The balance of nature and climate change

Edited by Klaus Rohde

Cambridge University Press

Chapter 5: Effective evolutionary time and the latitudinal diversity gradient

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5.1 Introduction

The relationship between climate and biodiversity is perhaps the most widely recognised and extensively studied pattern of nature on earth. Attempts to explain this relationship and the attendant latitudinal gradient in diversity began more than 200 years ago (von Humboldt, 1808, Wallace, 1878) and indeed the number of theories that attempt to address this question appears to be accumulating at an ever increasing rate. However, one theory which has received relatively little attention began with the observation by Rensch (1959) that animals living in warmer tropical climates have shorter generation times than those living at higher latitudes. He suggested that because natural selection accumulates change with each generation, shorter generation times found among tropical fauna might increase the pace of natural selection and thereby the pace at which evolution progresses. A faster **evolutionary speed** in the tropics would therefore lead to the evolution of more species there than at higher latitudes over an equivalent period of time.

Evidence suggesting that mutations can be induced by high temperatures prompted Rohde (1978, Rohde, 1992) to predict that not only might rates of selection increase with increasing ambient energy towards the tropics, but that rates of mutation may also be greater in lower latitude climates. It is predicted that the combined effects of faster rates of mutation and faster rates of selection will lead to greater rates of diversification. Over an equivalent period of time, regions experiencing generally faster rates of genetic evolution will therefore generate and accumulate more species and greater species richness than regions where genetic evolution is slower. Fundamental to this hypothesis is the precept that the incumbent diversity of species within communities is not at an equilibrium number set by contemporary environmental conditions. Instead, it suggests that communities continue to accumulate species at rates that depend on climatic variables. This theory is therefore quite different to those, such as the energy-richness or more individuals hypothesis (Brown, 1981, Hutchinson, 1959, Wright, 1983), that suggest that diversity is limited by energetic capacity of the environment and that species origination and extinction are therefore held in balance with climate.

Rohde also proposed that the time over which speciation had been able to occur would have a direct bearing on the number of extant species. Thus, species richness is predicted to be dependent on both the rate of evolution and the time over which species have had to accumulate; he called this the **effective evolutionary time hypothesis**.

5.2 Testing for a thermal gradient in rates of genetic evolution among ectotherms

If ambient energy directly affects the rate of mutation then we would expect genetic evolution among ectotherms, such as plants and cold blooded animals, to vary positively with ambient temperature, whereas, among endotherms (birds and mammals) that maintain a relatively constant body temperature of 35–40°C while active, regardless of ambient temperature, the same relationship should not be evident (Allen *et al.*, 2006).

In 2003, Wright *et al.* examined 24 species of plants within Myrtaceae that differed in latitudinal distribution and found the first evidence that species occupying tropical climates had faster rates of genetic evolution than those occupying cooler climates at higher latitudes. They found rates of genetic evolution in the ITS-ETS regions of rDNA of the tropical species were almost three times faster than those occupying temperate climates. Although this study lacked phylogenetically independent replication, confirmation of these results with well replicated studies for a diversity of genes soon followed: replication across 86 angiosperm families (Davies *et al.*, 2004) and 45 phylogenetically independent pairs of gymnosperm and angiosperm tree species (Wright et al., 2006, Gillman et al., 2010).

The same pattern is apparent among exothermic animals and microbes. Using 22 pairs of marine foraminifera that were dated to first appearance from fossil data, Allen et al. (2006) demonstrated an exponential increase in the rate of nuclear DNA evolution with increasing ocean temperature. Similarly, comparisons between 68 sister species pairs of teleost fish in which each member of the pair occurs at different depths or different

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latitudes revealed faster rates of evolution in both cytochrome *b* and ribosomal 12S and 16S genes for the species occurring in warmer waters (Wright *et al.*, 2011). Amphibians from 18 families of caudates and anurans (188 species) were also found to have faster rates of genetic evolution in the mitochondrial RNA genes, 12S and 16S, at both lower latitudes and lower elevations (Wright *et al.*, 2010).

Thus, empirical studies that have tested a range of nuclear and mitochondrial genes across a diversity of exothermic taxa support the hypothesis that rates of genetic evolution are faster within species that occupy warmer habitats. Furthermore, the association between ambient temperature and rates of evolution come from thermal dimensions that include both elevation and latitude in terrestrial environments and both depth and latitude in the marine environment. Although many variables vary with latitude, elevation and depth, temperature is the only one that varies consistently in the same way with all three. Taken together these results suggest a general link between thermal energy and the tempo of genetic evolution within ectotherms.

5.3 Plausible explanations

5.3.1 Metabolic rate

It has been suggested that metabolic rate influences mutagenesis within species either via the rate of cell division and consequential replication error in the germline, or via the rate of DNA damage due to the production of oxygen free-radicals (Martin and Palumbi, 1993). Metabolic rates increase with temperature towards the equator among

ectotherms consistent with faster rates of genetic evolution in warmer environments (Allen *et al.*, 2006). However, body temperatures and metabolic rates in endotherms increase with latitude rather than decreasing (Anderson and Jetz, 2005). For example, a mammal living at -10 ^{0}C at a high polar latitude has a body temperature approximately 2.7 ^{0}C warmer and a basal metabolic rate (BMR) approximately 40% higher than a tropical mammal of similar size living at 25 ^{0}C (Clarke *et al.*, 2010). Thus, a positive association between metabolic rate and genetic evolution would predict microevolution for birds and mammals, in contrast to ectotherms, to be faster at higher latitudes not slower.

Two studies that have tested for latitudinal variation in the rate of genetic evolution among birds failed to find statistically significant results (Bromham and Cardillo, 2003, Weir and Schluter, 2008), whereas two others involving endotherms report significant associations. The largest study involving endotherms was one using 131 independent sister pairs of mammal species from 10 orders and 29 families (Gillman *et al.*, 2009). In this study, rates of genetic evolution were found to be independently faster for species at both lower latitudes and at lower elevations. The second of these, using 30 phylogenetically independent bird species pairs, also found faster rates in warmer environments (Gillman *et al.*, in press). The latter two studies therefore show the opposite trend to that expected if BMR had a positive influence on rates of genetic evolution.

Early studies with limited data that tested for a direct relationship between BMR and rates of genetic evolution found positive correlations (Bleiweiss, 1998, Martin and

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Palumbi, 1993). However, studies using much larger data sets of mammals (61 species from 14 orders, Bromham *et al.*, 1996) and more generally of metazoans (>300 species for 12 different genes, Lanfear *et al.*, 2007) have found no support for such a relationship. Basal metabolic rate would not, therefore, appear to be instrumental in controlling rates of genetic evolution. However, average annual metabolic rates may nonetheless be important (see discussion below).

5.3.2 Body mass

Average body mass has been found to correlate positively with latitude and inversely with temperature (Ashton *et al.*, 2000). Body mass also correlates inversely with rates of genetic evolution (Martin and Palumbi, 1993, Gillooly et al., 2005, Nunn and Stanley, 1998) and therefore the slower rates of evolution reported in cooler climates towards the poles might be due to the tendency for average body size to increase with latitude. However, rates of genetic evolution were also faster for subsets of warmer climate species (occurring at a lower latitude, elevation or depth) of mammals and fishes that are heavier than their cold climate sisters (Gillman et al., 2009, Wright et al., 2011). Furthermore, the general pattern of faster rates of evolution for warmer climate mammal species was weaker amongst a data subset in which the cooler climate species was larger. Similarly, in a study involving birds, body size was only weakly related to rates of evolution, whereas latitude and elevation show a strong relationship (Gillman *et al.*, in press). Furthermore, Cooper & Purvis (2009) found strong positive, rather than negative, correlations between body size and phenotypic evolution. Body size asymmetries

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cannot therefore explain associations between thermal environment and rates of genetic evolution.

5.3.3 Generation time.

Simpson (1953) suggested that, because the frequency of genetic replication error increases with the frequency of reproduction, species that have shorter generation times might be expected to have more mutations occurring over any given time period. More mutations occurring per unit time is then posited to result in faster rates of evolution. This hypothesis assumes that, for multicellular sexual organisms, mutations are either, more likely during sexual reproduction, and in particular during meiosis, than during germ-line mitotic cell divisions, or that the total number of germ-line cell divisions does not increase commensurately with generation time. It has also been proposed that generation time correlates positively with latitude. Therefore, shorter generation times at lower latitudes might explain faster rates of genetic evolution and diversification in the tropics (Rohde, 1992).

Inverse correlations between genetic evolution and generation time have been found among some groups of invertebrates and angiosperms (Smith and Donoghue, 2008, Thomas et al., 2010). This relationship is apparent for both synonymous and non-synonymous substitutions. Synonymous mutations are assumed to have little effect on phenotypic evolution and therefore are unlikely to be implicated in speciation and diversification, whereas non-synonymous mutations have a direct bearing on protein synthesis and phenotypic evolution. Thus, generation time provides a plausible

explanation for the relationships found between latitude, genetic evolution and diversification for some ectotherms.

However, the influence of generation time on diversification via genetic evolution among mammals is much less clear because, although negative relationships have been observed between generation time and synonymous substitutions within both nuclear and mitochondrial DNA, no correlations with non-synonymous substitutions have been found (Bromham et al., 1996, Welch et al., 2008, Nikolaev et al., 2007, Nabholz et al., 2008). If speciation is dependent on genetic evolution, it will largely involve non-synonymous protein altering substitutions. Generation time is therefore unlikely to influence diversification in mammals and nor can it be invoked to account for the negative association between non-synonymous genetic change and latitude reported for mammals by Gillman *et al.* (2009). Therefore, generation time does not appear to be implicated in putative latitudinal effects on rates of protein evolution and diversification among mammals.

5.3.4 Annual metabolic activity

Basal metabolic rate may not reflect long-term metabolic activity and yet if metabolic activity has an effect on mutation rates it will not be the basal or resting rate that will be important. Instead, maximum or long-term average metabolic rates are more likely to be causally linked to mutations. Therefore, total metabolic activity measured over a full twelve month cycle may yet prove to be associated with rates of evolution (Gillman *et al.*, 2009). In cooler environments, periods of hibernation or torpor that conserve energy in

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response to low energetic supply (McKechnie and Lovegrove, 2002, Munro et al., 2005) may reduce total metabolic activity over full annual cycles. It is therefore possible that mutagenesis, and therefore rates of genetic evolution, among birds and mammals might reflect metabolic averages that are reduced in cooler less productive environments. Such a hypothesis may be testable in the future if real time field monitoring of metabolic activity becomes practicable.

5.3.5 UV radiation

Ultra violet radiation is known to induce mutations and has been proposed as a possible mechanism inversely linking mutation rate with latitude (Rohde, 1992). Of all the environmental variables tested by Davies *et al.* (2004), UV radiation correlated with rates of genetic evolution among angiosperms most strongly. However, the latitudinal diversity gradient applies equally well to taxa largely shielded from UV radiation such as forest floor plants and animals, and marine animals as it does for those taxa exposed fully to UV radiation such as canopy trees (Hillebrand, 2004) and UV radiation generally increases with elevation and with aridity, whereas species richness tends to decline along these gradients. Furthermore, rates of genetic evolution have been shown to be slower among plants in more arid environments where UV radiation is higher (Goldie *et al.*, 2010) and to be slower among mammals and amphibians at higher elevations where UV radiation can also be higher (Gillman et al., 2009, Wright et al., 2010).

5.3.6 The Red Queen Hypothesis

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A third explanation for an association between climate and rates of genetic evolution among both ectotherms and endotherms is that metabolic rates may influence the rate of genetic evolution of ectotherms directly via a metabolic effect, whereas the rate of evolution among endotherms in the same community may depend on the rate of evolution among co-evolving ectotherms via a Red Queen effect (VanValen, 1973). That is, if the rate of evolution of a given species in a particular ecosystem is dependent on the rate of evolution among other species within that community with which it is co-evolving, the rate of genetic evolution among endotherms might be linked to the corresponding rate of evolution among ectotherms within the same community (Gillman et al., 2009, Rohde, 1992).

Given that rates of genetic evolution among ectotherms are more rapid in warmer locations it is possible that the biotic environment engineered by ectotherms may also be more dynamic in warmer locations. The probability of a mutation possessing a positive selection coefficient may be greater, if it occurs within an endothermic population living among more rapidly changing ectotherms, than if that same mutation were to occur within a population of endotherms living in a cooler more static ectothermic milieu (Gillman *et al.*, 2009). For example, if a mutation in a warm climate amphibian produced a defence against a mammalian predator, a subsequent mutation within a mammalian predator species that overcame this defence would be rapidly selected and fixed within the mammal species population. However, if the same 'anti-defence' mutation were to occur in a mammalian predator occupying a cooler environment, where the amphibians being predated had not produced the relevant 'defensive' mutation - because they were evolving their defences more slowly - the

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corresponding anti-defence mutation would not be selected and fixed in the predator population.

Therefore, endotherms living within a community in which the ectotherms, with which they interact, are evolving more rapidly might also be evolving more rapidly. The rate of fixation of novel alleles in endotherms may, on average, be faster in warmer climates due to a greater proportion of mutations possessing a selective advantage.

If it is assumed that the rate of synonymous fixation is dependent on the rate of mutation, then a Red Queen effect would be evidenced by an increase in non-synonymous evolution due to positive selection without a corresponding increase in the mutation rate, or rate of synonymous evolution. Therefore, the ratio of dN/dS should be elevated in warm climate species relative to cold climate species if there has been a Red Queen effect. However, there was no such elevation in dN/dS detected among the warm climate mammals (Gillman *et al.*, 2009).

A "Red Queen" dynamic equilibrium may exist within climate zones in terms of the pace of evolution. However, there is no empirical evidence to support the hypothesis that elevated selection due to a Red Queen effect occurs among mammals in warmer climates. By contrast, there is a body of empirical evidence strongly suggesting that the pace of evolution varies across thermal differentials. A balance in nature may exist with similar rates of evolution occurring among taxa within communities experiencing a uniform climatic environment, but the pace of evolution appears to vary among taxa in a systematic manner across climatic zones.

5.4 Cause or effect

The effective evolutionary time hypothesis predicts that faster rates of genetic evolution at lower, warmer, latitudes produces faster rates of diversification and ultimately higher diversity at these latitudes. This is perhaps a parsimonious concept given that adaptation appears to be limited by the supply of novel mutations and not just on standing genetic variation (Gossmann et al., 2012).

Using a selected angiosperm species from each of 86 sister families, Davies *et al.* (2004) found relationships between environmental energy and species richness, energy and rates of genetic evolution, and genetic evolution and species richness. However, genetic evolution dropped out of the regression model as a significant predictor variable for species richness when the model was simplified. Davies *et al.* suggest this indicates that the influence of energy on species richness is independent of the rate of genetic evolution. However, the rate of genetic evolution within each sister family in that study was represented by one species and therefore it is unclear whether or not genetic evolution within a single species from each family is sufficiently free from error to adequately characterise the predictor variable.

The alternative hypothesis to the effective evolutionary time hypothesis, under nearly neutral theory, is that faster rates of diversification cause an increase in the rate of genetic evolution (Pagel et al., 2006, Cardillo, 1999). Nearly neutral theory posits that small populations will accumulate a greater number of mildly deleterious mutations over a given time than a larger population (Ohta, 1992). This might occur because in small populations purifying selection that eliminates such mutations will be less efficient.

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Therefore, a greater number of mildly deleterious mutations will drift to fixation, resulting in an overall faster rate of genetic evolution, within smaller populations. It is assumed that during speciation, population sizes are small causing a spike in the rate of genetic evolution and therefore where diversification rates have been high, such as at low latitudes, rates of genetic evolution are posited to be commensurately high.

As far as we are aware there have been no studies that have tested the assumption that population sizes are substantially reduced during speciation or that if such reductions do occur whether populations remain small for long enough on an evolutionary time scale for this to significantly affect rates of genetic evolution. There are also surprisingly few studies, using adequate sample replication and controls for confounding factors, which have tested for an influence of population size on genetic evolution. Most studies that have tested for population size effects have used comparisons that have suffered from a lack of phylogenetic independence and therefore have an effective sample size of one to three (Woolfit and Bromham, 2005). In many cases the compared lineages, such as rodents versus primates, differ substantially in their biology thereby potentially confounding the influence due to population size on rates of genetic evolution with variables such as body weight, metabolic rate, temperature, generation time, and DNA repair mechanisms (Wright et al., 2009, Gillooly et al., 2005). Furthermore, justification of the assumptions about relative population sizes inherent in examinations of evolutionary rate and population size has usually been lacking.

The first well replicated study of population size effects used 70 phylogenetically independent contrasts between island and mainland taxa (Woolfit and Bromham, 2005).

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However, this study did not find a statistically significant difference in rates of genetic evolution between large and small populations. This result may have been due to the many contrasts in the study that were only related at familial or ordinal levels. Such distantly related comparisons introduce the likelihood of ancestral population-size variation such that it is unclear whether the majority of genetic evolution that has been measured has occurred in large or small populations. Wright *et al.* (2009) addressed this issue by using 48 sister species comparisons of birds where one of each species occurred on a small island and the other on a landmass at least five times larger. However, this study reported that smaller populations had slower rates of genetic evolution, not faster rates as predicted by nearly neutral theory.

If greater rates of diversification at lower latitudes were responsible for the observed pattern of faster rates of genetic evolution at such low latitudes under the nearly neutral model, we would expect genera that have temperate diversity that is greater than tropical diversity to show a reverse pattern in rates of genetic evolution. Wright *et al.* (2006) tested this prediction using a data subset in which plant genera were more speciose at high latitudes. However, among this data subset rates of genetic evolution remained significantly faster in the tropical species. This finding therefore does not support the nearly neutral hypothesis; greater rates of cladogenesis are not the cause of accelerated genetic evolution in warmer climates.

A related hypothesis, again invoking nearly neutral theory, is that the greater number of species per unit area in warmer latitudes results in smaller average population sizes

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and again the smaller populations are posited to evolve faster (Stevens, 1989). This hypothesis might be able to potentially explain faster rates of genetic evolution in warmer latitudes, but faster rates of genetic evolution have also been found among mammals, amphibians and birds at lower, warmer, elevations and population sizes tend to be larger at lower elevations not smaller (e.g. Patterson *et al.,* 1989).

Nearly neutral theory predicts that smaller populations will evolve faster than large due to an increase in the number of mildly deleterious mutations moving to fixation in the smaller populations (Ohta, 1992). Deleterious mutations will in most cases be limited to those mutations that affect protein synthesis (i.e. they are non-synonymous). By contrast, fixation of synonymous mutations is not predicted to be influenced by population size. Therefore, nearly neutral theory also predicts that smaller populations will have a greater non-synonymous to synonymous substitution ratio (dN/dS) than larger populations. If faster rates of genetic evolution in warmer lower latitude or elevation species are due to nearly neutral effects related to smaller populations, then we would expect the ratio of dN to dS to be elevated in the warmer climate species. This prediction was tested for mammals, amphibians and fish and in all cases, despite faster overall rates of genetic evolution, there was no evidence of elevated dN/dS in the warmer climate species (Wright et al., 2010, Wright et al., 2011, Gillman et al., 2009).

Similarly, if correlations between speciation and rates of genetic evolution, which have been found for a range of taxa (e.g. Webster et al., 2003, Smith and Donoghue, 2008), are due to nearly neutral effects of small populations persisting following speciation, then faster evolving lineages in putatively small populations will have a higher ratio of

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dN/dS than those evolving more slowly in larger populations. Lanfear *et al.* (2010) found a significant correlation between bird diversity and rates of genetic evolution within clades. However, they found no evidence of elevated dN/dS in faster evolving lineages and therefore concluded that the correlation was not due to nearly neutral effects. By contrast, Goldie *et al.* (2011) failed to find a correlation between rates of mammal evolution and speciation.

A different approach to this question was taken by Lancaster (2010). She reasoned that if small population sizes during speciation cause an increase in rates of genetic evolution, then substitution rate heterogeneity should also be apparent among clades, with shorter branches (that have been in the process of speciation for a greater proportion of their span) exhibiting higher rates of genetic evolution than longer branches. Using aged lineages, Lancaster (2010) found a positive correlation between substitution rates and rates of diversification among 13 clades of angiosperms, but failed to find a correlation between substitution rate variation and diversification rate. She therefore rejected the hypothesis that speciation had caused an increase in substitution rate.

The balance of evidence therefore suggests that greater rates of speciation are unlikely to be the cause of the higher tempo of genetic evolution at lower latitudes. However, the Goldie *et al.* (2011) result for mammals is difficult to reconcile with the effective evolutionary speed hypothesis, unless higher rates of extinction have been occurring in more rapidly evolving and diversifying clades involved in their study. There is therefore

a need for more testing of the hypothesis that rates of genetic evolution influence rates of diversification.

5.5 Influence of climate change on rates of evolution and diversification

If rates of genetic evolution and diversification are underpinned by available energy either via annual metabolic activity, or via a direct metabolic influence on ectotherm evolution and an indirect 'Red Queen' effect among endotherms, an increase in global temperatures would suggest faster rates of contemporary evolution and diversification. There is evidence of rapid evolution over contemporary timeframes (Stockwell *et al.*, 2003). However, counteracting any putative affect due to faster evolution will be the disruptive influence of climate change on species and their habitats and the consequential enhanced extinction rate. If we also consider elevated rates of extinction due to other anthropogenic influences such as overharvesting, pollution and habitat destruction (e.g. Brook *et al.*, 2003), it is hard to imagine how a process of diversification which operates over millions of years could possibly compensate for the contemporary extinction event that is occurring within a time frame of decades.

5.5 Conclusion

There is a substantial body of empirical evidence showing that rates of genetic evolution are elevated in species occurring in warmer environments at lower latitudes, lower elevations and in shallower waters. By contrast, attempts to understand what factors might be responsible for this relationship have not been able to identify a likely

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mechanism: there is either no evidence in support of putative mechanisms or contradictory evidence. Additionally, although the weight of evidence indicates that nearly neutral effects do not generate the association between rates of genetic evolution and rates of diversification, there remains a lack of unequivocal evidence demonstrating that rates of diversification are driven by genetic evolution.

If the effective Evolutionary Time hypothesis (or Evolutionary Speed hypothesis) is valid then we might expect enhanced rates of genetic evolution across the planet as global temperatures increase. Given enough time this might eventually lead to an increase in speciation. Counteracting, and overwhelming this effect, however, will be the exceptionally high rates of human driven contemporary extinctions.

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