Clark, 1984; Sax, 2001; Mittelbach *et al.*, 2007; Schemske *et al.*, 2009; Comita *et al.*, 2010; Ricklefs, 2010; Swamy & Terborgh, 2010; Johnson *et al.*, 2012; Terborgh, 2012).

It is far from clear, however, how temperature, by increasing the rate of interactions and coevolution, generates and maintains higher species richness. Recent meta-analyses have collected and analysed published data on temperature dependence of rates of ecological interactions, including competition, predation, herbivory and parasitism (Brown *et al.*, 2004; Dell *et al.*, 2011; Englund *et al.*, 2011). The results are variable, sample sizes are generally small, and statistical reso-

lution is correspondingly limited. A more comprehensive compilation and analysis reveals a clear central tendency, with values clustering around the value of $E \approx 0.65$ as predicted by metabolic theory (W.R. Burnside, S.T. Hammond & J.H. Brown, unpublished). Additional theoretical and empirical studies are needed to show how warmer temperatures, by speeding up rates of interaction and coevolution, cause higher species diversity in the tropics.

Spatial relationships

The vast majority of empirical studies of the LDG have focused on alpha diversity or local species richness. Much less attention has been devoted to the spatial context of diversity, explicitly to beta diversity or spatial turnover in species composition. Higher beta diversity in the tropics, however, appears to be another pervasive feature of the LDG (Condit *et al.*, 2002; Qian *et al.*, 2004, 2009; Rodríguez & Arita, 2004; Qian & Ricklefs, 2007; Wang *et al.*, 2009; Kraft *et al.*, 2011). This phenomenon is expressed on a range of spatial scales. With decreasing latitude and increasing temperature: (1) similarity in species composition of local communities decreases more rapidly with increasing distance between samples (distance-decay relationships: e.g. Nekola & White, 1999); (2) the number of species increases more rapidly with increasing sample area (species–area relationships: Fig. 2, middle; e.g. Wang *et al.*, 2009); and (3) species occupy smaller geographical ranges and a narrower range of abiotic environmental conditions (Rapport's rule: e.g. Rapport, 1982; Stevens, 1989; Brown *et al.*, 1996).

These patterns of beta diversity are consistent with the effect of temperature on ecological interactions and coevolutionary processes as outlined above. In a spatial context, 'diversity begets diversity' because biotic resistance from other species restricts species to their specialized niches and limits their capacities to disperse and invade other environments, which also have a diverse complement of well-adapted species. The patterns of beta diversity are uniquely explained by biotic limiting factors; otherwise the relatively benign conditions in the tropics should allow species to be widespread (e.g. Terborgh, 1973; Gaston & Chown, 1999; Colwell, 2011).

Again, it remains to be explained how temperature generates and maintains these patterns of beta diversity. Critical here is the effect of temperature on dispersal. I suggest that in general, temperature tends to increase the rates but decrease the distances of dispersal. On the one hand, the large number of very rare species in tropical communities suggests that relatively high rates of colonization of species from some larger, more extensive metacommunity are essential to replenish local richness after stochastic extinctions. On the other hand, the small ranges and difficulty of invading distant sites due to biotic resistance suggest that long-distance dispersal is rare and probably maladaptive for most tropical species. Metabolic theory addresses the temperature dependence of metabolic rate, life history traits and dispersal

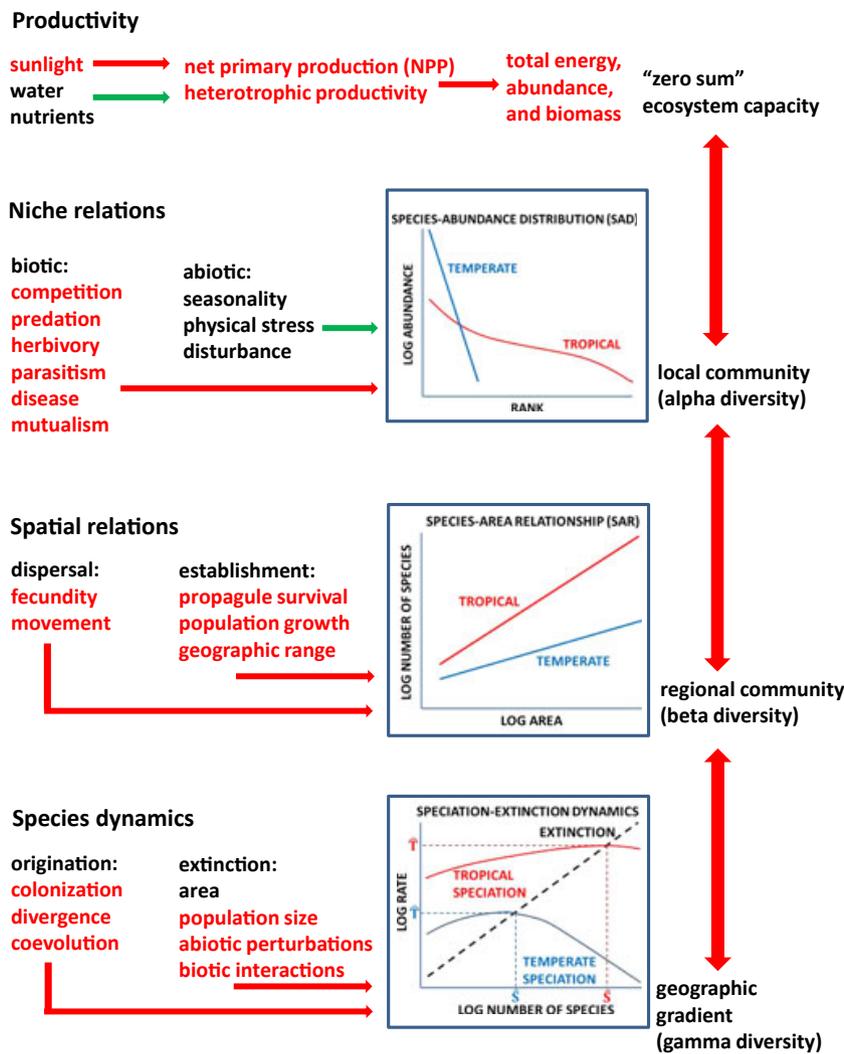


Figure 2 A tentative synthetic framework for the causal mechanisms that generate and maintain the latitudinal gradient of species diversity. Cause–effect relationships are indicated by arrows. Mechanisms that are at least in part temperature dependent, and hence consistent with the kinetics of metabolic theory, are in red. Other mechanisms are in green. Some emergent outcomes are shown in the graphs. The presentation is arranged in approximate order of increasing spatial scale and evolutionary time, starting with local ecological processes at the top and ending with regional species dynamics at the bottom. But the mechanisms operate both bottom-up and top-down, as indicated by the double-headed vertical arrows on the right, which indicate important feedbacks among processes and across scales. See text for additional explanation. \hat{S} , carrying capacity for species; \hat{T} , turnover rate of species.

distance in ectothermic organisms. The effect of temperature on development and lifespan predicts shorter dispersal distances in at least some tropical organisms. One example is planktonic larvae, the primary dispersal stage of benthic marine algae, invertebrates and fish. In warmer environments larvae develop more rapidly and consequently disperse over shorter distances (O'Connor *et al.*, 2007). And finally, higher rates of ecological interactions with enemies and the resulting mortality should additionally limit dispersal distances and establishment of propagules in the tropics.

Species dynamics

Ultimately the generation and maintenance of diversity depends on species dynamics, on how rates of colonization, speciation and extinction vary with the number of species. When speciation rate exceeds extinction rate, the number of species will tend to increase exponentially; when extinction rate exceeds speciation rate, the number of species will tend to decline exponentially towards zero. Because such exponential trajectories cannot be continued for very long, species

diversity must come to an approximate equilibrium or steady state between rates of origination and extinction. So, it is really this ‘carrying capacity for species’, rather than speciation and extinction rates per se, that maintains species diversity over both ecological and evolutionary time.

It is constructive to develop a simple graphical model, similar to MacArthur & Wilson’s (1967) equilibrium model of island biogeography (Fig. 2, bottom). Here, both speciation and extinction rates are depicted as increasing functions of species richness, but the extinction curve is steeper than the speciation curve so that they cross to give a stable equilibrium. I have drawn the graph with a single extinction curve for both temperate and tropical environments, but with a higher rate of speciation for any given richness, S , in the tropical environment, reflecting how ‘diversity begets diversity’ due to the rates of biotic interactions and coevolutionary processes (see also Emerson & Kolm, 2005). This model predicts a higher ‘carrying capacity’ for species, \hat{S} , in the tropics, maintained by a higher turnover rate of species, \hat{T} , i.e. higher rates of both speciation and extinction at this equilibrium. There is much room to elaborate and improve on this

model: e.g. changing the shapes and positions of the curves, making the extinction rates different in the tropic and temperate environments, and adding a colonization rate curve to depict species migrating out of the tropics into the temperate zone, and so on. Nevertheless, this simple model can be useful in guiding our thinking about the fundamentals of species dynamics and the temperature dependence of the underlying rate processes.

The model in Fig. 2 is at least qualitatively consistent with metabolic theory and empirical observations. There is increasing evidence that rates of evolution, from nucleotide and nucleic acid substitution to speciation and phyletic diversification, are higher in warmer environments and, when examined, exhibit a latitudinal gradient (Gillooly *et al.*, 2005; Allen *et al.*, 2006; Estabrook *et al.*, 2007; Gillooly & Allen, 2007; Mittelbach *et al.*, 2007; Gillman *et al.*, 2010; Wright *et al.*, 2010, 2011; Machac *et al.*, 2012). In particular, the model in the bottom panel of Fig. 2 predicts that at equilibrium both speciation and extinction rates are temperature dependent. This is supported by turnover of fossil morphospecies of planktonic organisms as a function of palaeolatitude and sea-surface temperatures (Allen *et al.*, 2006; Allen & Gillooly, 2006).

It remains to be explained just how higher rates of evolution and diversification generate and maintain higher species diversity in warmer environments and at tropical latitudes. The model of Allen *et al.* (2002) that predicted a universal temperature dependence of biodiversity has not been supported. A single value of E is unlikely on theoretical grounds (Storch, 2012), and empirical studies have shown that E varies with spatial scale (beta diversity: see above), taxon and geographical region (Wang *et al.*, 2009; Hawkins *et al.*, 2007). It is tempting to suggest that the temperature dependence of biodiversity and the LDG are not simply due to higher rates of evolution in warmer environments, but to higher rates of Red Queen coevolution due to more and faster biotic interactions. Given the evidence presented above, I am confident that 'the Red Queen runs faster when she is hot', but additional theoretical and empirical work will be required to elucidate the mechanisms.

Feedbacks

I have narrated the synthesis above from the bottom-up, starting with how productivity and niche relationships affect local (alpha) diversity and working up to spatial turnover (beta diversity) and finally to geographical scale species dynamics (gamma diversity). I do not mean to imply, however, that the causal relationships all flow in this direction. In fact, as depicted by the arrows on the right side of Fig. 2, there are top-down feedbacks at all these levels. The large-scale patterns of colonization, speciation and extinction feed down to influence regional diversity and the composition of metacommunities, and these feed down to affect the diversity and composition of local communities. Some of these cross-

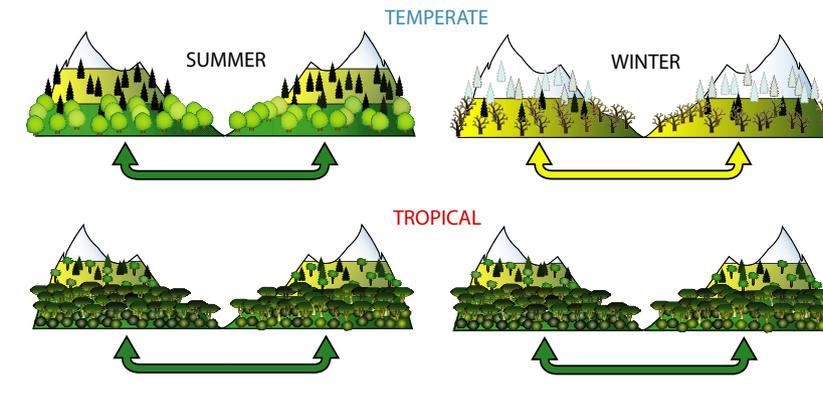
scale feedbacks are implicit in the presentation above and Fig. 2, but a few warrant some elaboration.

One, described by Darwin (1859), has been called the Dobzhansky–MacArthur phenomenon (DMP): the equatorial limits of species geographical ranges are usually due to biotic interactions, whereas the polar limits are due to stressful abiotic conditions. There is considerable empirical support for the DMP (e.g. MacArthur, 1972; Root, 1988; Stephens & Wiens, 2003; Lomolino *et al.*, 2010; Sunday *et al.*, 2011, 2012; and other cases summarized in Lomolino *et al.*, 2010). Perhaps the most convincing evidence comes from the latitudinal limits of geographical ranges of exotic species on continents and islands where they are native and where they have been introduced (e.g. Sax, 2001; Wiens & Graham, 2005). The DMP offers a way that the historical 'out of the tropics' dynamics and phylogenetic niche conservatism of lineages can be reconciled with the fact that the LDG is an ancient pattern, reflecting a steady-state relationship to climate dating back hundreds of millions of years (e.g. Stehli *et al.*, 1969; Crane & Lidgard, 1989; Crame, 2001). Needless to say, the DMP is consistent with the above suggestions that the LDG is due in large part to the temperature dependence of biotic interactions and Red Queen coevolution.

Another interesting cross-scale feedback is the influence of the geography of speciation on local and regional diversity. It has long been recognized that diversity is highest not just in the tropics, but in topographically diverse regions: mountain terrain on land, such as the slopes of the Andes and Himalayas, and island archipelagos in the sea, such as the Indo-West Pacific and Caribbean. Janzen (1967) called attention to the former in a wonderful paper entitled 'Why mountain passes are higher in the tropics'. He pointed out that because of seasonal variation in climate, a given change in elevation poses a greater barrier to dispersal in the tropics than at higher latitudes (Fig. 3, top). By dispersing in a particular season (winter or summer) an elevationally restricted temperate species can potentially cross mountain passes at lower or higher elevations without encountering temperatures outside the range that it normally experiences during an annual cycle. An elevationally restricted tropical species, by contrast, cannot cross over passes at substantially higher or lower elevations without being exposed to more extreme temperatures than it normally experiences. Janzen suggested that adaptations to such limited seasonal climatic variation result in tropical organisms with narrow thermal niches and restricted distributions. McCain (2009) has recently shown that elevational ranges are narrower in the tropics than at higher latitudes, a pattern consistent with both Janzen's hypothesis and Rapoport's rule (see above). Although Janzen was cautious about extrapolating his idea to explain higher speciation rates and species diversity in the tropics, it is easy to see how temperature-limited dispersal would have this effect.

I suggest that a somewhat similar phenomenon may facilitate speciation in marine organisms in tropical archipelagos (Fig. 3, bottom). Species richness of benthic marine organisms is highest in the islands of the Indo-West Pacific and

Mountain passes are higher in the tropics (Janzen, 1967)



Marine islands are farther apart in the tropics

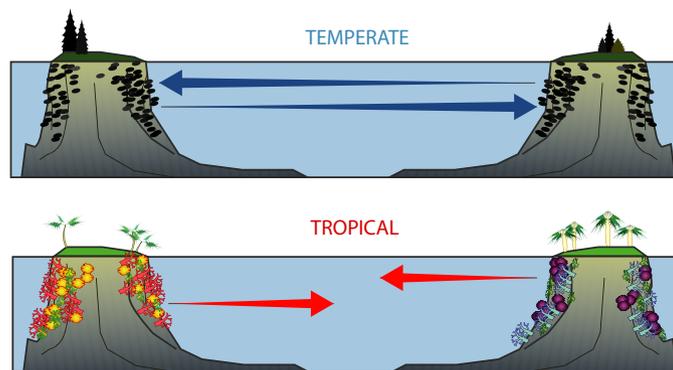


Figure 3 Schematic diagram illustrating a feedback between topography, temperature regime and speciation rates that plays a major role in the latitudinal diversity gradient. Above: Janzen's (1967) explanation for 'Why mountain passes are higher in the tropics'. Organisms confined to elevational zones can more easily disperse across mountain passes at either higher or lower elevations in temperate regions (yellow and green arrows) than in the tropics (green arrows only), because temperate organisms living at any elevation experience wider seasonal temperature fluctuations and have broader thermal tolerances than tropical organisms. Below: my explanation for 'Why marine islands are farther apart in the tropics'. Organisms that are confined to benthic habitats and disperse as planktonic larvae can travel longer distances in the temperate zones (blue arrows) than in the tropics (red arrows), because they have lower metabolic and developmental rates and longer survival in colder waters (O'Connor *et al.*, 2007). In both cases, shorter-distance dispersal in the tropics results in reduced gene flow and allows higher rates of diversification and speciation. In both cases, in addition to the direct effect of temperature on physiology, the higher diversity and activity of enemies in warm tropical environments create more severe barriers to dispersal.

Caribbean (Tittensor *et al.*, 2010; Bowen *et al.*, 2013). Benthic fish, invertebrates and algae disperse between suitable substrates as planktonic larvae. Metabolic theory predicts and empirical studies confirm that survival of larvae in the plankton is temperature dependent, because the rate of development depends on metabolic rate (Gillooly *et al.*, 2002; O'Connor *et al.*, 2007; O'Connor & Bruno, 2012). In warmer waters larvae develop to the settling stage more rapidly, so they spend less time in the plankton and disperse shorter distances. So, from the standpoint of barriers to dispersal and gene flow, 'islands are farther apart in the tropics'. Janzen emphasized the direct effect of environmental temperature as a barrier to dispersal in tropical mountains. Warm waters present somewhat similar physiological barriers to dispersal of planktonic marine larvae in archipelagos. In both cases, however, the effect is potentially exacerbated by biotic

resistance from enemies, which are more diverse and active where the temperatures are warmer.

These effects of topography on speciation appear to feed down to smaller scales to augment regional and local diversity. High origination rates would facilitate maintenance of higher equilibrium species richness by counteracting high extinction rates of rare species, (Hubbell, 2008). Additionally, the generation of new species with novel combinations of traits that more completely fill available niche space would tend to augment diversity at all spatial scales. So while temperature-dependent biotic interactions act from the bottom-up to promote local diversity by promoting the coexistence of many specialized rare species, temperature-dependent speciation rates act from the top-down to pump in new species and traits to fill the niches with specialized species.

FUTURE PROSPECTS

It should be clear from the above that we do not yet have a widely accepted, general, synthetic explanation for the LDG. Even if all or parts of the above synthesis are substantially correct, many parts are incomplete and many holes need to be filled. I am optimistic that substantial progress can be made. Several areas of research should be especially promising.

Comparative biogeography and macroecology

There has been great progress in documenting empirical patterns of biodiversity: across scales of space and time, levels of biological organization, taxa and habitats. There has been less progress in comparing and synthesizing the results, in part because systematists, ecologists and biogeographers tend to be specialists. This is unfortunate. On the one hand, the LDG is very general, suggesting that similar processes operate in similar ways on the different organisms in different habitats. On the other hand, the roles of historical events and contemporary environments, and of evolutionary and ecological processes, are not independent or mutually exclusive. Moreover, the LDG is just the most well known of several pervasive geographical patterns of biodiversity. Others are the gradients of species richness with elevation on land, depth in the ocean, and aridity in terrestrial environments (e.g. Lomolino *et al.*, 2010; Colwell, 2011).

There is much to be learned by taking advantage of ‘natural experiments’ and making comparisons among the different gradients, scales, levels of organization, taxa and habitats. The variables that potentially affect diversity – tectonic and glacial history, seasonality, temperature, productivity, abiotic stress, biotic interactions, abundance and biomass – sort out in different ways in these different systems, offering potentially valuable insights. For example, the correlations among seasonality, NPP, temperature and latitude, which potentially confound analyses of the LDG in the terrestrial realm are effectively absent in the marine realm. In the oceans NPP is controlled largely by nutrient supply and is highest in areas of upwelling and outflows of large rivers. So productivity is largely independent of temperature and latitude, but biodiversity is highest in tropical waters (e.g. Tittensor *et al.*, 2010). The historical effects of Pleistocene glaciations on pelagic marine organisms, although not inconsequential, were likely to have been quite different from those on plants and animals on the northern continents. Similarly, comparisons of elevational and latitudinal diversity patterns have the potential to separate the effects of glacial history and seasonality from those of productivity and temperature. Also relevant are mechanisms responsible for the frequently observed peak of diversity at intermediate elevations, a phenomenon seldom seen across latitude (e.g. McCain, 2004; Colwell, 2011).

Comparisons of diversity at different levels of biological organization will also be relevant. The LDG is not restricted to species; it also holds at higher and lower levels of

organization. Recent studies have documented LDGs of clades of multiple species (e.g. Hawkins *et al.*, 2012; Romdal *et al.*, 2012). Supplemented with information from the fossil record and molecular phylogenies on the timing and location of dispersal, speciation, divergence and extinction, such studies are elucidating historical patterns of biodiversity and providing insights into the dynamical processes. At the other extreme, there is increasing evidence of LDGs within species, including human cultures and languages (Collard & Foley, 2002; Pagel & Mace, 2004). Rapoport’s rule was originally based on within-species variation as expressed in range sizes of recognized subspecies. Finally, there appears to be a LDG of genetic diversity within populations, as evidenced by numbers of mitochondrial genotypes within local populations of several kinds of terrestrial vertebrates (Adams & Hadly, 2012).

Comparisons of species richness, genetic diversity, geographical range limits, local abundance and spatial distributions between alien and native species offer additional insights. Exotics introduced by humans within the last few hundred years provide invaluable ‘unintentional experiments’ in ecology and evolution (Sax, 2001; Sax *et al.*, 2002; Wiens & Graham, 2005). For example, the pattern that polar but not equatorial limits of geographical ranges of introduced terrestrial vertebrates are closely correlated, and that tropical continents but not islands, appear to be resistant to colonization by introduced species are consistent with the DMP, limitation by abiotic factors at high latitudes, and biotic interactions in the tropics (Sax, 2001). There is much to learn by expanding macroecological studies of exotics to other systems, such as terrestrial insects and marine organisms.

The most invasive organism is our own species. In only about 50,000 years anatomically modern humans have spread out of tropical Africa to colonize the entire Earth and become the most dominant species. Recent studies of subsistence cultures have documented a Rapoport’s rule of tribal ranges and a LDG of languages and cultures (Collard & Foley, 2002; Pagel & Mace, 2004; Burnside *et al.*, 2012; Gavin *et al.*, 2013). Because these patterns have been established rapidly and independently on different continents, they presumably reflect convergent responses to similar ecological conditions. They are consistent with effects of biotic interactions, especially with diseases and plant and animal food resources.

Theory and models

There is also a need for more and better theory to articulate promising questions, guide the design and analysis of empirical studies, and evaluate mechanistic hypotheses. To produce a widely accepted general synthetic theory of biodiversity will be a real challenge. Just to provide a relatively satisfying explanation of the LDG would be a major accomplishment, let alone to develop a more comprehensive theory that places the LDG in the context of other pervasive patterns of diversity across geographical space and evolutionary time.

A major challenge in developing biodiversity theory is the inherent complexity of the problem. Most efforts have used either qualitative verbal or graphical frameworks (Connell & Orias, 1964; Janzen, 1970; Connell, 1971; Rosenzweig, 1995), simple analytical treatments that incorporate only a few coexisting species (e.g. MacArthur, 1972; Tilman, 2004), or whole-system models that focus on emergent patterns rather than underlying mechanisms (e.g. Hubbell, 2008; Harte *et al.*, 2008; Harte, 2011; Storch, 2012). This is understandable, but for ideal interplay between theory and data we need models that can incorporate explicit mechanistic processes and make predictions for assemblages of tens to hundreds of species. This will necessarily entail computer simulation models.

I am fairly optimistic that considerable progress can be made using models that incorporate a relatively small number of assumptions and parameters and are firmly grounded in basic biophysical principles such as mass and energy balance, biomechanics and physiology, and metabolic scaling (e.g. Hammond & Niklas, 2009, 2011a,b).

Manipulative experiments

I also see considerable promise in using real experiments to address general questions about biodiversity. Such manipulations can be viewed as empirical models: deliberately oversimplified systems designed to make progress by using controlled conditions and standardized treatments to focus on the effects of critical variables and processes. Experiments with microbes in microcosms have been used to great effect to address questions in population ecology, interspecific interactions and evolution. So far, however, inferences about biodiversity have generally been limited, because most experiments have used a small number of genotypes or species. But the general approach could be extended by inoculating microcosms with high-diversity cultures from natural sources and using metagenomic molecular tools to quantify the outcomes, while manipulating and controlling environmental variables.

CONCLUDING REMARKS

More than three centuries after the spectacularly high biodiversity in the tropics became known, accounting for this phenomenon remains one of the greatest challenges for Western science. New databases and analytical techniques have increasingly documented the empirical manifestations of the LDG, both the pervasiveness of the gradient across different habitats, taxa, and levels of biological organization, and the variations and exceptions to the general pattern. Still missing, however, is a unified theory of biodiversity to explain these relationships.

In particular, I see a need for frameworks that show how the historical events and environmental conditions affect the dynamics of fundamental ecological and evolutionary processes to generate and maintain variation in standing stocks of biodiversity. In other words, we need to understand the link-

ages between the rates of mechanistic processes and the resulting states of diversity at different levels of organization. We can look to the fossil record, phylogenetic reconstructions, analyses of variation in genomes and niche traits, and metabolic theory to guide the search for these linkages. I suspect that the latitudinal gradient of biodiversity is so ancient and pervasive because the relationship of the Earth to the sun and the variation in solar energy input creates a gradient of environmental temperature. Temperature affects the rate of metabolism and all biological activity, including the rates of ecological interactions and coevolution. 'Diversity begets diversity' in the tropics, because 'the Red Queen runs faster when she is hot'.

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BIOSKETCH

James H. Brown grew up in upstate New York, attended Cornell University, and received his PhD from the University of Michigan. He held faculty appointments at the University of California at Los Angeles, University of Utah, University of Arizona, Santa Fe Institute, and University of New Mexico, where he has been Professor Emeritus since 2012. He is known for his empirical research in desert ecosystems and biogeography and his theoretical research in macroecology, biological scaling and metabolic ecology. He has trained many undergraduates, graduate students and postdocs. He has received several honors and awards, including election to the National Academy of Sciences and the American Academy of Arts and Sciences, the Wallace Award from the International Biogeography Society, the Odum and MacArthur Awards from the Ecological Society of America, the Merriam and Grinnell Awards from the American Society of Mammalogists, the Marsh Award from the British Ecological Society, and the Grinnell Medal from the University of California at Berkeley. In retirement he is trying to spend a bit less time doing science and a bit more time travelling and with family.

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