

REVIEW AND  
SYNTHESISEvolution and the latitudinal diversity gradient:  
speciation, extinction and biogeography

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## Abstract

A latitudinal gradient in biodiversity has existed since before the time of the dinosaurs, yet how and why this gradient arose remains unresolved. Here we review two major hypotheses for the origin of the latitudinal diversity gradient. The time and area hypothesis holds that tropical climates are older and historically larger, allowing more opportunity for diversification. This hypothesis is supported by observations that temperate taxa are often younger than, and nested within, tropical taxa, and that diversity is positively correlated with the age and area of geographical regions. The diversification rate hypothesis holds that tropical regions diversify faster due to higher rates of speciation (caused by increased opportunities for the evolution of reproductive isolation, or faster molecular evolution, or the increased importance of biotic interactions), or due to lower extinction rates. There is phylogenetic evidence for higher rates of diversification in tropical clades, and palaeontological data demonstrate higher rates of origination for tropical taxa, but mixed evidence for latitudinal differences in extinction rates. Studies of latitudinal variation in incipient speciation also suggest faster speciation in the tropics. Distinguishing the roles of history, speciation and extinction in the origin of the latitudinal gradient represents a major challenge to future research.

## Keywords

Biodiversity, biotic interactions, diversification, evolutionary speed, extinction, geographical isolation, latitudinal diversity gradient, speciation, tropics.

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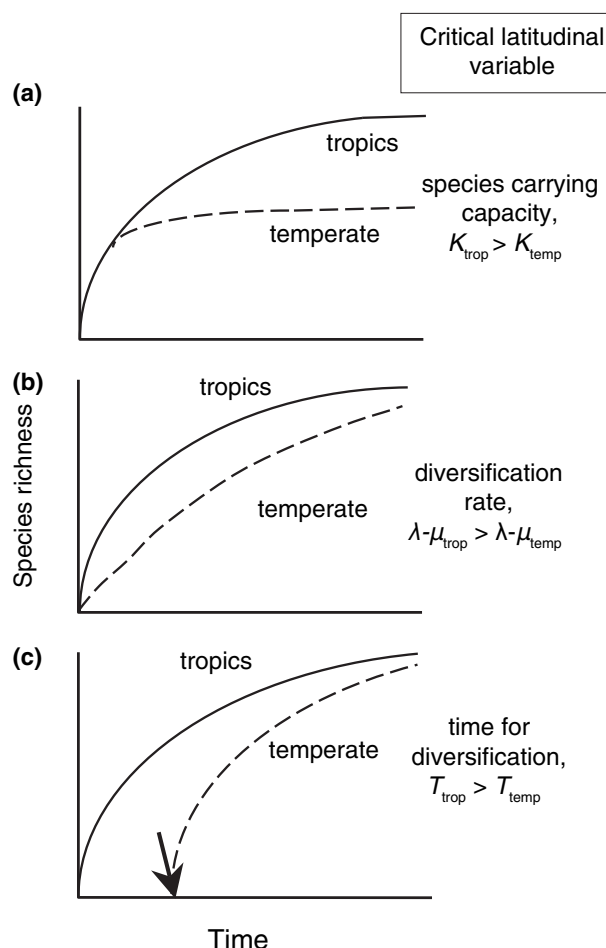
## INTRODUCTION

The latitudinal diversity gradient is one of the most striking patterns in the natural world. Hillebrand's (2004) recent meta-analysis of almost 600 studies documents its remarkable consistency across space, scale, habitat and taxonomic group. Species richness of most taxa increases towards the equator and this trend is substantially stronger at regional than local scales. The strength of the trend does not differ between northern and southern hemispheres (although it is not symmetrical around the equator), nor does it differ between marine and terrestrial groups, active and passive dispersers, or ectothermic and endothermic taxa (Hillebrand 2004). Yet, despite decades of study, a universally accepted explanation for the latitudinal diversity gradient remains elusive.

Three kinds of explanations have been proposed for the gradient: ecological hypotheses that focus on mechanisms of species coexistence and the maintenance of species diversity (Fig. 1a), evolutionary hypotheses that focus on rates of diversification (Fig. 1b), and historical hypotheses that focus on the duration and extent of tropical environments in Earth's history (Fig. 1c). Ecological hypotheses have predominated over the past 50 years and a number of recent reviews summarize these ideas (e.g. Willig *et al.* 2003). Evolutionary and historical hypotheses, despite their long history (e.g. Dobzhansky 1950; Fischer 1960; Fedorov 1966) have received far less attention (but see Ricklefs 1987, 2004; Rohde 1992; Jablonski 1993; Rosenzweig 1995; Schemske 2002; Wiens & Donoghue 2004; Allen *et al.* 2006; Jablonski *et al.* 2006). Recently, however, renewed interest in evolutionary and historical explanations for the gradient (Table 1) has been fuelled by the increased availability of phylogenetic, molecular, palaeontological and biogeographical data, and by the inadequacy of ecological hypotheses to account for the patterns (Currie *et al.* 2004). Our goal is to review these recent developments, and particularly to examine the roles that diversification and historical biogeography may have played in the origin of the latitudinal diversity gradient.

### Evolutionary and biogeographical hypotheses – a brief history

Early evolutionary explanations for the latitudinal gradient focused primarily on geographical differences in the nature and magnitude of natural selection. Both Darwin (1859) and Wallace (1878) suggested that adaptations in the temperate zone are governed by a harsh climate, while those in tropical regions are caused by biotic interactions: 'In the equatorial zone there is no such struggle against climate. Every form of vegetation has become alike adapted to its genial heat and ample moisture, ...and the never ceasing struggle for existence between the various species in the



**Figure 1** The accumulation of species richness through time (stylized) under three general mechanisms. (a) The tropics and temperate zone do not differ with respect to diversification rate, but richness asymptotes at different levels due to ecological factors (e.g. niche availability). (b) The tropics have a higher diversification rate (speciation rate–extinction rate) than the temperate zone and thus accumulate species richness faster. (c) The tropics have had more time for diversification than temperate areas. For example, the arrow could represent the end of the megathermal climate and the formation of the temperate zone (see text).

same area has resulted in a nice balance of organic forces...' (Wallace 1878, p. 66). Dobzhansky (1950) also proposed that relatively benign, stable tropical climates favoured adaptations in response to biotic interactions, whereas harsh temperate climates favoured adaptations to the physical environment.

Fischer (1960) hypothesized that tropical biotas diversify more rapidly than do temperate biotas and reach a higher equilibrium number of species, and also that tropical environments have had a longer and relatively undisturbed evolutionary history compared with temperate environments. Thus, Fischer's (1960) explanation for the latitudinal

**Table 1** Evolutionary hypotheses for the latitudinal diversity gradient. Notable papers associated with each hypothesis are listed, but space limitations prevent citing all who have contributed to the development of a hypothesis

Diversification rates are similar across regions, but the time for diversification is greater in the tropics (Fig. 1c):	
1.	Tropical environments are older and many extant clades originated in the tropics (Wallace 1878; Fischer 1960; Ricklefs & Schluter 1993; Futuyma 1998; Wiens & Donoghue 2004)
2.	Dispersal of clades out of the tropics is limited and recent (Farrell <i>et al.</i> 1992; Latham & Ricklefs 1993; Brown & Lomolino 1998; Futuyma 1998)
Diversification rates are higher in the tropics than in the temperate (Fig. 1b) due to	
Higher speciation rates	
1.	Genetic drift in small populations accelerates evolutionary rates (Fedorov 1966)
2.	Climatic variation results in higher speciation at lower latitudes (Haffer 1969; Dynesius & Jansson 2000)
3.	Higher likelihood of parapatric (Moritz <i>et al.</i> 2000) and sympatric speciation (Gentry 1989) in the tropics
4.	Larger area of the tropics provides more opportunities for isolation (Terborgh 1973; Rosenzweig 1995)
5.	Narrower physiological tolerances in tropical organisms reduce dispersal across unfavourable environments (Janzen 1967)
6.	Higher temperatures result in increased evolutionary speed (Rohde 1992; Allen <i>et al.</i> 2002)
7.	Stronger biotic interactions lead to greater specialization (Dobzhansky 1950) and faster speciation (Fischer 1960; Schemske 2002)
Lower extinction rates	
1.	Stability of tropical climates reduces the chance of extinction (Darwin 1859; Wallace 1878; Fischer 1960)
2.	Larger tropical area leads to higher population numbers, larger species ranges, and lower chance of extinction (Terborgh 1973; Rosenzweig 1995)

diversity gradient includes elements of regional differences in diversification rate and time for diversification. Stebbins (1974), in a discussion of the origin and diversification of flowering plants, asked whether tropical rain forests are a 'cradle' for the generation of new taxa, or a 'museum' for the preservation of existing diversity. Stebbins's favoured the idea that tropical rain and cloud forests '... are museums in which representatives of most families have been preserved because of low rates of extinction' (Stebbins 1974, p. 170). Although Stebbins's (1974) cradle/museum metaphor is useful in focusing attention on how speciation and extinction may lead to differences in net diversification rates between regions, the two processes are not mutually exclusive.

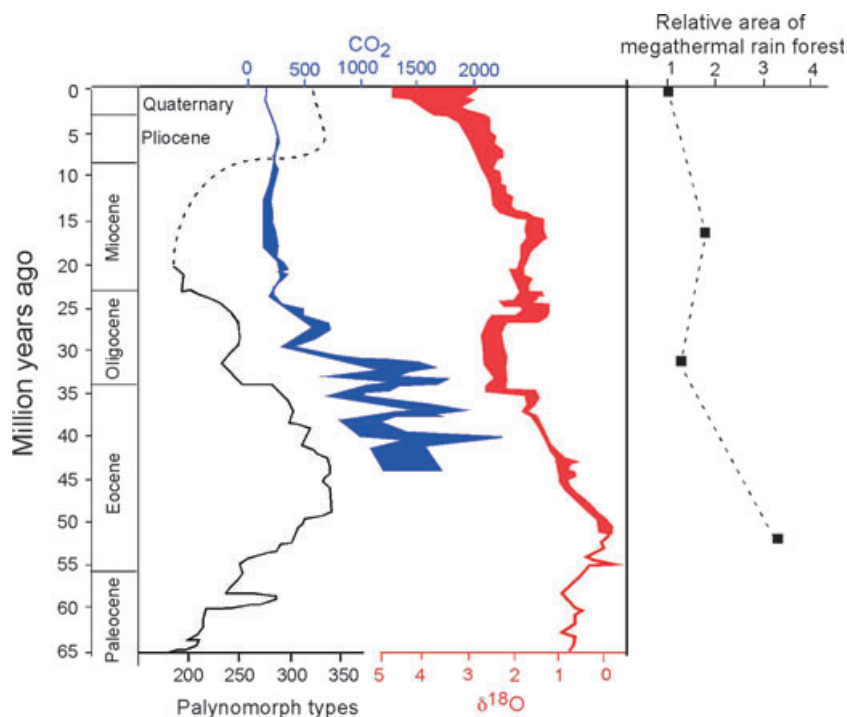
A number of authors have proposed that regional differences in speciation and/or extinction rates may be

unnecessary in generating the latitudinal diversity gradient, if tropical environments are simply older than temperate environments and if most groups originated in the tropics (e.g. Farrell *et al.* 1992; Ricklefs & Schluter 1993; Brown & Lomolino 1998; Futuyma 1998; Wiens & Donoghue 2004). We begin our review with this hypothesis and discuss the empirical evidence bearing on it. We then consider the question of latitudinal variation in diversification rates, discussing the hypothesized mechanisms that may drive regional differences in speciation and/or extinction rates, as well as the empirical evidence available. In our review, we have attempted to be as inclusive as possible in discussing the ideas and evidence for the evolution of the latitudinal diversity gradient. However, the literature on the topic is enormous and the diversity of opinion is great. We have focused on hypotheses that are, in our opinion, at the forefront of current study, and we acknowledge that other ideas may be relevant as well.

## THE TIME AND AREA HYPOTHESIS

The time and area hypothesis holds that the tropics have accumulated species over a longer period than temperate regions (Fig. 1c). This idea dates back to Wallace (1878), who argued that equatorial regions have suffered less from climatic changes, such as Pleistocene glaciations. As Wallace put it, 'in the one, evolution has had a fair chance; in the other it has had countless difficulties thrown in its way' (Wallace 1878, p. 123). While early statements of the time hypothesis focused on the impacts of Pleistocene glaciations and extinctions (e.g. Wallace 1878; Fischer 1960; Pianka 1966), we now know that the latitudinal diversity gradient has roots far deeper than the Pleistocene, extending back through the Mesozoic (180 Ma) and into the Palaeozoic (325 Ma) both on land and in the oceans (e.g. Ricklefs 1987; Crane & Lidgard 1989; Crame 2001; Leighton 2005). These ancient latitudinal diversity gradients, however, were probably less pronounced than seen today (Crame 2001); all evidence points to a substantial increase in the magnitude of latitudinal diversity gradients throughout the Cenozoic (65 Myr–present), when most of the modern components of the Earth's flora and fauna diversified.

Recent discussions of the time and area hypothesis have focused on the distribution of tropical environments during early portions of the Cenozoic. Climate history inferred from multiple proxies points to a pronounced warm period during the early Tertiary (Fig. 2), especially the mid Palaeocene to early Eocene (59–50 Ma), with warm (> 18 °C) surface waters extending to the arctic and a much reduced equator-to-pole temperature gradient (Sluijs *et al.* 2006). With this warmth, tropical floras existed as far north as London and the Midwest of North America. As these areas never lay within tropical latitudes, the term



**Figure 2** Cenozoic changes in palynomorph diversity in a lowland tropical setting (Jaramillo *et al.* 2006),  $\delta^{18}\text{O}$  as a proxy for temperature (Zachos *et al.* 2001; Pagani *et al.* 2005),  $\text{CO}_2$  concentrations (Zachos *et al.* 2001; Pagani *et al.* 2005), and megathermal rain forest extent (Morley 2000). The dotted line represents the inferred rebound of palynomorph diversity in the late Miocene or Pliocene that may even have exceeded modern diversity (Hoorn *et al.* 1995). Areas occupied by megathermal rain forest (relative to present rain forest area) are based on figures in Morley (2000), redrafted onto an equal area projection and then area of polygons summed.

'megathermal' best describes these tropical environments (Morley 2000). This thermal maximum was followed by a cooling trend beginning *c.* 45 Ma and continuing to the present, punctuated by occasional periods of warm climate such as occurred in the middle Miocene (Wolfe 1975, 1978; Behrensmeyer *et al.* 1992; Zachos *et al.* 2001). The glacial–interglacial cycles during the Pleistocene represent the latest climatic perturbations that disproportionately affected species and lineages living in high latitudes. Thus, tropical environments are older than temperate climates and therefore may have had a longer 'effective' time for diversity to accumulate (the 'time for speciation effect'; Stephens & Wiens 2003). In addition, the greater extent of tropical environments, especially during the early Cenozoic, could fuel higher diversification rates due to area effects on rates of speciation and extinction (Terborgh 1973; Rosenzweig 1995; Chown & Gaston 2000). Thus, the influence of time and area may be linked in the evolution of the latitudinal diversity gradient.

Fine & Ree (2006) examined the combined roles of time and area in generating the current latitudinal gradient in tree species diversity by comparing current tree species richness in three biomes (tropical, temperate and boreal) to the area of these three biomes integrated over three intervals of evolutionary time: the mid-Miocene (11 Ma) to the present, the mid-Oligocene (30 Ma) to the present and the early Eocene (55 Ma) to the present. They found no correlation between current tree richness and current biome area, but did find significant positive correlations between current

tree species richness and time-integrated biome areas for older time periods. Correlations were especially strong and consistent when using a time interval that included the Eocene tropical maximum. The authors concluded that biome area, integrated through evolutionary time, was the primary driver of the current latitudinal gradient in tree diversity. However, the presumed mechanisms by which area affects diversification rates (greater speciation and/or lower extinction) were not explored.

Additional evidence supporting the time hypothesis may be found in the phylogenetic relationships of temperate and tropical taxa. Many diverse lineages originated in tropical climates and temperate taxa are often nested within tropical clades, implying their origin from tropical groups with older evolutionary roots (Farrell *et al.* 1992; Farrell & Mitter 1993; Latham & Ricklefs 1993; Judd *et al.* 1994; Jablonski *et al.* 2006). Evidence from the palynological and macrofossil record indicates that flowering plants gradually spread from megathermal to cooler settings during the Cretaceous (130–65 Ma), replacing diverse gymnosperm-dominated floras (Crane & Lidgard 1989). For trees, most temperate taxa, including such major temperate clades as the Fagales (birches, beeches, oaks), are embedded within ancestrally tropical groups, again suggesting that tropical lineages have had more time to diversify (Ricklefs 2005). Wiens *et al.* (2006), in a detailed analysis of hylid frogs, found that the Hylidae originated in tropical South America and that current hylid species richness in a region is tightly correlated with the time since colonization.

The above analyses support the role of historical climates in generating the current latitudinal diversity gradient. However, while the Earth's environment was predominantly tropical up to  $\approx 45$  Ma, average species durations are in the range of 10–15 Myr (Stanley 1985). Thus, few of the species that comprise the current latitudinal diversity gradient likely arose during a time of maximum tropical extent. What then is the link between current species diversity and Cenozoic climates? Has species richness increased steadily through time, or has it followed an irregular course of advance and retreat? For example, the palynological record suggests that tropical plant species diversity of the Amazon lowlands decreased during late Eocene and early Miocene cooling, followed by a resurgence of species diversity in the late Miocene or Pliocene under different climatic conditions and mountain building (Fig. 2; Hoorn *et al.* 1995; Hooghiemstra & van der Hammen 1998; Jaramillo *et al.* 2006). Crame (2001, p. 182) notes that for many taxa '...the Cenozoic diversification event continued well past the prolonged late Palaeocene-middle Eocene interval of global warming. There was also a pronounced mid- to late Neogene phase of tropical diversification, and this coincided with both global cooling and the areal retraction of the tropics'. Thus, while the current wealth of tropical species may be strongly influenced by the greater time and area available to accumulate species, there also appear to be constraints on diversification within cooler and more arid environments, or on dispersal to temperate climates.

The idea that many clades originated in the tropics, but relatively few have made the transition to temperate climates, was proposed by Farrell *et al.* (1992), Latham & Ricklefs (1993), and others, and has recently been gathered under the 'tropical conservatism hypothesis' (Wiens & Donoghue 2004; Wiens *et al.* 2006). Wiens & Donoghue (2004) note that range limits in many taxa correspond to climatic isoclines, suggesting that certain traits such as freezing tolerance present significant barriers to colonizing the temperate zone (see Kleidon & Mooney 2000; Fine 2001; Wiens *et al.* 2006). Ricklefs & Renner (1994) note that half the families of flowering plants have no temperate representatives, even though some clades that have moved into the temperate zone have proliferated abundantly. Hawkins *et al.* (2006) also find evidence that the latitudinal gradient in New World bird species diversity is influenced by the differential extirpation of older, warm-adapted clades from temperate climates. Such ecophysiological barriers may present a filter through which only a fraction of some families or genera pass, and subsequent divergence is based on the few members that successfully pass through the filter.

While 'tropical conservatism' seems common among terrestrial organisms, the pattern is less evident in the ocean. The majority of molluscan families have distributions that encompass both tropical and temperate latitudes (Roy *et al.* 1996), and data from the fossil record show that most

marine invertebrate taxa that originate in the tropics subsequently expand their ranges into higher latitudes without losing their tropical presence (Jablonski 1993; Jablonski *et al.* 2006). This suggests that the degree of phylogenetic constraint on latitudinal patterns of speciation may differ between the land and the sea, or between taxonomic groups.

Species age distributions are another potential source of evidence relevant to the time hypothesis. If higher diversity in the tropics is primarily due to accumulation over a longer time, species at lower latitudes should be older on average relative to species in temperate and polar areas. Alternatively, if the tropics have higher speciation rates as well as a longer history, the tropics should have a greater variance in species ages than higher latitudes. Recent studies favour the latter hypothesis. Comparisons of species age distributions based on molecular phylogenies of bats (Stevens 2006) and birds (Weir & Schluter 2006), and on the fossil ages of genera of marine bivalves (Jablonski *et al.* 2006) and mammalian families (Stehli *et al.* 1969) show greater variance in taxon age in tropical than extratropical regions. Jablonski *et al.* (2006) also found that marine bivalves not only have more originations per unit time in the tropics (over the past 11 Myr), but that taxa also tend to persist there while expanding their ranges to higher latitudes. As a consequence, the older age of polar genera does not reflect *in situ* origination–extinction, but instead results from an accumulation of taxa that evolved in lower latitudes and then dispersed poleward (see also Goldberg *et al.* 2005). All of this suggests that while tropical habitats have indeed existed longer than temperate ones, the longer duration by itself does not explain the latitudinal diversity gradient; instead the key lies in understanding why tropical regions may diversify at higher rates than temperate regions. We explore this question below.

## MECHANISMS FOR LATITUDINAL VARIATION IN DIVERSIFICATION RATES

Many hypotheses have been put forth to explain why rates of speciation might differ between temperate and tropical regions, whereas fewer hypotheses focus on rates of extinction (Table 1). We provide an overview of these hypotheses below, discussing in greater length those hypotheses which are relatively new and/or are the primary subjects of active research.

### Genetic drift

Fedorov (1966) proposed that low average population density and consequently enhanced genetic drift in the tropics might contribute to rapid speciation. This mechanism requires that communities are already diverse, with

many rare species, and therefore cannot explain the origins of diversity (Schemske 2002), although it may contribute to rates of speciation once communities have diversified. Fedorov's conjecture has received little empirical investigation, but a possible first step would be to compare the genetically effective population sizes of representative temperate and tropical groups within a phylogenetic context to test the hypothesis that greater genetic drift in the tropics promotes higher rates of diversification.

### **Climate change**

Periodic change in the Earth's orbit and axis of rotation cause marked climatic changes on the time scale of 10–100 kyr – Milankovitch cycles. Dynesius & Jansson (2000) noted that the magnitude of Milankovitch cycles is greater at high latitudes and proposed that these orbitally driven climate changes would favour species with strong dispersal ability, whose ranges would shift to follow favourable conditions. Greater vagility could in turn reduce speciation rates in temperate regions by favouring more generalized adaptations and by increasing gene flow among populations, and this could contribute to the origin of the latitudinal diversity gradient (Dynesius & Jansson 2000). There are no direct empirical tests of this hypothesis, and it is unclear how one would distinguish climatic oscillations as a cause of latitudinal differences in speciation rates from other proposed mechanisms. In addition, the magnitude of climatic oscillations was greater in the Quaternary than in previous periods (Dynesius & Jansson 2000), yet the latitudinal diversity gradient was established long before the Quaternary. Milankovitch oscillations and increased vagility in species ranges at higher latitudes may also affect extinction rates, although the net outcome of these effects is unclear. Extinction rates are expected to be higher at high latitudes due to climatic variation, but selection for larger species ranges may decrease the probability of extinction (Dynesius & Jansson 2000).

Haffer (1969) also proposed that climatic changes associated with Pleistocene glaciation facilitated speciation at low latitudes by contracting tropical forest into refuges isolated by intervening dry habitats. These Pleistocene events are too recent to account for a diversity gradient that has persisted for > 100 Myr (Crame 2001), but they could contribute to current diversity patterns. However, palynological data casts doubt on Amazonian Pleistocene aridity (e.g. Colinvaux *et al.* 1996), and molecular phylogenetic data (e.g. Moritz *et al.* 2000) show no evidence for a concentration of Pleistocene speciation.

### **Mechanisms of speciation**

There is limited discussion of whether the mechanisms of speciation might differ with latitude. Moritz *et al.* (2000)

considered local processes that could promote diversification in rain forest faunas, including allopatric models of reduced gene flow caused by Amazonian river barriers and parapatric models of divergent selection across strong environmental gradients. They find some support for both models, and suggest that the latter mechanism in particular merits further research in light of the observation that tropical hybrid zones are often associated with ecotones. Nevertheless, latitudinal comparisons of the frequency of parapatric speciation are needed to determine if this mechanism might contribute to the biodiversity gradient.

Gentry (1989, p. 126) suggested that 'explosive and essentially sympatric speciation' has played an important role in the production of high species richness in the Neotropics, although his description of sympatric speciation is more akin to founder effect speciation on a microgeographical scale than to classical sympatric speciation. To date, there are few, well-supported examples of sympatric speciation (Coyne & Orr 2004; but see Barluenga *et al.* 2006; Savolainen *et al.* 2006 for possibilities), and it is impossible to assess whether latitudinal differences in speciation rates are due in part to latitudinal differences in the likelihood of sympatric speciation. Phytophagous insects might provide an interesting system for further study, as Berlocher & Feder (2002) suggest that sympatric speciation may play an important role in generating the extraordinary diversity of this group.

### **Geographical area**

Larger areas are predicted to have higher speciation rates and lower extinction rates and this may lead to differences in diversification rates between temperate and tropical regions (Terborgh 1973; Rosenzweig 1995). Area is expected to positively affect speciation rates if larger areas support larger species ranges, and if a large range is more likely to expose species to greater ecological heterogeneity and/or become fractured by geological barriers (Rosenzweig 1995). As area increases, the probability of extinction also may decline due to an increase in average population size and an increase in species range. However, as Chown & Gaston (2000) note, this simple argument for the influence of area on the evolution of the latitudinal diversity gradient ignores the fact that as species diversity increases, population sizes and species ranges may decrease.

The tropics encompass most of the Earth's current continental surface (Terborgh 1973) and this observation has been used to support the area hypothesis for the evolution of the latitudinal diversity gradient (see also Rosenzweig 1995). However, as Fine & Ree (2006) note, tropical and extratropical regions have varied in area through evolutionary time; thus, any tests of the area hypothesis must take into account the correlation between

age and area. Further, speciation rates need not increase monotonically with range size (Chown & Gaston 2000). Species with large ranges may have high dispersal ability and broad environmental tolerances (Jablonski & Roy 2003), attributes which could reduce the likelihood of speciation by facilitating gene flow. Indeed, gastropod genera from the late Cretaceous exhibit a strong negative correlation between speciation rate and range size (Jablonski & Roy 2003). Future evaluation of the area hypothesis will require research to partition the historical relationship between area and age (Fine & Ree 2006), examine latitudinal patterns in range size prior and during the diversification of tropical regions, and evaluate the diversification rates of lineages that differ in geographical range size.

### Physiological tolerances and dispersal limitation

Janzen (1967) proposed that species in lowland tropical environments experience a narrower range of temperature than those in temperate regions and that this should result in the evolution of greater physiological specialization and reduced opportunity for dispersal across unfavourable climatic regions (i.e. why mountain passes are 'higher' in the tropics). Although Janzen (1967) stated that his hypothesis was not an attempt to explain the evolution of tropical species diversity, the mechanism he describes could be generalized to any case of local adaptation along strong environmental gradients. Indeed, Janzen has since suggested that it might contribute to the latitudinal diversity gradient (Janzen, pers. comm.). Ghalambor *et al.* (2006) found support for many aspects of Janzen's model, including increases in thermal tolerance ranges and acclimation capacities of species with increases in latitude. However, a number of predictions, including whether the dispersal of tropical species up and down mountains should be less than temperate species, have never been directly tested. Further study is needed to determine if the geographical scale of physiological adaptation is narrower in tropical than temperate organisms, and if so, how this might contribute to latitudinal variation in speciation rates.

### Evolutionary speed

Rohde (1978, 1992) proposed that biodiversity peaks at the equator due to the kinetic effects of environmental temperature on rates of biological processes. Mechanistically, this 'evolutionary speed' hypothesis links biodiversity to temperature through its effects on mutation rates and generation times of individuals which, in turn, lead to faster rates of genetic divergence among populations, and higher rates of speciation in communities. At the molecular level, there is evidence that rates of molecular evolution increase with temperature. Martin & Palumbi (1993) found that rates

of nucleotide substitution are higher for warmer-bodied endotherms than for ectothermic animals of similar size, and decline with increasing body size. They proposed that this could be due to generation time (through its effects on rates of germline replication), or metabolic rate (through its effects on rates of mutagenic free-radical production).

Using mtDNA data, Gillooly *et al.* (2005) demonstrated that differences in evolutionary rates between endotherms and ectotherms agree with predictions based on differences in body temperature (after controlling for body size). Allen *et al.* (2006) also found that, after controlling for body size, rates of nuclear DNA evolution in planktonic foraminifera increased *c.* 15-fold from arctic ocean waters (*c.* 0 °C) to tropical waters (*c.* 30 °C), as predicted by Gillooly *et al.*'s (2005) model. However, the role of body size in molecular evolution has recently been called into question by the study of Thomas *et al.* (2006), which found no correlation between body size and substitution rates in invertebrates, although this study did not control for temperature. Other studies have found evidence of a positive association between temperature and the rate of molecular evolution in plants (Wright *et al.* 2003, 2006; Davies *et al.* 2004), but not in birds (Bromham & Cardillo 2003), which is expected given that temperature should not directly affect metabolic rate in endotherms. Thus, there is some evidence of a positive association between temperature and rate of molecular evolution in ectotherms, although more work is clearly needed.

Allen *et al.* (2006) formulated a model that links latitudinal variation in speciation rates of ectotherms to two variables – environmental temperature and the abundance of individuals – through their combined effects on total rates of genetic divergence among populations comprising communities. As predicted by their model, speciation rates for planktonic foraminifera increase exponentially with ocean temperature in the same way as metabolic rate, but only after controlling for latitudinal variation in the total abundance of foraminifera by expressing speciation on a *per capita* basis (species individual<sup>-1</sup> Myr<sup>-1</sup>).

Several formidable challenges to the evolutionary speed hypothesis remain. First, the evolutionary speed hypothesis applies only to ectotherms, but endotherms also exhibit pronounced latitudinal diversity gradients (Hillebrand 2004). Allen *et al.* (2002) discuss the importance of community abundance, and how it may contribute to diversity gradients in endotherms and ectotherms. Second, the association between temperature and substitution rates predicted by Gillooly *et al.* (2005) is based in part on Kimura's (1968) neutral theory, which Gillespie (1991) argued was inconsistent with a large body of data on molecular evolution. Finally, the evolutionary speed hypothesis does not yet adequately specify how temperature and speciation rates are linked (Evans & Gaston 2005). Allen *et al.* (2006) derived

their model assuming that the rate of production of new alleles that contribute to the evolution of reproductive isolation by natural selection is controlled by the mutation rate. Given that essentially any model of molecular evolution will predict increased rates of substitution as mutation rates rise (Gillespie 1991), this assumption is consistent with other theoretical work indicating that any mechanism that accelerates the accumulation of genetic differences between taxa will accelerate the accumulation of intrinsic postzygotic isolation, all else being equal (Orr & Turelli 2001). However, as of yet, there is little direct evidence of an association between molecular and phenotypic rates of change (Bromham *et al.* 2002).

### Biotic interactions

Wallace (1878), Dobzhansky (1950), Fischer (1960) and MacArthur (1969) all proposed that biotic interactions have contributed to high species richness in the tropics. Dobzhansky (1950) proposed that relatively benign, stable tropical climates favoured adaptations to biotic interactions and viewed natural selection in the tropics as 'a creative process that may lead to emergence of new modes of life and of more advanced types of organization' (Dobzhansky 1950, p. 221).

If geographical isolation is typically the first step in the origin of species (Coyne & Orr 2004), then differences in the pattern of speciation in tropical and temperate communities may result from latitudinal differences in the relative importance of biotic interactions and coevolution (Dobzhansky 1950; Schemske 2002). Schemske (2002) hypothesized that abiotic interactions play a greater role in the adaptation of temperate populations than do biotic interactions. Even though temperate regions may experience considerable temporal variation in abiotic factors, and hence the phenotypic optimum may change somewhat from year to year, adaptation to climatic fluctuations does not cause a change in climate. As a result, adaptation in temperate regions is towards a relatively fixed target, and the rates of phenotypic and genetic divergence between isolated populations may decline as populations approach their local optima. In contrast, Schemske (2002) suggested that natural selection in tropical populations is mainly due to geographical differences in the pattern and magnitude of species interactions, and could thus promote the rapid evolution and coevolution of adaptations, and ultimately speciation. Newly isolated tropical populations are forced into new coevolutionary pathways and hence species evolve along new trajectories. In this scenario, the optimum phenotype in the tropics is a moving target, as interacting species constantly adapt to the shifting selective landscape (Schemske 2002). Tropical environments are thus an example of Van Valen's Red Queen hypothesis (Van Valen 1973),

where coevolution continually drives phenotypic change (Stenseth 1984).

A greater importance of biotic interactions may simply increase the number of niche dimensions along which species can differentiate (e.g. Schemske 2002; Vermeij 2005). Because each new niche axis results in a geometric increase in the number of possible niches (MacArthur 1969), a greater importance of biotic interactions could greatly increase opportunities for differentiation and thus speciation. In addition, with increasing tropical species richness, mean species density decreases, so there could be greater stochasticity in the species composition of nascent communities. Variation in local community composition may favour different adaptations in each isolated population as species coevolve locally, which would generate a much greater variety of local adaptations and a much greater potential for speciation (Thompson 1994; Schemske 2002).

Are biotic interactions stronger in the tropics than in the temperate zone? Studies of nest predation in birds suggest that tropical species experience greater predation rates (Kulesza 1990; Robinson *et al.* 2000) when compared with similar data from temperate zones (Conway & Martin 2000). Coley & Barone (1996) find significantly higher rates of herbivory on trees in the tropics, despite higher levels of defense in tropical plants. Jeanne (1979) measured ant predation of wasp larvae along a latitudinal gradient extending from New Hampshire (USA) to Brazil, and found greater risk of predation at lower latitudes. Bertness *et al.* (1981) showed experimentally that the incidence of shell crushing of marine gastropods was higher in a tropical than a temperate area. Parasitoid attack shows no relationship with latitude (Stireman *et al.* 2005), and ichneumonid parasitoids show a reverse gradient, i.e. lower diversity in the tropics (Sime & Brower 1998).

There are caveats to be considered in evaluating such studies. First, the current species richness in the tropics might confound interpretation of the historical strength of biotic interactions. Second, a critical element of the biotic interactions hypothesis is that species interactions are not simply stronger in the tropics; they must also comprise a greater fraction of the total selection. To address this question would require detailed studies that estimate the selective impacts of a variety of abiotic and biotic factors along a latitudinal gradient.

The biotic interactions hypothesis predicts that traits related to biotic interactions should evolve faster in tropical than temperate taxa. To test this hypothesis, one could investigate the extent of trait divergence between temperate and tropical taxa as a function of genetic distance, or estimate the rate of trait evolution using phylogenies (Collar *et al.* 2005). Dodd *et al.* (1999) used a phylogenetic approach to examine trait evolution and diversification in flowering plants, and concluded that animal pollination was associated



with higher diversity at the family level, but biotic dispersal was not. These results supported the findings of Ricklefs & Renner (1994), but mode of pollination is just one of many factors that influence the diversification of plant families (Ricklefs & Renner 2000). In a study of the Neotropical plant genus *Costus*, Kay *et al.* (2005) found that approximately a fifth of speciation events involved a shift to hummingbird pollination – a high rate compared with other plant lineages that have been studied.

The biotic interactions hypothesis is virtually unexplored from either a theoretical or an empirical perspective. Studies are needed to determine if the magnitude of biotic interactions varies with latitude, if biotic interactions contribute more to the evolution of adaptations in tropical than temperate regions, and if a greater role for biotic interactions in tropical regions can facilitate the coevolutionary diversification of populations and communities.

## EXAMINING LATITUDINAL VARIATION IN DIVERSIFICATION RATES

Are diversification rates higher in the tropics than outside the tropics, and how do rates of speciation and extinction contribute to this pattern? We examine this question below, drawing on evidence from palaeontological and phylogenetic studies, and as well as alternative approaches such as comparisons of rates of evolution of reproductive isolation (Coyne & Orr 1989, 1997) and incipient speciation.

### Palaeontological studies

A number of palaeontological studies have examined how diversification rates vary with latitude, and most support the hypothesis that net diversification rates (origination–extinction) are higher in the tropics. For corals, bivalves, benthic and planktonic foraminifera and some mammals, average age of genera and families decreases with decreasing latitude, suggesting that the tropics have more geologically young taxa (Stehli *et al.* 1969; Stehli & Wells 1971; Durazzi & Stehli 1972; Flessa & Jablonski 1996; but see Van Valen 1969). Similarly, the geologically youngest families of extant marine bivalves tend to have the steepest latitudinal gradient in species richness (Crame 2000, 2002), consistent with the idea that net diversification rates at the species level are higher in the tropics. Other evidence for high tropical diversification rates at the species level comes from benthic foraminifera, which have exhibited a higher rate of increase in within-habitat species richness over the last 10 Myr in the tropics than in the temperate zone (Buzas *et al.* 2002). While these results show that tropical regions tend to have higher net diversification rates, they cannot ascertain whether this differential reflects higher origination rates, lower extinction rates, or both. Areas with high net diversification rates are

likely to have higher origination rates, but high latitude regions where diversification rates are low may have experienced either high or low extinction rates (Crame 2002; Jablonski *et al.* 2006).

In addition to revealing a latitudinal gradient in diversification rates, palaeontological data provide direct evidence for higher origination rates in the tropics. Individual orders of marine invertebrates tend to preferentially originate in the tropics (Jablonski 1993), as do genera of marine bivalves over the last 11 Myr (Jablonski *et al.* 2006). Among marine planktonic organisms, species of fossil foraminifera tend to originate at lower latitudes (Allen *et al.* 2006), but nanoplankton and radiolarians apparently do not (Allen & Gillooly 2006), although the rate of first appearance is positively correlated with species richness in all three groups (Allen & Gillooly 2006). Similarly, ‘per capita speciation rate’ (the first occurrences of species in the geological record expressed as a function of present-day species abundance) of planktonic foraminifera appears to be higher in warmer waters (Allen *et al.* 2006).

At present, we know relatively little about regional differences in extinction rates. Marine bivalve genera and subgenera show higher extinction rates in polar regions compared with lower latitudes during the Cenozoic (Goldberg *et al.* 2005; Jablonski *et al.* 2006). In contrast, other studies of marine molluscs and foraminifera have found little evidence for latitudinal differences in extinction rates (Stanley *et al.* 1980; Wei & Kennett 1983). Negative impacts of cooling climates on diversity at high latitudes have been documented during the late Tertiary for terrestrial plants (Sauer 1988; Latham & Ricklefs 1993; Svenning 2003). However, past episodes of climatic cooling that led to increased extinctions of marine ectotherms have often disproportionately affected warm water taxa (Clarke 1993; Roy & Pandolfi 2005). In general, robust estimates of how extinction rates vary with respect to latitude remain scarce for both terrestrial and marine organisms, and more analyses of extinction rates are sorely needed.

In addition to origination and extinction rates, broad-scale patterns of biodiversity depend on changes in geographical distributions over time. However, few studies have examined the role of past distributional changes in shaping the present-day latitudinal diversity gradient (Fine & Ree 2006). Most palaeontological as well as phylogenetic studies implicitly assume that the latitudinal diversity gradient reflects *in-situ* differences in origination and extinction rates (Cardillo 1999; Chown & Gaston 2000; Cardillo *et al.* 2005). However, this simplifying assumption is contradicted by data showing shifts in the geographical range limits of many taxa, both marine and terrestrial, in response to climatic changes (Valentine & Jablonski 1993; Roy *et al.* 2001; Jackson & Williams 2004; Roy & Pandolfi 2005; Coope 1995, 2004). Recently, Jablonski *et al.* (2006)

examined the combined effects of origination and extinction rates, plus shifts in taxon range limits, in a global analysis of marine bivalve genera over the past 11 Myr. Their work suggests an 'out of the tropics' model for the latitudinal diversity gradient, where taxa (genera and subgenera) preferentially originate in the tropics and expand towards the poles without losing their tropical presence.

In summary, palaeontological data for many taxonomic groups are consistent with the hypothesis that the latitudinal diversity gradient is a result of higher rates of diversification in the tropics compared with temperate and polar regions, and the available evidence suggests that this difference is due to higher origination rates and lower extinction rates in the tropics. In addition, taxa originating in the tropics tend to subsequently expand their geographical ranges into high latitudes without losing their tropical presence; such range expansions play an important role in determining the strength and nature of the present-day latitudinal diversity gradient (Goldberg *et al.* 2005; Jablonski *et al.* 2006). Despite these insights, the full potential of palaeontological data for understanding the evolutionary dynamics underlying the latitudinal diversity gradient has yet to be realized. Tropical fossil assemblages remain poorly sampled (Jablonski 1993; Jackson & Johnson 2001; Valentine *et al.* 2006) and the temperate bias in palaeontological data presents methodological challenges in comparing origination and extinction rates along latitudinal gradients. While the effects of such biases can be accounted for statistically, until the tropical fossil record is better sampled, the true magnitude of these differences will remain unknown, especially given the high endemism and the preponderance of rare taxa in the tropics.

### Phylogenetic studies

Phylogenies also provide important information for studying geographical variation in diversification rates. The earliest use of phylogenetic methods to test diversification hypotheses compared the species richness of sister clades that differ in the trait of interest. Because sister clades are, by definition, of equal age, differences in species richness reflect differences in net rates of diversification, and hypotheses about the influence of ecological, biogeographical, or other factors can be tested statistically if multiple pairs of sister clades can be identified that differ in these factors (Barracough *et al.* 1998). Three studies have used sister-clades whose members are primarily in lower vs. higher latitudes to evaluate the effect of latitude on diversification rates. Farrell & Mitter (1993) found no effect of latitude on diversification rates in herbivorous insects, whereas Cardillo (1999) found a significantly higher rate of diversification at lower latitudes in passerine birds and swallowtail butterflies. Davies *et al.* (2004) also found higher diversification rates in angiosperm sister taxa located at

lower latitudes, although energy was a better predictor than latitude.

Sister-group comparison is elegant in its simplicity and powerful in its ability to control for the non-independence of taxa and other confounding variables (Barracough *et al.* 1998), but the approach has significant limitations when applied to the latitudinal gradient (summarized in Cardillo *et al.* 2005; Ricklefs 2006). In particular, sister taxa tend to retain their ancestral ecological traits, including geography, which may result in low sample size and statistical power for latitudinal comparisons (e.g. the study of Farrell & Mitter 1993 had only five tropical-temperate sister-clade comparisons). 'Topological approaches' (Chan & Moore 2002), which use an extension of phylogenetically independent contrast analysis (Agapow & Isaac 2002; Isaac *et al.* 2003), use more of the information conveyed by trees and allow multiple potential correlates of diversity to be tested simultaneously. Using this approach, no correlation between latitude and diversification rate was found in agamid lizards (Stuart-Fox & Owens 2003) or a tribe of old-world monkeys (Böehm & Mayhew 2005). Bayesian techniques for identifying changes in diversification rates (Ree 2005) incorporate estimates of time between events (i.e. branch lengths) as well as topology. Applications of such new analytical techniques to the growing number of phylogenetic data sets may help evaluate the mixed evidence for latitudinal effects on diversification rates shown in sister group comparisons.

An alternative to the sister-clade approach is to compare diversification rates in clades whose ages are estimated by molecular methods. For example, Cardillo *et al.* (2005) and Ricklefs (2005, 2006) investigated latitudinal effects on diversification rates of birds using the DNA-DNA hybridization-based phylogeny of Sibley & Ahlquist (1990), supplemented with more recent molecular phylogenetic analyses. These studies found that clades at lower latitudes diversified faster than clades at higher latitude. Wiens *et al.* (2006), however, found no significant relationship between latitude and diversification rate in hylid frogs, although only two of the 11 clades examined had their distributional mid-points outside the tropics.

Phylogenetic approaches to studying latitudinal variation in diversification rates have several important caveats. For example, our knowledge of species diversity in many tropical clades is inadequate, and underestimating tropical diversity will underestimate the rate of diversification. Also, how to best define traits of interest (e.g. the geographical range of a clade) and how to best incorporate these traits into phylogenetic analyses is an outstanding problem (see Cardillo *et al.* 2005 and Ricklefs 2005 for discussion with regard to temperate/tropical comparisons). Finally, as noted earlier, differences in diversification rates may be driven by differences in speciation and/or extinction, and extracting

information about extinction rates from phylogenies is notoriously difficult (Paradis 2004).

Speciation and extinction rates can be estimated from phylogenies using a lineage through time-plot, LTT (Harvey *et al.* 1994; Nee *et al.* 1994a,b; Kubo & Iwasa 1995). In an LTT, as the earliest lineages accumulate, the slope of the relationship between  $\ln(\text{number of lineages})$  and time reflects the long-term net rate of diversification (i.e. speciation minus extinction). As the most recently produced lineages are added, however, few of these recent lineages will have had time to go extinct; therefore, the slope of the LTT during recent diversification should approximate the speciation rate. If we assume constancy in rates over time, extinction rate can be estimated as the difference between diversification rate and speciation rate. No studies have attempted to apply LTT plots to partition the contributions of speciation and extinction to differences in diversification rates across latitude, and indeed the assumption of rate constancy may be difficult to overcome. However, two recent studies have used LTT plots to estimate speciation rates in South American passerine birds (Ricklefs 2005; Weir 2006) and illustrate how this method might be applied to latitudinal comparisons. Recently, Weir & Schluter (2006) used a different approach to try to disentangle the roles of speciation and extinction in producing the latitudinal diversity gradient. Fitting rate constant birth–death models to the age distributions of recent ( $< 10$  Ma) sister species of New World birds and mammals, they found that rates of speciation and extinction were both higher at higher latitudes, and that net diversification (speciation minus extinction) followed the same trend as shown by Cardillo *et al.* (2005) and Ricklefs (2006) – net diversification was faster near the equator than near the poles. If this pattern is representative of past millennia, then Weir & Schluter's (2006) findings suggest a significant role for extinction in generating the latitudinal diversity gradient.

### Evolution of reproductive isolation

In accord with the biological species concept (Mayr 1942), speciation occurs when populations evolve as independent gene pools due to the accumulation of sufficient reproductive isolating barriers. Evolutionary biologists often separate those forms of reproductive isolation that act before fertilization (prezygotic barriers) from those that operate after fertilization (postzygotic barriers) (Coyne & Orr 2004). Several prezygotic barriers may arise as a direct consequence of ecological conditions experienced by allopatric populations such as isolation involving differences in habitat, timing of reproduction or pollinators. Other forms of prezygotic isolation such as mating isolation or gametic isolation are not necessarily as tightly linked to ecology,

though may still arise as a pleiotropic by-product of ecological divergence. Extrinsic postzygotic isolation is directly related to ecology, as it arises when hybrids are less fit than their parents due to ecological maladaptation.

Intrinsic postzygotic isolation, in contrast, results from fixation of alternate negatively interacting alleles in separated populations, often referred to as Dobzhansky–Muller incompatibilities (DMIs) (Dobzhansky 1937; Muller 1940; Orr & Turelli 2001). These genetic incompatibilities can be, but are not necessarily linked to ecology. Divergent selection due to ecological conditions experienced by allopatric populations could potentially increase the rate at which DMIs are fixed (Schluter 2000). The few times these loci have been identified, a strong signature of selection was found (Barbash *et al.* 2003; Presgraves *et al.* 2003; Brideau *et al.* 2006). However, DMIs can also be fixed by non-ecological mechanisms that involve selection. For example, a new mutation may be favoured because it increases male fertilization success, and this may lead to reproductive incompatibilities if different mutations spread in different populations (Rice 1998). Similarly, intragenomic conflicts will lead to DMIs that are likely to be non-ecological (Burt & Trivers 2006).

Evolutionary biologists interested in the patterns and process of speciation have benefited greatly from the employment of the comparative method in examining reproductive isolation between pairs of taxa. The method, as first applied by Coyne & Orr (1989, 1997), consists of measuring components of reproductive isolation between species pairs, and regressing the strength of isolation on genetic distance. The slope of the regression indicates the rate at which components of reproductive isolation evolve. Coyne and Orr's (1989, 1997) pioneering work in *Drosophila* demonstrated that mating isolation and intrinsic postzygotic isolation both increased with genetic distance. Comparative studies of isolation have now been conducted in other taxa (e.g. Presgraves 2002; Price & Bouvier 2002; Mendelson 2003; Moyle *et al.* 2004; Bolnick & Near 2005), although these have focused almost exclusively on intrinsic postzygotic reproductive isolation.

Coyne and Orr's method could be employed to investigate how divergence patterns differ between tropical and temperate groups. For example, the biotic interactions hypothesis proposes that speciation rates are higher in the tropics because isolated populations are more likely to experience divergent selection linked to coevolving biotic pressures than their temperate counterparts. Under this hypothesis, an analysis based on the approach of Coyne and Orr would show that reproductive isolation directly linked to ecology, including some forms of prezygotic isolation and extrinsic postzygotic isolation, would evolve at a faster rate in the tropics relative to temperate zones. This approach offers some advantages over phylogenetic tree-based

methods for investigating the relationship between speciation rates and latitude (though a phylogeny is still needed to perform the analysis). As discussed above, there are significant difficulties in distinguishing speciation from extinction as the ultimate source of differences in diversification determined by tree-based methods. Because the Coyne and Orr method only examines the rate at which reproductive isolation evolves between extant taxa, it allows a direct comparison of components of speciation between tropical and temperate groups without the confounding effects of extinction.

The ideal data for utilizing this method to study the latitudinal gradient would be detailed comparative studies of reproductive isolation for many taxa (with both pre- and postzygotic isolation), including both temperate and tropical species pairs. These data do not currently exist. The comparative studies published to date either suffer the drawback of considering only intrinsic postzygotic isolation (Presgraves 2002; Price & Bouvier 2002) or examine only temperate species (Mendelson 2003; Moyle *et al.* 2004; Bolnick & Near 2005). Only Coyne and Orr's (1989, 1997) *Drosophila* study includes both pre- and postzygotic isolation and includes tropical and temperate comparisons. Their measure of prezygotic isolation was the relative preference for conspecific over heterospecific matings under experimental laboratory conditions, and postzygotic isolation consisted of intrinsic inviability and sterility. In a preliminary examination of isolation between the tropical *D. willistoni* species group and the temperate *D. virilis* group within this data set, it appears that both the pre- and postzygotic forms of isolation studied by Coyne and Orr evolve faster in the tropical group (J. Sobel, unpublished data). The *Drosophila* results illustrate the potential utility of this method and highlight the need for additional studies on the nature of isolation between species, especially in tropical systems.

### Incipient speciation

The magnitude of genetic divergence among populations within a species may be considered an indicator of incipient speciation (Avice 2000), as total reproductive isolation increases with genetic distance (Coyne & Orr 1989, 1997). If speciation rates increase towards the equator, then the divergence among populations of current biological species should parallel the latitudinal gradient in species richness. In a review of genetic data for vertebrates, Martin & McKay (2004) confirmed this hypothesis, although it should be noted that few of the species included in their study were tropical inhabitants. They proposed that range shifts and gene flow resulting from repeated glaciation reduced speciation rates in temperate regions. However, the time scale of post-Pleistocene range expansions (*c.* 10 kyr) is much shorter than the time-scale of most speciation. Hence,

is it not clear if current levels of population differentiation provide a reliable indicator of speciation rates over the past 10–20 Myr. In a review of the geographical distribution of intraspecific variation, Martin & Tewksbury (in review) found that for those species with five or more subspecies, the mean number of subspecies was greater at lower latitudes. Bernatchez & Wilson (1998) also found that the degree of differentiation among fish populations increased with decreasing latitude.

The incipient speciation approach assumes that populations will eventually reach species status, and requires that the metrics and criteria used for comparing different taxa are comparable. However, it may have an advantage over phylogenetic approaches such as lineage through time plots, because it requires no assumption about rates of extinction, and is complementary to studies of reproductive isolation as a function of genetic distance conducted at the level of populations and species.

### CONCLUSIONS

For 200 years naturalists have pondered the latitudinal diversity gradient and more than half a century has passed since Dobzhansky (1950) postulated how such geographical variation in diversity may have evolved. Current evidence points to the tropics as both a museum and a cradle (*sensu* Stebbins 1974); taxa not only preferentially originate in the tropics but tend to also persist there longer (Jablonski *et al.* 2006; McKenna & Farrell 2006). Tropical environments are older and were more wide-spread than temperate climates for much of the Earth's history, and for many lineages, a tropical centre of origin is strongly supported. This historical pattern provides an explanation for the latitudinal gradient in diversity at higher taxonomic levels (e.g. orders, families, genera). There is also accumulating evidence for higher rates of diversification in the tropics compared with the temperate zone in many taxa, and this appears to be due, in part, to greater tropical speciation. This evidence is based on both palaeontological and phylogenetic studies, and exists for marine and terrestrial groups, plants and animals, vertebrates and invertebrates. However, we know little about latitudinal variation in extinction rates and future work evaluating the relative contributions of speciation and extinction to patterns of diversification across latitude is clearly needed.

There are many hypothesized mechanisms for latitudinal variation in diversification rates (Table 1) and for most we lack the data to evaluate their significance. Janzen's (1967) hypothesis, for example, is almost 40 years old, yet we still do not know whether selection for narrower physiological tolerances and species ranges in the tropics contributes to greater opportunities for isolation and speciation. Other hypotheses (e.g. 'evolutionary speed', 'biotic interactions')

are in their initial stages of development and testing. Early evidence points to more rapid molecular evolution in some tropical taxa compared with temperate taxa, but a general link between substitution rates and speciation rates remains to be shown. Likewise, biotic interactions appear stronger in the tropics, but do they facilitate speciation? Research on both questions is sorely needed.

Although we can reject few of the hypotheses in Table 1, we are optimistic about the future. We are in a new era of inquiry into the evolution of the latitudinal diversity gradient, one that is being facilitated by rapid advances in molecular biology, phylogenetics, palaeontology and biogeography, as well as investigations into the evolutionary mechanisms contributing to other spatial patterns (e.g. altitudinal gradients in diversity). These new tools, coupled with the timeless observations of naturalists and field biologists, are providing the keys to understanding how the Earth's predominant diversity pattern arose.

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## REFERENCES

- Agapow, P.-M. & Isaac, N.J.B. (2002). MacroCAIC: revealing correlates of species richness by comparative analysis. *Div. Distrib.*, 8, 41–43.
- Allen, A.P. & Gillooly, J.F. (2006). Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.*, 9, 947–954.
- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.
- Allen, A.P., Gillooly, J.F., Savage, V.M. & Brown, J.H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl. Acad. Sci. USA*, 103, 9130–9135.
- Avise, J. (2000). *Phylogeography*. Harvard University Press, Cambridge, MA.
- Barbash, D.A., Siino, D.F., Tarone, A.M. & Roote, J. (2003). A rapidly evolving MYB-related protein causes species isolation in *Drosophila*. *Proc. Natl. Acad. Sci. USA*, 100, 5302–5307.
- Barluenga, M., Stolting, K.N., Salzburger, W., Muschick, M. & Meyer, A. (2006). Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature*, 439, 719–723.
- Barraclough, T.G., Nee, S. & Harvey, P.A. (1998). Sister-group analysis in identifying correlates of diversification. *Evol. Ecol.*, 12, 751–754.
- Behrensmeyer, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D. & Wing, S.L. (1992). *Terrestrial Ecosystems Through Time. Evolutionary Paleocology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago, IL.
- Berlocher, S.H. & Feder, J.L. (2002). Sympatric speciation in phytophagous insects: moving beyond controversy. *Annu. Rev. Entomol.*, 47, 773–815.
- Bernatchez, L. & Wilson, C.C. (1998). Comparative phylogeography of Nearctic and Palearctic fishes. *Mol. Ecol.*, 7, 431–452.
- Bertness, M.D., Garrity, S.D. & Levings, S.C. (1981). Predation pressure and gastropod foraging: a tropical-temperate comparison. *Ecology*, 35, 995–1007.
- Böehm, M. & Mayhew, P.J. (2005). Historical biogeography and the evolution of the latitudinal gradient of species richness in the Papionini (Primates: Cercopithecidae). *Biol. J. Linn. Soc. Lond.*, 85, 235–246.
- Bolnick, D.I. & Near, T.J. (2005). Tempo of hybrid inviability in centrarchid fishes (Teleostei: Centrarchidae). *Evolution*, 59, 1754–1767.
- Brideau, N.J., Flores, H.A., Wang, J., Maheshwari, S., Wang, X. & Barbash, D.A. (2006). Two Dobzhansky-Muller genes interact to cause hybrid lethality in *Drosophila*. *Science*, 314, 1292–1295.
- Bromham, L. & Cardillo, M. (2003). Testing the link between the latitudinal gradient in species richness and rates of molecular evolution. *J. Evol. Biol.*, 16, 200–207.
- Bromham, L., Woolfit, M., Lee, M.S.Y. & Rambaut, A. (2002). Testing the relationship between morphological and molecular rates of change along phylogenies. *Evolution*, 56, 1921–1930.
- Brown, J.H. & Lomolino, M.V. (1998). *Biogeography*, 2nd edn. Sinauer Associates, Sunderland, MA, USA.
- Burt, A. & Trivers, R. (2006). *Genes in Conflict: the Biology of Selfish Genetic Elements*. Harvard University Press, Cambridge, MA.
- Buzas, M.A., Collins, L.S. & Culver, S.J. (2002). Latitudinal differences in biodiversity caused by higher tropical rate of increase. *Proc. Natl. Acad. Sci. USA*, 99, 7841–7843.
- Cardillo, M. (1999). Latitude and rates of diversification in birds and butterflies. *Proc. R. Soc. Lond. B*, 266, 1221–1225.
- Cardillo, M., Orme, C.D.L. & Owens, I.P.F. (2005). Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology*, 86, 2278–2287.
- Chan, K.M.A. & Moore, B.R. (2002). Whole-Tree methods for detecting differential diversification rates. *Syst. Biol.*, 51, 855–865.
- Chown, S.L. & Gaston, K.J. (2000). Areas, cradles and museums: the latitudinal gradient in species richness. *Trends Ecol. Evol.*, 15, 311–315.
- Clarke, A. (1993). Temperature and extinction in the sea – a physiologists view. *Paleobiology*, 19, 499–518.
- Coley, P.D. & Barone, J.A. (1996). Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.*, 27, 305–335.
- Colinvaux, P., DeOliveira, P., Moreno, J., Miller, M. & Bush, M. (1996). A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science*, 274, 85–88.
- Collar, D.C., Near, T.J. & Wainwright, P.C. (2005). Comparative analysis of morphological diversity: does disparity accumulate at the same rate in two lineages of centrarchid fishes? *Evolution*, 59, 1783–1794.

- Conway, C.J. & Martin, T.E. (2000). Evolution of passerine incubation behavior: influence of food, temperature, and nest predation. *Evolution*, 54, 670–685.
- Coope, G.R. (1995). Insect faunas in Ice age environments: why so little extinction? In: *Extinction rates* (ed Lawton, J.H. & May, R.M.), pp. 55–74. Oxford University Press.
- Coope, G.R. (2004). Several million years of stability among insect species because of, or in spite of, Ice Age climatic instability. *Philos. Trans. R. Soc. Lond. B*, 359, 209–214.
- Coyne, J.A. & Orr, H.A. (1989). Patterns of speciation in *Drosophila*. *Evolution*, 43, 362–381.
- Coyne, J.A. & Orr, H.A. (1997). Patterns of speciation in *Drosophila* revisited. *Evolution*, 51, 295–303.
- Coyne, J.A. & Orr, H.A. (2004). *Speciation*. Sinauer Associates, Sunderland, MA.
- Crame, J.A. (2000). Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of Recent bivalve faunas. *Paleobiology*, 26, 188–214.
- Crame, J.A. (2001). Taxonomic diversity gradients through geological time. *Div. Distrib.*, 7, 175–189.
- Crame, J.A. (2002). Evolution of taxonomic diversity gradients in the marine realm: a comparison of late Jurassic and Recent bivalve faunas. *Paleobiology*, 28, 184–207.
- Crane, P.R. & Lidgard, S. (1989). Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science*, 246, 675–678.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A. *et al.* (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.*, 7, 1121–1134.
- Darwin, C.R. (1859). *The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London, UK.
- Davies, T.J., Savolainen, V., Chase, M.W., Moat, J. & Barraclough, T.G. (2004). Environmental energy and evolutionary rates in flowering plants. *Proc. R. Soc. Lond. B*, 271, 2195–2200.
- Dobzhansky, T. (1937). *Genetics and the Origin of Species*. Columbia University Press, New York, NY.
- Dobzhansky, T. (1950). Evolution in the tropics. *Am. Sci.*, 38, 209–221.
- Dodd, M.E., Silvertown, J. & Chase, M.W. (1999). Phylogenetic analysis of trait evolution and species diversity variation among angiosperm families. *Evolution*, 53, 732–744.
- Durazzi, J.T. & Stehli, F.G. (1972). Average generic age, the planetary temperature gradient, and pole location. *Syst. Zool.*, 21, 384–389.
- Dynesius, M. & Jansson, R. (2000). Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. USA*, 97, 9115–9120.
- Evans, K.L. & Gaston, K.J. (2005). Can the evolutionary-rates hypothesis explain species-energy relationships? *Func. Ecol.*, 19, 899–915.
- Farrell, B.D. & Mitter, C. (1993). Phylogenetic determinants of insect/plant community diversity. In: *Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 253–266.
- Farrell, B.D., Mitter, C. & Futuyma, D.J. (1992). Diversification at the insect-plant interface. *BioScience*, 42, 34–42.
- Fedorov, A.A. (1966). The structure of tropical rain forest and speciation in the humid tropics. *J. Ecol.*, 54, 1–11.
- Fine, P.V.A. (2001). An evaluation of the geographic area hypothesis using the latitudinal gradient in North American tree diversity. *Evol. Ecol. Res.*, 3, 413–428.
- Fine, P.V.A. & Ree, R.H. (2006). Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *Am. Nat.*, 168, 796–804.
- Fischer, A.G. (1960). Latitudinal variations in organic diversity. *Evolution*, 14, 64–81.
- Flessa, K.W. & Jablonski, D. (1996). The geography of evolutionary turnover: a global analysis of extant bivalves. In: *Evolutionary Paleobiology* (eds Jablonski, D., Erwin, D.H. & Lipps, J.H.). University of Chicago Press, Chicago, IL, pp. 376–397.
- Futuyma, D.J. (1998). *Evolutionary Biology*, 3rd edn. Sinauer, Sunderland, MA.
- Gentry, A.H. (1989). Speciation in tropical forests. In: *Tropical Forests: Botanical Dynamics, Speciation and Diversity* (eds Holm-Nielsen, L.B., Nielsen, I.C. & Balslev, H.). Academic Press, San Diego, CA, pp. 113–134.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.*, 46, 5–17.
- Gillespie, J.H. (1991). *The Causes of Molecular Evolution*. Oxford University Press, Oxford.
- Gillooly, J.F., Allen, A.P., West, G.B. & Brown, J.H. (2005). The rate of DNA evolution: effects of body size and temperature on the molecular clock. *Proc. Natl. Acad. Sci. USA*, 102, 140–145.
- Goldberg, E.E., Roy, K., Lande, R. & Jablonski, D. (2005). Diversity, endemism, and age distributions in macroevolutionary sources and sinks. *Am. Nat.*, 165, 623–633.
- Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, 165, 131–147.
- Harvey, P.H., May, R.M. & Nee, S. (1994). Phylogenies without fossils. *Evolution*, 48, 523–529.
- Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006). Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of new World birds. *J. Biogeogr.*, 33, 770–780.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.*, 163, 192–211.
- Hooghiemstra, H. & van der Hammen, T. (1998). Neogene and Quaternary development of the neotropical rain forest: the forest refugia hypothesis, and a literature overview. *Earth Sci. Rev.*, 44, 147–183.
- Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. (1995). Andean tectonics as a cause for changing drainage patterns in Miocene northern South-America. *Geology*, 23, 237–240.
- Isaac, N.J.B., Agapow, P.M., Harvey, P.H. & Purvis, A. (2003). Phylogenetically nested comparisons for testing correlates of species-richness: a simulation study of continuous variables. *Evolution*, 57, 18–26.
- Jablonski, D. (1993). The tropics as a source of evolutionary novelty through geological time. *Nature*, 364, 142–144.
- Jablonski, D. & Roy, K. (2003). Geographical range and speciation in fossil and living mollusks. *Proc. R. Soc. Lond. B*, 270, 401–406.
- Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, 314, 102–106.

- Jackson, J.B.C. & Johnson, K.G. (2001). Paleoecology-measuring past biodiversity. *Science*, 293, 2401–2404.
- Jackson, S.T. & Williams, J.W. (2004). Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annu. Rev. Earth Planet. Sci.*, 32, 495–537.
- Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.
- Jaramillo, C., Rueda, M.J. & Mora, G. (2006). Cenozoic plant diversity in the Neotropics. *Science*, 311, 1893–1896.
- Jeanne, R.L. (1979). A latitudinal gradient in rates of ant predation. *Ecology*, 60, 1211–1224.
- Judd, W.S., Sanders, R.W. & Donoghue, M.J. (1994). Angiosperm family pairs: preliminary phylogenetic analyses. *Harr. Pap. Bot.*, 5, 1–51.
- Kay, K.M., Reeves, P., Olmstead, R. & Schemske, D.W. (2005). Rapid speciation and the evolution of hummingbird pollination in Neotropical *Costus* subgenus *Costus* (Costaceae): evidence from nrDNA ITS and ETS sequences. *Am. J. Bot.*, 92, 1899–1910.
- Kimura, M. (1968). Evolutionary rate at the molecular level. *Nature*, 217, 624–626.
- Kleidon, A. & Mooney, H.A. (2000). A global distribution of biodiversity inferred from climatic constraints: results from a process-based modeling study. *Global Change Biol.*, 6, 507–523.
- Kubo, T. & Iwasa, Y. (1995). Inferring the rates of branching and extinction from molecular phylogenies. *Evolution*, 49, 694–704.
- Kulesza, G. (1990). An analysis of clutch-size in New World passerine birds. *Ibis*, 132, 407–442.
- Latham, R.E. & Ricklefs, R.E. (1993). Continental comparisons of temperate-zone tree species diversity. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 294–314.
- Leighton, L.R. (2005). The latitudinal diversity gradient through deep time: testing the ‘Age of the Tropics’ hypothesis using Carboniferous productidine brachiopods. *Evol. Ecol.*, 19, 563–581.
- MacArthur, R.H. (1969). Patterns of communities in the tropics. *Biol. J. Linn. Soc.*, 1, 19–30.
- Martin, A.P. & Palumbi, S.R. (1993). Body size, metabolic rate, generation time, and the molecular clock. *Proc. Natl. Acad. Sci. USA*, 90, 4087–4091.
- Martin, P.R. & McKay, J.K. (2004). Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution*, 58, 938–945.
- Martin, P.R., Bonier, R. & Tewksbury, J.J. (in review). Cladogenesis and range expansion explain latitudinal variation in taxonomic richness.
- Mayr, E. (1942). *Systematics and the Origin of Species*. Harvard University Press, Cambridge, MA, USA.
- McKenna, D.D. & Farrell, B.D. (2006). Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proc. Natl. Acad. Sci. USA*, 103, 10947–10951.
- Mendelson, T.C. (2003). Sexual isolation evolves faster than hybrid inviability in a diverse and sexually dimorphic genus of fish (Percidae: *Etheostoma*). *Evolution*, 57, 317–327.
- Moritz, C., Patton, J.L., Schneider, C.J. & Smith, T.B. (2000). Diversification of rainforest faunas: an integrated molecular approach. *Ann. Rev. Ecol. Syst.*, 31, 533–563.
- Morley, R.J. (2000). *Origin and Evolution of Tropical Rain Forests*. John Wiley and Sons, Chichester.
- Moyle, L.C., Olson, M.S. & Tiffin, P. (2004). Patterns of reproductive isolation in three angiosperm genera. *Evolution*, 58, 1195–1208.
- Muller, H.J. (1940). Bearing of the *Drosophila* work on systematics. In: *The New Systematics* (ed. Huxley, J.S.). Clarendon Press, Oxford, pp. 185–268.
- Nee, S., Holmes, E.C., May, R.M. & Harvey, P.H. (1994a). Extinction rates can be estimated from molecular phylogenies. *Philos. Trans. R. Soc. Lond. B*, 344, 77–82.
- Nee, S., May, R.M. & Harvey, P.H. (1994b). The reconstructed evolutionary process. *Philos. Trans. R. Soc. Lond. B*, 344, 305–311.
- Orr, H.A. & Turelli, M. (2001). The evolution of postzygotic isolation: accumulating Dobzhansky-Muller incompatibilities. *Evolution*, 55, 1085–1094.
- Pagani, M., Zachos, J.C., Freeman, K.H., Tipple, B. & Bohaty, S. (2005). Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. *Science*, 309, 600–603.
- Paradis, E. (2004). Can extinction rates be estimated without fossils? *J. Theor. Biol.*, 229, 19–30.
- Pianka, E.R. (1966). Latitudinal gradients in species diversity: a review of concepts. *Am. Nat.*, 100, 33–46.
- Presgraves, D.C. (2002). Patterns of postzygotic isolation in Lepidoptera. *Evolution*, 56, 1168–1183.
- Presgraves, D.C., Balagopalan, L., Abmayr, S.M. & Orr, H.A. (2003). Adaptive evolution drives divergence of a hybrid inviability gene between two species of *Drosophila*. *Nature*, 423, 715–719.
- Price, T.D. & Bouvier, M.M. (2002). The evolution of F-1 postzygotic incompatibilities in birds. *Evolution*, 56, 2083–2089.
- Ree, R.H. (2005). Phylogeny and the evolution of floral diversity in *Pedicularis* (Orobanchaceae). *Int. J. Plant Sci.*, 166, 595–613.
- Rice, W.R. (1998). Intergenomic conflict, interlocus antagonistic evolution, and the evolution of reproductive isolation. In: *Endless Forms: Species and Speciation*. (eds Howard, D.J. & Berlocher, S.H.). Oxford University Press, New York, pp. 261–270.
- Ricklefs, R.E. (1987). Community diversity: relative roles of regional and local processes. *Science*, 235, 167–171.
- Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.*, 7, 1–15.
- Ricklefs, R.E. (2005). Phylogenetic perspectives on patterns of regional and local species richness. In: *Rainforest: Past, Present and Future* (eds Bermingham, E., Dick, C. & Moritz, C.). University of Chicago Press, Chicago, IL, pp. 3–40.
- Ricklefs, R.E. (2006). Global variation in the diversification rate of passerine birds. *Ecology*, 87, 2468–2478.
- Ricklefs, R.E. & Renner, S.S. (1994). Species richness within families of flowering plants. *Evolution*, 48, 1619–1636.
- Ricklefs, R.E. & Renner, S.S. (2000). Evolutionary flexibility and flowering plant familial diversity: a comment on Dodd, Silvertown, and Chase. *Evolution*, 48, 1619–1636.
- Ricklefs, R.E. & Schluter, D. (1993). Species diversity: regional and historical influences. In: *Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 350–363.
- Robinson, W.D., Robinson, T.R., Robinson, S.K. & Brawn, J.D. (2000). Nesting success of understory forest birds in central Panama. *J. Avian Biol.*, 31, 151–164.

- Rohde, K. (1978). Latitudinal gradients in species-diversity and their causes. I. A review of the hypotheses explaining the gradients. *Biol. Zent. Bl.*, 97, 393–403.
- Rohde, K. (1992). Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, 65, 514–527.
- Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Roy, K. & Pandolfi, J.M. (2005). Responses of marine species and ecosystems to past climate change. In: *Climate Change and Biodiversity* (eds Lovejoy, T.E. & Hannah, L.). Yale University Press, New Haven, CT, USA, pp. 160–175.
- Roy, K., Jablonski, D. & Valentine, J.W. (1996). Higher taxa in biodiversity studies: patterns from eastern Pacific marine molluscs. *Philos. Trans. R. Soc. Lond. B*, 351, 1605–1613.
- Roy, K., Jablonski, D. & Valentine, J.W. (2001). Climate change, species range limits and body size in marine bivalves. *Ecol. Lett.*, 4, 366–370.
- Sauer, J.D. (1988). *Plant Migration: The Dynamics of Geographic Pattern in Seed Plant Species*. University of California Press, Berkeley, CA.
- Savolainen, V., Anstett, M.C., Lexer, C., Hutton, I., Clarkson, J.J., Norup, M.V. *et al.* (2006). Sympatric speciation in palms on an oceanic island. *Nature*, 441, 210–213.
- Schemske, D. (2002). Tropical diversity: patterns and processes. In: *Ecological and Evolutionary Perspectives on the Origins of Tropical Diversity: Key Papers and Commentaries* (eds Chazdon, R. & Whitmore, T.). University of Chicago Press, Chicago, IL, pp. 163–173.
- Schluter, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, New York.
- Sibley, C.G. & Ahlquist, J.H. (1990). *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. Yale University Press, New Haven, CT.
- Sime, K.R. & Brower, A.V.Z. (1998). Explaining the latitudinal gradient anomaly in ichneumonid species richness: evidence from butterflies. *J. Anim. Ecol.*, 67, 387–399.
- Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Sinninghe Damsté, J.S. *et al.* (2006). Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature*, 441, 610–613.
- Stanley, S.M. (1985). Rates of evolution. *Paleobiology*, 11, 13–26.
- Stanley, S.M., Addicott, W.O. & Chinzei, K. (1980). Lyellian curves in paleontology: possibilities and limitations. *Geology*, 8, 422–426.
- Stebbins, G.L. (1974). *Flowering Plants: Evolution above the Species Level*. The Belknap Press of Harvard University Press, Cambridge, MA.
- Stehli, F.G. & Wells, J.W. (1971). Diversity and age patterns in hermatypic corals. *Jyst. Zool.*, 20, 114–126.
- Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969). Generation and maintenance of gradients in taxonomic diversity. *Science*, 164, 947–949.
- Stenseth, N.C. (1984). The tropics: cradle or museum? *Oikos*, 43, 417–420.
- Stephens, P.R. & Wiens, J.J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *Am. Nat.*, 161, 112–128.
- Stevens, R.D. (2006). Historical processes enhance patterns of diversity along latitudinal gradients. *Proc. R. Soc. Lond. B*, 273, 2283–2289.
- Stireman, J.O., Dyer, L.A., Janzen, D.H., Singer, M.S., Lill, J.T., Marquis, R.J. *et al.* (2005). Climatic unpredictability and parasitism of caterpillars: implications of global warming. *Proc. Natl. Acad. Sci. USA*, 102, 17384–17387.
- Stuart-Fox, D. & Owens, I.P.F. (2003). Species richness in agamid lizards: chance, body size, sexual selection or ecology. *J. Evol. Biol.*, 16, 659–669.
- Svenning, J.-C. (2003). Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecol. Lett.*, 6, 646–653.
- Terborgh, J. (1973). On the notion of favorableness in plant ecology. *Am. Nat.*, 107, 481–501.
- Thomas, J.A., Welch, J.J., Woolfit, M. & Bromham, L. (2006). There is no universal molecular clock for invertebrates, but rate variation does not scale with body size. *Proc. Natl. Acad. Sci. USA*, 103, 7366–7371.
- Thompson, J.N. (1994). *The Coevolutionary Process*. University of Chicago Press, Chicago, IL.
- Van Valen, L. (1969). Climate and evolutionary rate. *Science*, 166, 1656–1658.
- Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory*, 1, 1–30.
- Valentine, J.W. & Jablonski, D. (1993). Fossil communities: compositional variation at many time scales. In: *Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). University of Chicago Press, Chicago, IL, pp. 341–349.
- Valentine, J.W., Jablonski, D., Kidwell, S.M. & Roy, K. (2006). Assessing the fidelity of the fossil record by using marine bivalves. *Proc. Natl. Acad. Sci. USA*, 103, 6599–6604.
- Vermeij, G.J. (2005). From phenomenology to first principles: towards a theory of diversity. *Proc. Cal. Acad. Sci.*, 56(Suppl. I, No. 2), 12–23.
- Wallace, A.R. (1878). *Tropical Nature and Other Essays*. Macmillan, New York.
- Wei, K.-Y. & Kennett, J.P. (1983). Nonconstant extinction rates of Neogene planktonic foraminifera. *Nature*, 305, 218–220.
- Weir, J.T. (2006). Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, 60, 842–855.
- Weir, J.T. & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* (in press).
- Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology and species richness. *Trends Ecol. Evol.*, 19, 639–644.
- Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006). Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: tree frogs unearth the roots of high tropical diversity. *Am. Nat.*, 168, 579–596.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Ann. Rev. Ecol. Syst.*, 34, 273–309.
- Wolfe, J.A. (1975). Some aspects of plant geography of the northern hemisphere during the late cretaceous and tertiary. *Ann. Mo. Bot. Gard.*, 62, 264–279.
- Wolfe, J.A. (1978). A paleobotanical interpretation of tertiary climates in the Northern Hemisphere. *Am. Sci.*, 66, 694–703.
- Wright, S., Gray, R.D. & Gardner, R.C. (2003). Energy and the rate of evolution: inferences from plant rDNA substitution rates in the western Pacific. *Evolution*, 57, 2893–2898.



- Wright, S., Keeling, J. & Gilman, L. (2006). The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proc. Natl. Acad. Sci. USA*, 103, 7718–7722.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to Present. *Science*, 292, 686–693.

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