Species richness and evolutionary speed: the influence of temperature, water and area

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ABSTRACT
There are a few patterns in nature that are striking even to casual observers. These include patterns of species richness associated with latitude, elevation, rainfall and area. Current thinking suggests that a number of primary mechanisms determine richness variation and that these differ depending on the type of pattern and the biome to which they apply. Prominent among the many hypotheses that attempt to explain the latitudinal diversity gradient (LDG) are those based either on climate or on historical factors such as past biome area. Climate-based and historically-based hypotheses have been regarded as competing alternatives, but there is growing acknowledgement that both are important. The evolutionary speed hypothesis (ESH) is one of several climate-based hypotheses. According to this hypothesis the LDG is generated by thermally mediated asymmetries in evolutionary speed and diversification. Here we identify five relationships predicted by the ESH and survey the literature for empirical evidence for and against these relationships. We find these five relationships are supported by a number of empirical studies. However, there are gaps in this evidence that require further work and, because the relationship between temperature and species richness is negative when water is limited, a modification to the ESH is necessary. Additionally, we suggest that diversity patterns associated with area, temperature and water availability might all be influenced by a common mechanism associated with biologically available energy and its influence on the tempo of evolution. Rates of genetic evolution might also be influenced by spatial heterogeneity and rates of biotic and abiotic environmental change, potentially introducing positive feedbacks between diversification and genetic evolution.

Keywords
Diversification, energy, evolutionary speed hypothesis, latitude, latitudinal diversity gradient, productivity, species diversity gradients, species richness, water availability.

INTRODUCTION
The latitudinal diversity gradient (LDG) is one of the most well recognized and best documented of the global patterns in biotic systems. Diversity patterns relating to latitude apply to biomes on land and in water and they apply to life forms that range from bacteria and viruses to trees and vertebrates, including both ectotherms and endotherms (Willig et al., 2003; Guernier et al., 2004; Hillebrand, 2004; Pommier et al., 2007). Furthermore, the LDG appears to have existed more than 300 million years ago (Stehli et al., 1969; Powell, 2007).

The long-term generality of this pattern across taxa suggests a unitary set of primary controlling factors that have been extant throughout the history of life. Other well-recognized regional to global scale biodiversity patterns include the positive relationship with bioregion area and island area (MacArthur & Wilson, 1967), water availability (e.g. Gentry, 1988) and productivity (Gillman & Wright, 2006; Cusens et al., 2012). The influence on diversity due to the interplay between water availability and temperature is also well recognized (O’Brien, 1998; Francis & Currie, 2003; Hawkins et al., 2003).
There is evidence that tropical climates have existed for longer and were more extensive than temperate climates for much of Earth’s history (Mittelbach et al., 2007), suggesting that area (Rosenzweig & Abramsky, 1993) and evolutionary time (Rohde, 1992) influence current diversity. By contrast, the long standing energy–richness (or more individuals) hypothesis, as described by Hutchinson (1959), Brown (1981) and Wright (1983), explains the LDG as a function of productivity. This hypothesis suggests that greater productivity can support more individuals and therefore a greater number of minimum-viable-populations of species. However, key predictions of this theory appear to be contradicted by empirical evidence (e.g. Currie et al., 2004) and productivity appears to have an effect on richness beyond that expected on the basis of the number of individuals (Hurlbert & Jetz, 2010). Recently, a model that integrated area and productivity over geological time together with temperature succeeded in explaining 77% of current-day species richness of the four major terrestrial vertebrate groups (Jetz & Fine, 2012).

Hypotheses based on differential rates of diversification are also gaining increasing support (Mittelbach et al., 2007). The idea that global species richness gradients derive from origination and diversification asymmetries that favour tropical climates has been with us in one form or another for more than 130 years (Wallace, 1878; Fisher, 1930; Rensch, 1959; Stehli et al., 1969; Rohde, 1992; Jablonski, 1993; Briggs, 2004). One of several potential explanations for such an asymmetry is the evolutionary speed hypothesis (ESH; Rensch, 1959), elaborated as the effective evolutionary time hypothesis by Rohde (1992).

Rensch (1959) suggested that shorter generation times in warmer tropical climates might increase the pace of selection and consequently the overall pace of evolution. Faster rates of evolutionary speed would then lead to faster rates of diversity accumulation within the tropics. Rohde (1992) proposed that temperature might limit the rate of genetic evolution via an influence on the rate of mutagenesis and/or via an indirect influence on average generation times and rates of selection. According to Rohde, time is also an integral component, such that species richness becomes a function of the rate of evolution multiplied by the time that there has been available for species to accumulate.

Unlike theories that are based on species richness attaining equilibrium with the environment, the ESH makes no such assumption, implying that if species could undergo substantial range expansion without limitation then high latitudes would attain the same diversity as low latitudes. Therefore, the ESH makes the implicit assumption that diversity gradients are maintained by barriers to dispersal and range expansion. Barriers include the putatively hostile nature of both the biotic and abiotic receiving environment and the lag time for adaptation to novel environments (niche conservatism). They also include any potentially hostile intermediate environments required for dispersal and limitations due to the biotic and abiotic nature of dispersal vectors.

This implicit assumption of the ESH is equivalent to the main tenet of the tropical niche conservatism hypothesis (TNCH; Wiens & Donoghue, 2004). Tests that demonstrate climatic limits to clade expansion are therefore also consistent with the ESH. The TNCH differs from the ESH, however, because it assumes that the rate of diversification is independent of latitude (Wiens et al., 2006). In summarizing the TNCH, Wiens & Donoghue (2004) suggest that greater clade origination occurred in the tropics prior to 30–35 Ma due to larger tropical extent (i.e. the species–area hypothesis). Although niche conservatism, along with other limitations to dispersal, might explain how the LDG is maintained, in isolation it does not explain how the LDG originated. A separate mechanism such as that relating to area, or stability, must be invoked to explain greater origination of clades in the tropics.

The ESH involves three mechanistic steps between environmental temperature, rate of genetic evolution, rate of diversification and species richness. Two additional indirect relationships are therefore also predicted; that is, between temperature and richness and between temperature and speciation (Fig. 1). Here we begin by reviewing the empirical evidence for and against the relationships predicted by the ESH hypothesis and then we discuss developments that enable us to propose a link between environmental temperature, water availability and area via a common causative mechanism under an integrated theory of evolutionary speed. Thus, we present a model of evolutionary speed that might influence speciation rates and general patterns of diversity. However, in presenting this model we recognize that overlaying such a mechanism there will be other processes that have important, and in some cases dominant, influences on speciation and the maintenance of diversity. Nonetheless, this model provides a synthetic context and focus for future empirical testing.

**Prediction 1: Rates of genetic evolution depend on ambient temperature**

Greater rates of genetic evolution involving several different genes have been found at lower (warmer) latitudes for a broad range of taxa, including rain forest plants (Wright et al., 2006; Gillman et al., 2010), angiosperm families (Davies et al., 2004), marine foraminifera (Allen et al., 2006),

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*Figure 1* Direct relationships (1, 2 & 4) and indirect correlations (3 & 5) predicted by the evolutionary speed hypothesis (ESH). Possible feedback influences are indicated by dashed lines.
marine fishes (Wright et al., 2011), amphibians (Wright et al., 2010), turtles (Lourenço et al., 2013), mammals (Gillman et al., 2009) and birds (Gillman et al., 2012) (Table 1). Most of these studies have employed large data sets that replicate comparisons between closely related pairs of species from a diverse array of families and involve a range of different genes from both nuclear and mitochondrial genomes. By contrast, Bromham & Cardillo (2003) did not find a significant latitudinal effect, although one component of their study was only marginally non-significant.

Greater within-species genetic divergence in lower latitude populations has also been demonstrated among vertebrates (Martin & McKay, 2004; Adams & Hadly, 2013), plants (Eo et al., 2008) and birds (Chek et al., 2003) and greater phenotypic differentiation among bird populations at lower latitudes has been reported (Martin & Tewksbury, 2008). Genetic divergence among populations is important if such divergence is a necessary precursor to speciation.

In addition to these latitudinal patterns, faster rates of genetic evolution have been found among birds, amphibians and mammals occurring at lower elevations (Bleiweiss, 1998; Gillman et al., 2009; Wright et al., 2010) and among fishes occupying shallower water (Wright et al., 2011) (Table 1). Mean temperatures are lower at higher latitudes and elevations and at greater ocean depths. Seasonal temperature variation also increases with latitude and elevation on land but it decreases below the thermocline in oceans and peaks at mid-latitudes, not high latitudes, in surface ocean waters (Clarke & Gaston, 2006). Range size increases with latitude but not with elevation. Therefore, although other factors such as population size may account for the patterns observed, we suggest that temperature, or a temperature-related variable such as productivity, is linked with rates of genetic evolution. Increased resource concentration has been shown to produce faster rates of genetic evolution in microbes (Stevens et al., 2007). However, further studies that manipulate temperature and measure rates of genetic change among microbes would be able to test for the independent effect of temperature. In conclusion, the evidence to date is consistent with the prediction that rates of genetic evolution are generally faster in warmer (or more productive) environments, but is not conclusive. For a discussion of putative mechanisms that might underpin these relationships see Gillman & Wright (2013).

Table 1 Empirical studies that have tested for relationships between environmental variables and rates of genetic evolution.

| Taxa | Extent | Gene(s) | Variables | P-values | n | Reference |
|------|--------|---------|-----------|----------|---|----------|
| Mammals | Global | cyt b | Elevation | 0.006 | 29 | Gillman et al. (2009) |
| 10 orders, 29 families | | | Latitude | 0.008 | 101 | |
| Birds a | Global | cyt b | Elevation/latitude | 0.0003 | 130 | |
| Birds | Global DNA hybridization | Latitudes | 0.36 | 33 | Bromham & Cardillo (2003) |
| 21 families | | | 0.06 | 22 | |
| Hummingbirds | Regional DNA hybridization | Elevation | 0.004 | 30 | Gillman et al. (2012) |
| 18 families (caudates and anurans) | | | 0.004 | 30 | |
| Turtles | Global RAG1, RAG2 and c-mos | Elevation | 0.050 | 234 | Lourenço et al. (2013) |
| 30 families and 8 orders | Global 12S, 16S, cyt b | Depth | 0.026 | 42 | Wright et al. (2011) |
| Angiosperms and conifers | Global ITS | Latitude | 0.006 | 26 | |
| 27 families | | Depth/latitude | 0.0004 | 68 | |
| Angiosperms and conifers | Global 18S | Temperature | 0.001 | 45 | |
| 27 families | | | 0.001 | 45 | |
| Plants | Australia ITS | Aridity | 0.003 | 30 | Goldie et al. (2010) |
| 15 families | | | | | |
| Angiosperms 86 sister families | Not given 18S, rbcL, atpB c | Temperature | 0.001 | 86 | Davies et al. (2004) |

aIncluded migratory birds but did not account for migratory distribution. Some tropical species appeared in the column under temperate species and vice versa.

bThe 24 hummingbird species were not phylogenetically independent and therefore the P-value is based on an inflated number of degrees of freedom.

cThird position sites of the protein coding genes.

Non-significant after phylogenetic control.
Prediction 2: Diversification rates depend on rates of genetic evolution

Given that genetic evolution is necessary for speciation in allopatric populations (Martin & McKay, 2004) and necessary for both reproductive isolation and speciation in sympatric populations, it might be expected, with other factors being equal, that greater underlying rates of genetic evolution lead to greater rates of speciation.

Correlations between both diversification rate and genetic evolution, and between current species richness and genetic evolution in nuclear, mitochondrial and chloroplast genes have been demonstrated (Guo & Ricklefs, 2000; Barraclough & Savolainen, 2001; Jobson & Albert, 2002; Eo & DeWoody, 2010; Duchene & Bromham, 2013). However, the assumption that speciation is dependent on genetic evolution is not without challenge. Correlations between species level genetic evolution and species richness have often been interpreted as accelerated rates of evolution in response to speciation, rather than the converse (e.g. Webster et al., 2003). This alternative interpretation is based on the hypothesis that reduced population sizes (assumed to occur during speciation events) may cause a spike in the number of nearly neutral non-synonymous mutations (dN) (i.e. those that result in amino acid replacement).

Investigation of this question has taken five approaches: (1) testing the assumption under nearly neutral theory (Ohta, 1992) that rates of genetic evolution are faster in small populations; (2) testing for the relative strengths of correlations among rates of genetic evolution, ambient temperature and speciation rate (Davies et al., 2004); (3) testing the prediction that if greater rates of speciation increase substitution rates due to the birth of new species with small populations, then greater variation in the rate of substitution will also occur among species (Lancaster, 2010); (4) testing the prediction, under nearly neutral theory, that reduced population sizes during speciation will have increased the rate of nearly neutral, non-synonymous, substitutions among clades that have undergone faster rates of diversification (Lanfear et al., 2010) (note that synonymous substitution rate is predicted not to be affected by population size under nearly neutral theory); and (5) testing the prediction, under nearly neutral theory, in circumstances where genera have more species at temperate latitudes rather than less, that rates of genetic evolution are also faster among the temperate species (Wright et al., 2006).

Are rates of genetic evolution faster in smaller populations?

Under nearly neutral theory deleterious mutations with selection coefficients so small that they act like neutral mutations are fixed at greater rates in smaller populations where purifying selection is thought to be less efficient. Therefore, genetic evolution is expected to be faster in smaller populations. Several studies spanning three decades have tested for a relationship between population size and rates of genetic change and although there has been some empirical support for nearly neutral theory, overall the results have been equivocal (Woolfit & Bromham, 2005). Hawks et al. (2007), for example, show increasing rates of genetic evolution with increasing human population size. The study with greatest replication (n = 70), used pairs of distantly related species from islands and continents and found no overall difference in the rate of genetic change between small and large populations (Woolfit & Bromham, 2005). Recently, Wright et al. (2009) used 48 pairs of closely related bird species (mostly sister species) of contrasting population sizes and found, contrary to expectations under nearly neutral theory, that bird species with smaller populations had experienced a slower pace in genetic evolution than those with larger populations. Nearly neutral effects probably occur, but there is a lack of evidence suggesting that they predominate and thereby underpin the relationship between rates of diversification and genetic evolution.

What are the relative strengths of correlations among rates of genetic evolution, ambient temperature and speciation rate?

Using a selected angiosperm species from each of 86 sister families, Davies et al. (2004) found relationships between: temperature and species richness; temperature and rates of substitution and; substitution rate and species richness. However, although the relationship between substitution rate and species richness was significant (P = 0.004), substitution rate dropped out of the regression model as a significant predictor variable of species richness when the model was simplified. Davies et al. suggest this indicates that temperature independently influences species richness and the rate of genetic evolution, but that the rate of genetic evolution does not influence species richness. However, the rate of genetic evolution within each sister family in that study was represented by just one species using only the third codon position. A single branch length from each family may be adequate to represent the dependent variable when regressed with temperature. However, it is unclear, given the diversity of branch lengths among species within angiosperm families, whether or not a single branch length from each family is sufficiently free from error to adequately characterize the predictor variable in a regression with speciation rate, where strength of correlations are to be used for comparative purposes.

Do clades with greater speciation rates contain greater variation among species in the rate of genetic evolution as expected if speciation causes a short-term spike in substitutions?

Using fossil-aged lineages, Lancaster (2010) found a positive correlation between substitution rates and rates of diversification among 13 clades of angiosperms as expected if rates of DNA evolution influence speciation. However, she did not
find a correlation between substitution rate variation and diversification rate. She therefore rejected the hypothesis that speciation itself had caused an increase in substitution rate.

**Is non-synonymous genetic change elevated relative to synonymous change among clades that have undergone faster rates of diversification?**

If reduced population size leads to accelerated genetic evolution during speciation via nearly neutral effects it is predicted that the ratio of non-synonymous to synonymous (dN/dS) substitutions should be elevated in more rapidly diversifying clades, while synonymous substitutions should not be affected. Contrary to this prediction, Lanfear et al. (2010) found a positive correlation between the rate of diversification of birds and the rate of synonymous substitutions, but no relationship with dN/dS, suggesting that speciation was not the cause of the increase in rate of genetic evolution. Similar results have been found among Eutherian mammals for nuclear DNA, but not for mitochondrial DNA, and no significant correlations for either nuclear or mitochondrial DNA were found for non-Eutherian mammals (Goldie et al., 2011).

**Do species in temperate climates have faster rates of genetic evolution than those in tropical climates, in contrast to the typically faster rates in the tropics, when the genera are more species rich at temperate latitudes?**

Wright et al. (2006) tested this prediction among plant species and found that, contrary to the expectation under nearly neutral theory, temperate species had slower rates of genetic evolution even when they belonged to genera that were more species rich at higher latitudes.

Taken together these studies provide little support for the hypothesis that reduced population size during speciation is the cause of the association between rates of genetic evolution and diversification. By contrast, results from empirical studies are generally, but not always, consistent with the alternative hypothesis that the rate of genetic evolution influences the rate of diversification.

**Prediction 3: Rates of origination depend on latitude and ambient temperature**

Empirical studies testing for associations between net diversification rates and latitude have been conducted for a diverse range of taxa using a variety of approaches. The fossil record shows lower average ages of taxa and greater rates of diversification towards the equator (Stehli et al., 1969; Stehli & Wells, 1971; Jablonski, 1993; Buzas et al., 2002; Crame, 2002; Jablonski et al., 2006).

Further evidence comes from phylogenetic data. Sister clades with a common ancestral node are, by definition, of equivalent evolutionary age and therefore the number of extant species within each clade can be used to compare rates of diversification. Comparisons involving sister clades have demonstrated faster rates of net diversification at lower latitudes for passerine birds, swallowtail butterflies (Cardillo, 1999), ferns (Schneider et al., 2013) and angiosperms (Davies et al., 2004; Jansson & Davies, 2008), whereas three studies, involving Old World primates (Bohm & Mayhew, 2005), herbivorous insects (Farrell & Mitter, 1993) and damselflies (McPeek & Brown, 2000), failed to find statistically significant relationships. However, the latter studies lacked statistical power due to the small sample sizes employed (n = 9, 5 and 1, respectively).

In order to overcome limitations due to a lack of available sister clades of equivalent age, several studies have estimated diversification rates using clade ages derived from node depths of DNA-based phylogenies. Using this technique, negative relationships between latitude and net diversification rates have been found for birds (Cardillo et al., 2005; Ricklefs, 2005, 2006), New World palms (Svenning et al., 2008), squamate reptiles (Ricklefs et al., 2007) and amphibians (Wiens, 2007). Tests using subsets of amphibia (Hylidae & Ranidae) did not, however, produce significant results (Wiens et al., 2006, 2009) and nor did a recent test for a relationship between latitude and diversification among mammal genera (Soria-Carrasco & Castresana, 2012). A positive relationship between temperature and diversification rate was found for plethodontid salamanders, whereas a negative relationship was found for carnivoran mammals (Machac et al., 2012). However, because genetic evolution is generally faster at lower, warmer latitudes, studies that derive divergence dates using DNA-based phylogenies and then use these to estimate diversification rates, suffer from a bias that underestimates the rate of diversification at lower latitudes. Similarly, greater genetic divergence among pairs of species from lower latitudes has been interpreted as indicating slower rates of origination at these latitudes (Weir & Schluter, 2007). Again, this result is a likely artefact of faster rates of genetic evolution at lower latitudes (Gillman et al., 2009, 2011).

Both palaeoecological and phylogenetic studies have the potential to under-represent tropical taxa due to greater sampling effort within temperate latitudes and the relative paucity of fossil deposits in the tropics (Johnson, 2003; Tobias et al., 2008). This data bias can be assumed to have had a conservative influence on the studies reported above, the majority of which provide evidence of increasing net diversification towards the equator. However, net diversification rates provide little insight into the relative contributions of origination, dispersal and extinction.

Studies that differentiate between these components are few, but faster rates of origination at lower latitudes have been found among marine bivalves (Flessa & Jablonski, 1996; Jablonski et al., 2006), 26 invertebrate orders (Jablonski, 1993; Martin et al., 2007) and marine foraminifera (Allen et al., 2006). Higher latitudes appear also to be net receivers of taxa dispersing ‘out of the tropics’ (Jablonski et al., 2006). This leakage of taxa from low to high latitudes may therefore act to ameliorate the LDG.
Although extinction appears, in many cases, to contribute to net diversification asymmetries favouring the tropics (Jablonski et al., 2006), and other areas of high diversity such as California (Lancaster & Kay, 2013), extinction rates among some taxa have been greater in tropical regions (Roy & Pandolfi, 2005; Martin et al., 2007; Powell, 2007). Among marine bivalves, extinction rates were found to be highest in temperate regions and lowest in Polar Regions during the last 5 million years (Valentine et al., 2008). Thus, the extinction pattern is not always consistent with the LDG and would therefore not appear to be the primary mechanism driving net diversification heterogeneity, although it may contribute to the pattern in many cases.

Although it is a parsimonious explanation that latitudinal patterns in diversification rates are due to a negative covariance of temperature with latitude (relationship 3, Fig. 1), this is not necessarily the case as other variables related to latitude may underpin patterns of diversification. However, a recent study of biodiversity patterns over the last 540 million years using fossil marine invertebrates, while controlling for sampling effort, found strong temporal associations between temperature and biodiversity and temperature and origination rates (Mayhew et al., 2012).

There have been alternative mechanisms suggested to account for latitudinal gradients in origination. Schemske (2002) suggested that biotic interactions are more important for evolution and origination in the tropics and because biotic interactions are also more spatially variable in the tropics, geographically isolated populations face different evolutionary pressures and this enhances divergence into different species. However, this hypothesis relies on high pre-existing diversity at low latitudes in order for there to be greater heterogeneity in biotic selection pressure. Therefore, it is unclear as to how this mechanism could act as a primary generator of diversification gradients. Such a mechanism may, nonetheless, contribute to a positive feedback system that enhances or maintains diversity (Fig. 1). Dynesius & Jansson (2000) suggested that at higher latitudes more extreme climate changes in the past might have favoured selection for strong dispersal capabilities and large range sizes, because these traits better enable species to track favourable conditions as they shift across latitudes. In turn, such traits could reduce speciation at high latitudes by enhancing gene flow and favouring more generalized adaptations.

In summary, there is strong evidence that a broad range of life forms have experienced faster net rates of diversification at lower latitudes. Evidence from marine taxa suggests that this differential is likely to be due to greater rates of origination in the tropics. Extinction rates, rather than consistently contributing to net diversification differentials, might in some cases have been greater at lower, not higher, latitudes. Similarly, range shifts tend to be tropical to polar, thus acting to counter the LDG rather than enhancing it. However, there is a clear need for further work to explore whether or not there is a relationship between temperature and diversification that is independent of latitude, because there are alternative hypotheses that might explain latitudinal gradients in diversification that do not invoke average temperatures.

**Prediction 4: Species richness is dependent on diversification rate**

Several studies (reviewed above) have found rates of origination that are consistent with the LDG (e.g. Cardillo et al., 2005; Jablonski et al., 2006) and that are therefore also consistent with this prediction (relationship 4 in Fig. 1). However, if diversity patterns derive from rates of diversification then patterns in diversity that are either independent of, or contrary to, the LDG should also be associated with the same atypical pattern in the tempo of diversification. Such tests are few. However, Ricklefs et al. (2006) report that mangrove species richness patterns, which could not be attributed to climatic variation, were nonetheless related to rates of origination. Marine bivalves, nanoplankton and radiolarians that have had greater rates of origination at mid-latitudes, rather than at low latitudes, also have atypical species richness maxima at mid-latitudes (Allen et al., 2006; Krug et al., 2007). Despite similar climates, the species richness of Gladiolus is an order of magnitude greater in the Cape of South Africa than in the Mediterranean Basin where diversification has been three to five times slower (Valente et al., 2011). These studies are therefore consistent with the prediction that diversity patterns are dependent on rates of origination. However, a high diversification rate among carnations has also been found in temperate Europe where plant diversity is not high (Valente et al., 2010), suggesting there is a need for more investigation in this area.

**Prediction 5: Species richness is dependent on ambient temperature**

The ESH was formulated to explain the positive relationship between species richness and latitude. However, it assumes that the important latitudinal variable controlling species richness is ambient temperature and therefore it predicts a positive monotonic relationship between temperature and species richness (relationship 5 in Fig. 1). At this point the ESH runs into the problem that the observed relationship between ambient temperature and species richness tends to be unimodal if richness is measured across a gradient that includes environments where water becomes a limiting factor. As temperature increases, species richness tends to increase up to a maximum, beyond which water deficits then begin to depress richness (O’Brien, 1998; Francis & Currie, 2003; Hawkins et al., 2003, 2005; Field et al., 2005). Given that water and warm temperatures are both necessary for high species richness, with some exceptions such as reptiles (e.g. Whittaker et al., 2007), it suggests that productivity or energy flux rather than ambient temperature is the primary factor that limits species richness. Indeed, for plants, species richness is best predicted by actual evapotranspiration (AET).
(Kreft & Jetz, 2007) and generally increases with productivity at both fine and coarse grains and at all but very small spatial extents (Gillman & Wright, 2006, 2010). Both water and temperature have also been found to be important for species richness patterns in birds, mammals, amphibians (Kalmar & Currie, 2007; Whittaker et al., 2007; McCain, 2009) and invertebrates (e.g. Kaspari et al., 2000; Hawkins & Porter, 2003). Productivity may therefore be a better predictor of total species richness than solar energy (e.g. Honkanen et al., 2010). A recent meta-analysis of 273 published studies (Cusens et al., 2012) demonstrates that for both terrestrial and freshwater animals, the predominant relationship between species richness and productivity at all spatial scales is positive. In general, warm dry climates have low productivity and are species poor and warm wet climates are productive and species rich.

If evolutionary speed is an important factor in determining species richness patterns we would then expect to find that evolutionary speed is also dependent on water in environments where water is a limiting factor. Indeed, this was the observed result in a recent study that compared rates of genetic evolution between 28 xeric Australian outback plant species with congeneric rain forest species at similar latitudes (Goldie et al., 2010). Therefore, the ESH requires modification to a construct that predicts a positive relationship between both available water and temperature with rates of genetic evolution, rather than just between temperature and rates of genetic evolution. Water and temperature may affect rates of genetic evolution via a combined influence on productivity. Alternatively, they may have independent effects (Fig. 2) or the relationship may not be causal. If productivity has a causal effect it can be further predicted that variables other than temperature and water, such as soil nutrient status, that influence productivity will also be associated with the speed of genetic evolution.

**ENVIRONMENTAL HETEROGENDERITY AND FEEDBACK EFFECTS**

If evolutionary speed limits speciation and potential species richness at regional to global scales then other factors known to influence species richness are likely to overlay this influence, especially at smaller scales. Speciation is also likely to depend on the environmental receptivity for niche differentiation (Fischer, 1960) associated with environmental gradients of heterogeneity (Doebel & Dieckmann, 2003) and/or the development of new environments. Spatial heterogeneity appears as a significant variable after accounting for temperature and water availability in many global models for species richness (e.g. Davies et al., 2007; Kreft & Jetz, 2007; Menéndez et al., 2007; Meynard & Quinn, 2008). For example, frugivorous bird diversity in a given community may depend, first, on the rate of genetic evolution of birds in a given bioregion and, second, on the potential for niche differentiation among these birds. The potential for niche differentiation might be limited, for example, by the number of fruit-producing plant species in the community (e.g. Kissling et al., 2007), or by the elevational relief available to provide novel environments.

In addition to the well-recognized influence of promoting reproductive isolation, spatial heterogeneity might also influence rates of diversification by enabling greater within-species genetic diversity both to derive and survive. Any given mutation occurring in a species that occupies a niche that encompasses a variable environment, might have a higher probability of having a selective advantage within a subset of this niche, relative to the same mutation occurring within a species that occupies a more homogeneous niche. If for example, a species occupies five distinct habitat types, any given mutation will have five times the probability of possessing a selective advantage for at least one of those habitat types relative to the same mutation occurring in a species population that occupies only one habitat. A new mutation that has selective advantage in one component of a heterogeneous niche is unlikely to be fixed within the species population, but if the selection coefficient relevant to that niche component is strong, the mutation may be maintained within the species as a polymorphism residing within a subpopulation. Biotic and abiotic heterogeneity, including that affected by species richness, may thereby promote

**Figure 2** An integrated evolutionary speed model in which temperature, water and the number of reproducing individuals are all primary influences on the rate of evolutionary speed and genetic diversity acting via biome level rates of mutation and the commensurate rate at which mutations with positive selection coefficients are produced. Water and temperature might have independent influences on rate of genetic evolution or they might act through their combined influences on productivity. If productivity has a causal influence on rates of genetic evolution then other factors that influence productivity will also be predicted to influence these rates. Area is proposed to influence rates of genetic evolution via the total number of reproducing individuals. Secondary influences on evolutionary speed and genetic diversity are proposed due to rates of biotic and abiotic environmental change and via environmental heterogeneity.
within-species genetic diversity and increase the opportunity for subsequent adaptive change and cladogenesis (Fig. 1).

A second potential feedback pathway (Fig. 1) may exist between the rate of speciation and the rate of genetic evolution. In an environment that is changing more rapidly due to higher rates of speciation, any given mutation within a population is likely to have a higher probability of having a positive selection coefficient than an equivalent mutation that occurs in a population occupying a more stable environment (Gillman et al., 2009). This is because in more stable environments populations are assumed to have a greater goodness of fit. For example, a single point mutation that allows a tropical animal species to overcome a recently evolved chemical defence mechanism in plants will confer a selective advantage to that species and the mutation is then likely to be fixed rapidly within the population by selection. Whereas, if plants are evolving more slowly in a less productive temperate environment and this chemical defence has not yet evolved, an exactly equivalent mutation occurring in a temperate animal species will not have a selective advantage and is likely to be lost from the population. A feedback mechanism such as this has the potential to enhance the relationship between productivity and genetic evolution. By contrast, this feedback loop may also become negative with respect to within-clade diversity (Ricklefs et al., 2007; Phillimore & Price, 2008) as opportunities for niche differentiation become increasingly limited by density dependent effects (Rabosky & Lovette, 2008). How these two conflicting feedback processes might play out is unclear and the balance between the two may differ among ecosystems.

**AREA AND EVOLUTIONARY SPEED**

Like the latitudinal diversity gradient, the species–area relationship holds for both aquatic and terrestrial realms and for a broad range of taxa (e.g. Drakare et al., 2006; Kalmar & Currie, 2006; Kref et al., 2008), and integrating area and productivity over geological time has been found to provide the best explanation of current-day species richness of the four major terrestrial vertebrate groups within the world’s 32 main bioregions (Jetz & Fine, 2012). The species–area relationship has also been shown to hold independently of habitat diversity among both plants and animals (Simberloff, 1976; Buckley, 1985; Deshaye & Morisset, 1988; Kohn & Walsh, 1994; Ricklefs & Lovette, 1999; Hannus & von Numers, 2008; Kallimanis et al., 2008).

The species richness of a bioregion or island necessarily depends on migration, extinction and speciation and all three have been theoretically associated with area (Preston, 1962; MacArthur & Wilson, 1967; Rosenzweig, 1995). Greater rates of net diversification, due to greater origination rates and/or lower extinction rates, have been demonstrated for larger areas among plants, mammals, birds, reptiles, arthropods and marine foraminifera (Cardillo et al., 2003; Allen et al., 2006; Ricklefs, 2006; Ricklefs et al., 2007; Borges & Hortal, 2009; Kisel et al., 2011; Zobel et al., 2011).

However, the putative mechanisms linking speciation with area have received little attention. Larger areas provide more opportunities for geographical isolation and allopatric speciation (Rosenzweig, 1995), but these cannot always explain greater rates of origination there. For example, *in situ* speciation of *Anolis* lizards was found to increase with island area, but could not be attributed to differential opportunities for reproductive isolation or differences in habitat diversity (Losos & Schluter, 2000).

Almost four decades ago, Stehli & Wells (1971) suggested an additional mechanism linking area to species richness that has largely been ignored in the intervening years (but see Allen & Gillooly, 2006; Kisel et al., 2011). Stehli & Wells suggested that larger areas contain larger population sizes and that larger populations have the capacity to evolve faster.

Greater genetic diversity is found in species with larger populations (e.g. Bazin et al., 2006; Hughes, 2010), suggesting that the potential for incipient speciation is also greater in species with larger populations. This empirical research is supported by microbial experimental work by Stevens et al. (2007). They demonstrated that when either population size or resource concentration was experimentally increased, genetic diversity within *Escherichia coli* also increased.

As discussed above, the occurrence of faster rates of evolution in smaller populations is embodied in the nearly neutral theory of evolution due to stronger selection against deleterious mutations in larger populations. However, selection for nearly neutral mutations with positive selection coefficients is also predicted to be more efficient in populations with larger effective population sizes (Ohta, 1992) and selectively advantageous genetic evolution is likely to be more important than deleterious genetic evolution for adaptive change and diversification. Furthermore, the total number of mutations produced within a species will increase with population size and the small proportion of these that convey a strong adaptive advantage will increase commensurately (Wright et al., 2009). Thus, greater rates of adaptive evolution are predicted for larger populations.

As previously stated, Wright et al. (2009) found that rates of genetic evolution were faster among birds with larger population sizes. However, more significantly, a recent study by Gossmann et al. (2012) showed that the rate of adaptive evolution amongst eukaryotes increased with effective population size. If these results prove to have widespread applicability among different taxa it would suggest that larger bioregions with more individuals will have an overall rate of adaptive genetic evolution that is faster than smaller bioregions – evolutionary speed may not only underpin the LDG, but it may also be a mechanism that contributes to species–area relationships.

**SYNTHESIS**

There is strong support for latitudinal gradients in the rate of evolution from a wide range of taxa, a pattern which
appears to be associated with environmental temperature (Davies et al., 2004; Allen et al., 2006; Wright et al., 2006, 2010, 2011; Gillman et al., 2009, 2010). Support for temperature or productivity acting as the primary cause of evolutionary rate differentials comes from data showing slower rates of genetic evolution at higher elevations where temperatures are lower and growing seasons are shorter (Bleiweiss, 1998; Gillman et al., 2009) and at greater ocean depths where temperatures are also lower (Wright et al., 2011). Slower rates of genetic evolution in plants growing in xeric conditions suggest that water availability, not just temperature, might limit rates of genetic evolution. There is also evidence to suggest that the rate of adaptive genetic evolution increases with area and population size (Hawks et al., 2007; Wright et al., 2009; Gossmann et al., 2012) although nearly neutral effects are also likely. Finally, there is increasing evidence to support a latitudinal gradient in speciation rate and an association between species richness and diversification rate that is independent of latitude. However, further work is required to resolve the question of whether or not the relationship between the rate of genetic evolution and that of speciation is causal.

These recent findings suggest an integrated evolutionary speed hypothesis that might contribute to the primary patterns of species richness (Fig. 2). Because the relationship between temperature, water availability and area are all positively associated with evolutionary speed and/or genetic diversity, it suggests that there may be a common underlying influence on species richness patterns due to rates of genetic evolution. Under such a scenario, evolutionary speed is likely to be a key mechanism contributing to the three most prevalent global patterns of species richness.

In addition, greater environmental heterogeneity and/or faster rates of environmental change (biotic and abiotic) may increase the probability that any given mutation will have a positive selection coefficient sufficiently strong for its maintenance as a polymorphism. Enhanced genetic diversity may then contribute to speciation (Fig. 2). Therefore, in biologically productive environments such as wet tropical forest, where the rate of diversification is high, rapid change in the biotic environment may provide a positive feedback mechanism enhancing microevolution and speciation (Figs 1 & 2).

In conclusion, we have reviewed evidence that on balance is largely consistent with an integrated evolutionary speed hypothesis that might contribute to global patterns of species richness associated with temperature, water and biome area. We anticipate that this synthesis will precipitate greater interest in investigating issues related to evolutionary speed that will in turn further develop our understanding of diversity.

ACKNOWLEDGEMENTS

We thank N. Gotelli and A. Clarke for constructive comments on an earlier version of this manuscript.

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Editor: Richard Ladle