Diversity **2013**, *5*, 811-823; doi:10.3390/d5040811

OPEN ACCESS

diversity

ISSN 1424-2818

www.mdpi.com/journal/diversity

Review

Patterns of Evolutionary Speed: In Search of a Causal Mechanism

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Received: 25 October 2013; in revised form: 21 November 2013 / Accepted: 25 November 2013 / Published: 2 December 2013

Abstract: The "integrated evolutionary speed hypothesis" proposes that the rate of genetic evolution influences all major biogeographical patterns of diversity including those associated with temperature, water availability, productivity, spatial heterogeneity and area. Consistent with this theory, rates of genetic evolution correspond with patterns of diversity and diversification. Here we review the mechanisms that have been proposed to explain these biogeographic patterns in rates of genetic evolution. Tests of several proposed mechanisms have produced equivocal results, whereas others such as those invoking annual metabolic activity, or a "Red Queen" effect, remain unexplored. However, rates of genetic evolution have been associated with both productivity mediated rates of germ cell division and active metabolic rates and these explanations therefore justify further empirical investigation.

Keywords: evolutionary speed; genetic evolution; latitude; population size; metabolic rate; diversity gradients

1. Introduction

The relationship between climate and biodiversity is now well established and, although attempts to explain this relationship along with the attendant latitudinal diversity gradient (LDG) began early in the nineteenth century [1], none of the many proposed hypotheses have yet to emerge as entirely satisfactory.

Rensch in 1959 [2] suggested that rates of evolution might be related to latitude via a generation time effect and that the LDG may be underpinned by the rate at which evolution can produce new species. The "effective evolutionary time hypothesis" by Rohde [3] proposed that this link might occur due to a relationship between temperature and both the rate of mutation and the rate of selection. However, Rohde's hypothesis was largely ignored for more than a decade before an attempt to test for a latitudinal pattern in the rate of genetic evolution was made [4]. Recently, Gillman and Wright [5] proposed the "integrated evolutionary speed hypothesis", which suggests that rates of genetic evolution influence all major biogeographic patterns of diversity including those associated with latitude, elevation, ocean depth, water availability, biome area, productivity and spatial heterogeneity.

Rates of genetic evolution are largely consistent with patterns of diversity and diversification [5]. However, the mechanisms that underpin geographic patterns in rates of genetic evolution are less clear. Several explanations have been suggested that invoke biotic mechanisms such as body size, metabolic rate, population size, generation time and longevity [6–10]. Others invoke abiotic factors such as temperature, water availability and biome productivity as primary causes that nonetheless act via biotic pathways [11,12]. Unfortunately, many of the proposed mechanisms are inconsistent with the empirical evidence. Here we briefly review the biogeographical patterns in variable rates of genetic evolution and then discuss potential mechanisms underpinning these patterns.

2. Biogeographical Patterns in Rates of Genetic Evolution

Wright *et al.* [4] were the first to test for a differential rate in genetic evolution among related species from different latitudes. They examined 24 *Metrosideros* species that occurred either in tropical or temperate latitudes and found evidence that greater genetic evolution had occurred among tropical species than had occurred among those from temperate regions. Rates of genetic evolution in the ITS-ETS regions of rDNA of the temperate species were approximately a third as fast as those occurring in tropical regions. In the same year Bromham and Cardillo [13] tested for a relationship between latitude and rates of cytochrome *b* and ND2 evolution (N = 33 and 22 respectively) using pyhlogenetically independent pairs of bird species. However, differences were not significant for either gene ($p = 0.36$ and $p = 0.06$).

A series of well replicated studies using more closely related species and a diversity of genes followed. These studies demonstrated faster rates of genetic evolution at lower latitudes in: (1) 18S, *rbcL* and *atpB* genes across 86 angiosperm families [14]; (2) ITS and 18S genes across 45 phylogenetically independent pairs of gymnosperm and angiosperm tree species [12,15]; (3) Cyt *b* and ribosomal 12S and 16S genes of 68 sister species pairs of teleost fish [16]; (4) mitochondrial RNA, 12S and 16S, genes across 188 species of Amphibians from 18 families of caudates and anurans [17] and; (5) RAG1, RAG2, C-mos, COX1, ND4 and Cyt *b* genes from turtles [18]. The same pattern is apparent among marine foraminifera. Using 22 pairs of marine foraminifera that were dated to first appearance from the fossil record, Allen *et al.* [19] demonstrated an exponential increase in the rate of nuclear DNA evolution with increasing ocean temperature. Faster rates of genetic evolution were also found for amphibians occurring at lower, warmer elevations and for marine teleost fish occurring in warmer, shallower waters [16,17].

All of the above studies involved exothermic organisms for which it can be assumed that environmental temperature is roughly equal to body temperature and therefore suggesting a link between body temperature and rates of genetic evolution. Thus, for a range of nuclear and mitochondrial genes from across a diversity of exothermic organisms, rates of genetic evolution are faster within species that have higher body temperatures. These associations between body temperature and rates of genetic evolution come from spatial dimensions that include elevation, latitude and oceanic depth on both land and within oceans.

What has surprised many researchers in the discipline is that the same patterns have emerged among endothermic mammals and birds. Bleiweiss [20] found faster rates of genetic evolution among hummingbird species occupying lower elevations and subspecies of Leaftossers in humid neotropical forests show a decreasing rate of genetic evolution with increasing elevation [21]. Although these studies did not involve phylogenetically independent sampling, they are consistent with a larger study using 30 independent pairs of bird species from 21 families that found faster rates of genetic evolution of cytochrome *b* in warmer environments, either at lower elevations, or at lower latitudes [22]. The largest study involving endotherms, however, was one using 131 independent sister pairs of mammal species from 10 orders and 29 families [23,24]. In this study, rates of genetic evolution in cytochrome *b* were found to be faster for species at both lower latitudes and at lower elevations.

Genetic diversity among populations within species has been shown to increase towards the tropics among plants, mammals, birds, reptiles, amphibians and fish [25–27] and greater phenotypic diversity at lower latitudes has been reported among bird species [28]. These intraspecific patterns of genetic diversity are consistent with interspecific patterns of evolutionary speed and the LDG.

Water availability is a key predictor of gradients in species richness, especially in warm climates where water is a limiting factor for productivity, and therefore it was predicted that evolutionary speed would also depend on precipitation [11]. Australia provided the ideal landscape for a natural experiment to test this prediction due to its longitudinal gradient in rainfall. Closely related tree species with similar latitudinal distributions were contrasted from wet and dry climates and as predicted the rate of genetic evolution was found to be faster among those species occurring in wet climates [29]. It remains to be seen whether further testing for this pattern affirms this as a general pattern or not.

Soil quality is a third key physical factor that influences species richness at continental scales; in natural systems greater diversity is generally found where soil productivity is also greater [30,31]. Preliminary as yet unpublished data from South America suggest that rates of genetic evolution are faster for species occupying richer more productive soils [32].

3. In Search of a Causal Mechanism

3.1. Body Mass

Many studies have found depressed rates of genetic evolution in larger bodied animals [7,33–39]. Body mass also correlates inversely with temperature (Bergmann's rule) [40] and inversely with population size [41]. Therefore, body mass offers a possible explanation for the faster rates of genetic evolution found for species with larger populations [42] and for species that occupy warmer environments, if these species have on average smaller body weights. It has been proposed that heat

loss mitigation arising from reduced surface area to volume ratios in larger animals acts to lower the metabolic activity required to maintain a given temperature set-point. The consequent reduction in metabolic rates in larger animals is thought to reduce rates of genetic evolution and speciation [6].

Larger plants are also associated with depressed rates of genetic evolution. Treeferns have slower rates than ferns that do not produce trunks [43], perennial flowering plants have slower rates than annuals [44], and a recent study of 138 families of flowering plants found that those that obtain greater maximum heights have slower rates of synonymous substitution within both nuclear and chloroplast genes [45]. The latter study took account of variation in species richness, temperature, ultraviolet radiation, latitude and growth form, and found no significant relationships with these variables.

By contrast, a body size effect on rates of evolution was not detected among 21 species of rodents [46], or among 330 species of invertebrates [47], or 54 species of poison frogs [48]. Cooper and Purvis [49] found a strong positive correlation between body size and phenotypic evolution rather than a negative correlation. Mammal and fish species occurring at warmer latitudes, that were heavier than their cold-climate sister species, were nonetheless also found to have faster rates of genetic evolution relative to their smaller cold-climate sister species; the opposite pattern to that expected due to body weight. Furthermore, the general pattern of slower rates of evolution for cold-climate species was weaker for contrasts in which the cold-climate species were larger than their warm-climate sister species [16,24].

Substitution rates among 214 species of turtles were correlated with latitude but not with body mass [18] and when closely related bird species (88 pairs) were compared, a much stronger pattern in evolutionary speed was found for latitude and elevation than for body size. Furthermore, when the data were pruned of comparisons in which latitude or elevation confounded the body size contrast, the body size effect was no longer detectable [22].

The results of these studies indicate that, although body mass may have an effect on rates of genetic evolution, body mass cannot provide an explanation for climate related rates of evolution. Furthermore, it is possible that climate is the underlying cause of slower rates of genetic evolution in species with larger bodies. Therefore, further investigations into the influence of body size that take account of biogeographic variables are required to resolve this question.

3.2. Generation Time and Longevity

Simpson [50] suggested in 1953 that species with longer generation times might be expected to incur mutations less frequently, because the opportunity for genetic replication error increases with the frequency of reproduction, and therefore such species might be expected to have slower rates of genetic evolution. Under this hypothesis mutations are expected to occur more often during meiosis than during germ-line mitotic cell divisions, or that there is not a commensurate increase in the total number of germ-line cell divisions with increasing generation times. The latter of these may be a reasonable assumption for some animal species but it is not likely to hold for plants [45]. Rensch [2] suggested that the LDG may have evolved because shorter generation times among animals at lower latitudes might have resulted in greater rates of evolutionary speed and diversification at these latitudes.

Inverse relationships between both synonymous and non-synonymous substitutions and generation time have been found among invertebrates and angiosperms [44,51,52]. However, although generation time among mammals has been negatively correlated with synonymous substitution rate in both nuclear and mitochondrial DNA, no such correlations have been found with non-synonymous substitutions [10,53–55]. Generation time therefore, does not appear to provide an explanation for faster rates of both synonymous and non-synonymous genetic evolution in lower latitude mammals. Furthermore, if diversification is dependent on molecular evolution, it will mostly occur via non-synonymous substitutions that produce protein evolution.

Greater longevity might reduce the species level mutation rate because longer lived organisms are likely to have more efficient DNA repair mechanisms [7]. Similarly, mammal longevity has been negatively correlated with synonymous substitution rate, but not with non-synonymous substitution rate [10,54] and longevity was not related to synonymous substitution rate among turtles [18]. The results of these studies, although few in number, suggest that gradients in average longevity are not likely to be the dominant cause of latitudinal patterns in genetic evolution or speciation.

3.3. Metabolic Rate

Metabolic rate is thought to influence the rate of mutation within species either via the number of cell divisions occurring over a given time, thereby affecting the replication error in the germ cell line, or via the rate of DNA damage due to the production of oxidative free radicals, or both [7]. Martin and Palumbi [7] found a relationship between basal metabolic rate (BMR) of mammals and rates of genetic evolution, and Bleiweiss [35] found a similar relationship among birds. By contrast, more recent studies using much larger data sets (61 species of mammals from 14 orders and more than 300 species of metazoans) have failed to support those earlier findings [34,56].

Allen *et al.* [19] developed a model for a relationship between mass specific metabolic rate (calculated from body mass and environmental temperature) and both genetic evolution and diversification. They presented empirical data in support of this model using marine foraminifera. There is also empirical support for such a relationship among North American fresh water fish [57,58]; whereas, studies using large data sets have found no support for a relationship between BMR and rates of genetic evolution in animals [34,56].

Metabolic rates and rates of genetic evolution both increase with temperature towards the equator among ectotherms, e.g., [6,17]. However, body temperatures and BMR in endotherms increase with latitude rather than decreasing [59,60]. Therefore, under the metabolic theory we would expect genetic evolution to be slower at lower latitudes for birds and mammals in contrast to the observed pattern of faster rates at lower latitudes for these taxa.

However, BMR may not reflect long-term metabolic activity over a full twelve month cycle and may not therefore be the relevant variable to measure when seeking to uncover a role for metabolic activity in governing the tempo of evolution. In cooler environments at higher latitudes or elevations, periods of torpor or hibernation among birds and mammals that conserve energy [61,62] may reduce total metabolic activity over full reproductive cycles. Therefore, average annual metabolic rates or maximum active metabolic rates are more likely to be variables associated with mutation rates and diversification [24].

Periods of slower growth caused by water stress, cooler temperatures or shorter growing seasons will reduce annual metabolic activity in plants and animals and therefore potentially reduce damage to DNA by oxidative free radicals, and fewer cell divisions per unit of time associated with slower growth rates should also reduce DNA replication error [12,24]. Reduced replication error and/or DNA damage should result in fewer mutations and slower genetic evolution. Testing the influence of annual metabolic activity on rates of genetic evolution is likely to become possible in the future when real time field monitoring of metabolic activity becomes available.

Lanfear *et al.* [45] lend support to the idea that growth rates, or productivity, influence rates of genetic evolution. As described above, they found that plant families with taller average maximum heights have slower rates of synonymous genetic evolution than families with shorter plants. The rate of growth in plants slows as they get larger and reproductive tissue develops from somatic tissue at the meristem. Therefore, Lanfear *et al.* [45] suggest that the average rate of cell division preceding reproduction is lower in taller plants than in shorter plants. Lower mutation rates associated with slower growth rates therefore provides a parsimonious explanation for the slower rates of genetic evolution they found in taller plants.

Santos [48] found no association between rates of genetic evolution and mass-specific BMR in poison fogs (54 species), but instead found a strong positive association between active metabolic rates and rates of both mitochondrial and nuclear evolution among these species. He suggests the mechanism involving active metabolic rate might be the occurrence of partial hypoxia in germ cells during high levels of physical activity when oxygen is targeted to skeletal muscles, or the occurrence of hyperoxia immediately following physical activity as increased blood flow and reoxygenation produces a pulse in oxidative free radicals. Both hypoxia and hyperoxia have been associated with DNA damage in flies, fish, amphibians, reptiles and endotherms, references within [48].

Therefore, both average metabolic rate and active metabolic rate might influence rates of genetic evolution in a systematic manner across climate gradients; the former acting via cell division rate (replication error) and the later via DNA damage during or following physical activity. Both of these possibilities require further empirical examination.

3.4. The Red Queen Hypothesis

If metabolic rates influence the evolutionary speed of ectotherms, but not endotherms, the rate of genetic evolution among endotherms may nonetheless depend on that of co-evolving ectotherms in the same community via a Red Queen effect [24,63]. More rapid evolution among ectotherms in warmer locations via a direct effect of body temperature on mutation rate will result in more rapid changes in the biotic environment of homeotherms. The probability of a given mutation having a selective advantage will be greater, if it occurs within an endothermic population living in an environment that is changing more rapidly than if exactly the same mutation were to occur within a population of endotherms living in a cooler more stable biotic environment [24]. That is, the substitution rate among endotherms might be faster in warmer climates at lower latitudes where a greater proportion of mutations have a selective advantage due to a more rapidly changing biotic environment.

Thus, endotherms living among ectotherms that are evolving and diversifying more rapidly might themselves also evolve and diversify more rapidly. However, this hypothesis is yet to be tested and therefore remains speculative at this time.

3.5. UV Radiation

Rohde [3] proposed that ultra violet radiation, known to induce mutations, might increase mutation rates at low latitudes. UV radiation has been correlated with rates of genetic evolution among angiosperm families [14]. However, the LDG applies equally to taxa such as marine biota and sub-canopy plants and animals as it does to taxa more heavily exposed to UV radiation [64]. Furthermore, UV radiation often increases with elevation and with decreasing water availability. Both of these patterns are contrary to patterns of species richness and rates of genetic evolution, e.g., [17,24,29].

3.6. Population Size

Faster rates of genetic evolution in warmer climates (at lower latitudes or elevations or water depth) could be due to nearly neutral population size effects if effective population sizes in warm climates are small relative to those in cooler climates. Nearly neutral theory predicts an inverse relationship between substitution rate and population size [65,66], because a greater proportion of mildly deleterious mutations are expected to survive in small populations where purifying selection is less efficient [67]. Mutations that are mildly deleterious will be largely confined to those genes that affect protein synthesis (*i.e.*, non-synonymous substitutions). Fixation of synonymous mutations under nearly neutral theory, by contrast, is predicted to be independent of population size. Therefore, the ratio of non-synonymous to synonymous substitutions (dN/dS) will be elevated in populations in warmer climates if nearly neutral effects account for faster overall rates of evolution in these climates [68].

Despite the four decades that have passed since the inception of this theory, empirical tests of these key predictions have been few and the results equivocal [69]. Until recently tests have suffered from design limitations that include a lack of phylogenetic independence between contrasts [68], population size comparisons that are confounded by fundamental physiological differences or involve comparisons across large phylogenetic distances such as contrasts between free living microbes and endosymbiotics [70], or humans *versus* rodents [33]. Contrasts have also been made that confound population size with differences in body sizes, or latitudinal distributions. Furthermore, justification of assumptions about relative population sizes has often been weak.

The first well replicated study to test for a relationship between effective population size (EPS) and rates of overall genetic evolution, using 70 independent contrasts between island taxa (small EPS) and continental taxa (large EPS), produced a non-significant result and although dN/dS was elevated in island taxa, this was not statistically significant when applying a two-tail test [68]. Many of the contrasts in this study, however, were between different genera or different families and so a large proportion of the genetic divergence between the contrasted taxa was likely to have occurred in populations that differed substantially in size and location to those of the extant species. Wright *et al.* [42] followed with a study that was similar but instead used 48 closely related bird species (mostly sister species) occurring on land masses that differed in extent, by a factor of five or more. This study found faster rates of genetic evolution in the species occurring on larger land masses where it is reasonable to

assume that on average they have existed with a larger EPS since divergence. Rates of genetic evolution also appear to have increased as human populations have grown [71]. However, preliminary work on passerines suggests faster rates of non-synonymous substitution in smaller populations, consistent with the predictions of nearly neutral theory [72] and therefore putatively smaller populations at lower latitudes and elevations and in shallower waters could potentially explain faster rates of genetic evolution in these environments.

Neutral mutations (synonymous mutations) are not predicted to be influenced by population size so a population size effect will result in elevated non-synonymous substitutions and elevated dN/dS in those species with smaller population sizes. This prediction was tested in two of the studies reporting faster rates of genetic evolution in warmer environments (one involving fish and one involving mammals). In both cases dN/dS was found to be similar for species in cool and warm environments at different latitudes, elevations and ocean depths [16,24], suggesting the results were unlikely to be due to nearly neutral effects. Rates of genetic evolution in non-functional gene regions, not predicted to be affected by population size, have also been found to be faster in warmer climates [12]. However, dS may not be entirely neutral and therefore elevated dS might also occur in warm climates due to small populations, thereby ameliorating any effect on dN/dS.

The second possibility is that the greater number of speciation events that lead to higher diversity in lower latitude taxa involve population bottlenecks that cause temporary spikes in dN/dS and therefore elevate overall rates of genetic evolution in these species. Although the mechanism is slightly different, the prediction for dN/dS is the same as above and so the empirical studies cited above also fail to support this explanation. In addition, under this hypothesis we would expect atypical taxa with greater temperate diversity than tropical diversity to also have atypically faster overall rates of genetic evolution among species in temperate zones. This prediction was tested by Wright *et al.* [12] using a data subset of plant genera with more species at high latitudes rather than at low latitudes. Within this data subset, rates of genetic evolution were nonetheless faster in the low latitude species. Again this result fails to support a nearly neutral explanation for faster rates of evolution in warm-climate species.

The integrated evolutionary speed hypothesis, in contrast to the nearly neutral theory, predicts that faster rates of genetic evolution in larger populations will produce faster rates of genetic evolution, adaptive speciation and ultimately higher diversity. This premise is based on the potential for adaptive mutations arising in a population increasing with the number of reproducing individuals in the population. It has been well established that larger populations generally contain greater genetic diversity than smaller populations, e.g., [73,74] and experimental work with *Escherichia coli* has demonstrated that increasing population size leads to increased genetic diversity [75] and such diversity is likely to be an important precursor for adaptive speciation. Adaptive genetic evolution was found to increase in eukaryotes as population size increases [76] and, although not all speciation is adaptive, adaptive genetic evolution associated with populations size might be more pertinent to putative links with diversity patterns than is nearly neutral deleterious evolution. Clearly there is a requirement for much more empirical investigation into these questions.

In summary, there is conflicting evidence on the effect population size has on rates of genetic evolution, but on the basis of the limited data available, population size does not appear to be the cause of faster rates in warmer environments. The component of genetic evolution predicted to be elevated in small populations under nearly neutral theory is slightly deleterious, whereas the component of genetic

evolution predicted to increase with increasing population size is that which is selectively positive and this latter component might be more likely to contribute to adaptive evolution and speciation.

4. Conclusions

The speed of genetic evolution within a range of genes appears to be higher among both ectothermic and endothermic taxa occupying warmer, wetter or more productive climates and adaptive evolution appears to be greater in larger populations. All of these patterns in rates of genetic evolution are consistent with patterns of diversity and may therefore provide a common mechanism underpinning such patterns of diversity.

A general explanation for biogeographic patterns in rates of genetic evolution does not appear to be due to body size, nearly neutral population size effects, UV radiation, or basal metabolic rate, although these factors may nonetheless have some influence. Total annual metabolic activity or a red Queen effect linking the rate of evolution in homeotherms to that of ectotherms, remain as possible explanations, but neither hypothesis has been tested empirically. There is some evidence that the average rate of cell division, as determined by maximum plant size and/or productivity, influences the real time mutation rate. Active metabolic rate may also influence mutation rate. These relationships potentially provide a general explanation for geographical patterns in both genetic evolution and species richness.

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Von Humboldt, A. *Ansichten der Natur mit wissenschaftlichen Erlauterungen* (in German); Stuttgart, J.G. Cotta: Tubingen, Germany, 1808.
2. Rensch, B. *Evolution above the Species Level*; Methuen: London, UK, 1959.
3. Rohde, K. Latitudinal gradients in species diversity: The search for the primary cause. *Oikos* **1992**, *65*, 514–527.
4. Wright, S.D.; Gray, R.D.; Gardner, R.C. Energy and the rate of evolution: Inferences from plant rDNA substitution rates in the western Pacific. *Evolution* **2003**, *57*, 2893–2898.
5. Gillman, L.N.; Wright, S.D. Species richness and evolutionary speed: The influence of temperature, water and area. *J. Biogeogr.* **2013**, doi:10.1111/jbi.12173.
6. Allen, A.P.; Gillooly, J.F. Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecol. Lett.* **2006**, *9*, 947–954.
7. Martin, A.P.; Palumbi, S.R. Body size, metabolic rate, generation time, and the molecular clock. *Proc. Natl. Acad. Sci. USA* **1993**, *90*, 4087–4091.
8. Cardillo, M. Latitude and rates of diversification in birds and butterflies. *Proc. Biol. Sci.* **1999**, *266*, 1221–1225.
9. Stevens, G.C. The latitudinal gradient in geographical range: How so many species coexist in the tropics. *Am. Nat.* **1989**, *133*, 240–256.

10. Nabholz, B.; Glémin, S.; Galtier, N. Strong variations of mitochondrial mutation rate across mammals—the longevity hypothesis. *Mol. Biol. Evol.* **2008**, *25*, 120–130.
11. Gillman, L.N.; Wright, S.D. Molecular evolution has wheels in the tropics. *Biologist* **2007**, *54*, 195–199.
12. Wright, S.; Keeling, J.; Gillman, L. The road from Santa Rosalia: A faster tempo of evolution in tropical climates. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 7718–7722.
13. Bromham, L.; Cardillo, M. Testing the link between the latitudinal gradient in species richness and rates of molecular evolution. *J. Evol. Biol.* **2003**, *16*, 200–207.
14. Davies, T.; Savolainen, V.; Chase, M.; Moat, J.; Barraclough, T. Environmental energy and evolutionary rates in flowering plants. *Proc. Biol. Sci.* **2004**, *271*, 2195–2200.
15. Gillman, L.N.; Keeling, D.J.; Gardner, R.C.; Wright, S.D. Faster evolution of highly conserved DNA in tropical plants. *J. Evol. Biol.* **2010**, *23*, 1327–1330.
16. Wright, S.D.; Ross, H.A.; Keeling, D.J.; McBride, P.; Gillman, L.N. Thermal energy and the rate of genetic evolution in marine fishes. *Evol. Ecol.* **2011**, *25*, 525–530.
17. Wright, S.D.; Gillman, L.N.; Ross, H.A.; Keeling, D.J. Energy and the tempo of evolution in amphibians. *Global Ecol. Biogeogr.* **2010**, *19*, 733–740.
18. Lourenço, J.M.; Glémin, S.; Chiari, Y.; Galtier, N. The determinants of the molecular substitution process in turtles. *J. Evol. Biol.* **2013**, *26*, 38–50.
19. Allen, A.P.; Gillooly, J.F.; Savage, V.M.; Brown, J.H. Kinetic effects of temperature on rates of genetic divergence and speciation. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 9130–9135.
20. Bleiweiss, R. Slow rate of molecular evolution in high-elevation hummingbirds. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 612–616.
21. D'Horta, F.M.; Cuervo, A.M.; Ribas, C.C.; Brumfield, R.T.; Miyaki, C.Y. Phylogeny and comparative phylogeography of Sclerurus (Aves: Furnariidae) reveal constant and cryptic diversification in an old radiation of rain forest understorey specialists. *J. Biogeogr.* **2013**, *40*, 37–49.
22. Gillman, L.N.; McCowan, L.S.C.; Wright, S.D. The tempo of genetic evolution in birds: Body mass, population size and climate effects. *J. Biogeogr.* **2012**, *39*, 1567–1572.
23. Gillman, L.N.; McBride, P.; Keeling, D.J.; Ross, H.A.; Wright, S.D. Are rates of molecular evolution in mammals substantially accelerated in warmer environments? Reply. *Proc. Biol. Sci.* **2011**, *278*, 1294–1297.
24. Gillman, L.N.; Ross, H.A.; Keeling, J.D.; Wright, S.D. Latitude, elevation and the tempo of molecular evolution in mammals. *Proc. Biol. Sci.* **2009**, *276*, 3353–3359.
25. Adams, R.I.; Hadly, E.A. Genetic diversity within vertebrate species is greater at lower latitudes. *Evol. Ecol.* **2013**, *27*, 133–143.
26. Chek, A.A.; Austin, J.D.; Lougheed, S.C. Why is there a tropical–temperate disparity in the genetic diversity and taxonomy of species? *Evol. Ecol. Res.* **2003**, *5*, 69–77.
27. Eo, S.H.; Wares, J.P.; Carroll, J.P. Population divergence in plant species reflects latitudinal biodiversity gradients. *Biol. Lett.* **2008**, *4*, 382–384.
28. Martin, P.R.; Tewksbury, J.J. Latitudinal variation in subspecific diversification of birds. *Evolution* **2008**, *62*, 2775–2788.
29. Goldie, X.; Gillman, L.N.; Crisp, M.; Wright, S.D. Evolutionary speed limited by water in arid Australia. *Proc. Biol. Sci.* **2010**, *277*, 2645–2653.

30. Gillman, L.N.; Wright, S.D. The influence of productivity on the species richness of plants: A critical assessment. *Ecology* **2006**, *87*, 1234–1243.
31. Gillman, L.N.; Wright, S.D. Mega mistakes in meta-analyses: Devil in the detail. *Ecology* **2010**, *91*, 2550–2552.
32. Mazinani, P.; Gillman, L.N.; Wright, S.D. *The relationship between Amazonian Soils and Rates of Genetic Evolution*; University of Auckland, Auckland, New Zealand, 2013; unpublished work.
33. Wu, C.I.; Li, W.H. Evidence for higher rates of nucleotide substitution in rodents than in man. *Proc. Natl. Acad. Sci. USA* **1985**, *82*, 1741–1745.
34. Bromham, L.; Rambaut, A.; Harvey, P.H. Determinants of rate variation in mammalian DNA sequence evolution. *J. Mol. Evol.* **1996**, *43*, 610–621.
35. Bleiweiss, R. Relative-rate tests and biological causes of molecular evolution in hummingbirds. *Mol. Biol. Evol.* **1998**, *15*, 481–491.
36. Nunn, G.B.; Stanley, S.E. Body size effects and rates of cytochrome *b* evolution in tube-nosed seabirds. *Mol. Biol. Evol.* **1998**, *15*, 1360–1371.
37. Bromham, L. Molecular clocks in reptiles: Life history influences rate of molecular evolution. *Mol. Biol. Evol.* **2002**, *19*, 302–309.
38. Gillooly, J.F.; Allen, A.P.; West, G.B.; Brown, J.H. The rate of DNA evolution: Effects of body size and temperature on the molecular clock. *Proc. Natl. Acad. Sci. USA* **2005**, *102*, 140–145.
39. Fontanillas, E.; Welch, J.J.; Thomas, J.A.; Bromham, L. The influence of body size and net diversification rate on molecular evolution during the radiation of animal phyla. *BMC Evol. Biol.* **2007**, doi:10.1186/1471-2148-7-95.
40. Ashton, K.G.; Tracy, M.C.; de Queiroz, A. Is Bergmann's rule valid for mammals. *Am. Nat.* **2000**, *156*, 390–415.
41. White, E.P.; Ernest, S.K.M.; Kerkhoff, A.J.; Enquist, B.J. Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* **2007**, *22*, 323–330.
42. Wright, S.D.; Gillman, L.N.; Ross, H.A.; Keeling, J.D. Slower tempo of microevolution in island birds: Implications for conservation biology. *Evolution* **2009**, *63*, 2276–2287.
43. Korall, P.; Schuettpelz, E.; Pryer, K.M. Abrupt deceleration of molecular evolution linked to the origin of arborescence in ferns. *Evolution* **2010**, *64*, 2786–2792.
44. Smith, S.A.; Donoghue, M.J. Rates of molecular evolution are linked to life history in flowering plants. *Science* **2008**, *322*, 86–89.
45. Lanfear, R.; Ho, S.Y.W.; Davies, T.J.; Moles, A.T.; Aarssen, L.; Swenson, N.G.; Warman, L.; Zanne, A.E.; Allen, A.P. Taller plants have lower rates of molecular evolution. *Nat. Commun.* **2013**, *4*, Article 1879.
46. Spradling, T.A.; Hafner, M.S.; Demastes, J.W. Differences in rate of cytochrome-*b* evolution among species of rodents. *J. Mammal.* **2001**, *82*, 65–80.
47. Thomas, J.A.; Welch, J.J.; Woolfit, M.; Bromham, L. There is no universal molecular clock for invertebrates, but rate variation does not scale with body size. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 7366–7371.
48. Santos, J.C. Fast molecular evolution associated with high active metabolic rates in poison frogs. *Mol. Biol. Evol.* **2012**, *29*, 2001–2018.

49. Cooper, N.; Purvis, A. What factors shape rates of phenotypic evolution? A comparative study of cranial morphology of four mammalian clades. *J. Evol. Biol.* **2009**, *22*, 1024–1035.
50. Simpson, G.G. *The Major Features of Evolution*; Columbia University Press: New York, NY, USA, 1953.
51. Thomas, J.A.; Welch, J.J.; Lanfear, R.; Bromham, L. A generation time effect on the rate of molecular evolution in invertebrates. *Mol. Biol. Evol.* **2010**, *27*, 1173–1180.
52. Andreasen, K.; Baldwin, B.G. Unequal evolutionary rates between annual and perennial lineages of checker mallows (Sidalcea, Malvaceae): Evidence from 18S–26S rDNA internal and external transcribed spacers. *Mol. Biol. Evol.* **2001**, *18*, 936–944.
53. Nikolaev, S.I.; Montoya-Burgos, J.I.; Popadin, K.; Parand, L.; Margulies, E.H.; National Institutes of Health Intramural Sequencing Center Comparative Sequencing Program; Antonarakis, S.E. Life-history traits drive the evolutionary rates of mammalian coding and noncoding genomic elements. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 20443–20448.
54. Welch, J.; Bininda-Emonds, O.; Bromham, L. Correlates of substitution rate variation in mammalian protein-coding sequences. *BMC Evol. Biol.* **2008**, doi:10.1186/1471-2148-8-53.
55. Tsantes, C.; Steiper, M.E. Age at first reproduction explains rate variation in the strepsirrhine molecular clock. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 18165–18170.
56. Lanfear, R.; Thomas, J.A.; Welch, J.J.; Brey, T.; Bromham, L. Metabolic rate does not calibrate the molecular clock. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 15388–15393.
57. April, J.; Hanner, R.H.; Mayden, R.L.; Bernatchez, L. Metabolic rate and climatic fluctuations shape continental wide pattern of genetic divergence and biodiversity in fishes. *PLoS One* **2013**, *8*, e70296.
58. Estabrook, G.F.; Smith, G.R.; Dowling, T.E. Body mass and temperature influence rates of mitochondrial DNA evolution in North American cyprinid fish. *Evolution* **2007**, *61*, 1176–1187.
59. Anderson, K.J.; Jetz, W. The broad-scale ecology of energy expenditure of endotherms. *Ecol. Lett.* **2005**, *8*, 310–318.
60. Clarke, A.; Rothery, P.; Isaac, N.J.B. Scaling of basal metabolic rate with body mass and temperature in mammals. *J. Anim. Ecol.* **2010**, *79*, 610–619.
61. McKechnie, A.E.; Lovegrove, B.G. Avian facultative hypothermic responses: A review. *Condor* **2002**, *104*, 705–724.
62. Munro, D.; Thomas, D.W.; Humphries, M.M. Torpor patterns of hibernating eastern chipmunks *Tamias striatus* vary in response to the size and fatty acid composition of food hoards. *J. Anim. Ecol.* **2005**, *74*, 692–700.
63. Van Valen, L.M. A new evolutionary law. *Evol. Theory* **1973**, *1*, 1–30.
64. Hillebrand, H. On the generality of the latitudinal diversity gradient. *Am. Nat.* **2004**, *163*, 192–211.
65. Ohta, T. Population size and the rate of evolution. *J. Mol. Evol.* **1972**, *1*, 305–314.
66. Ohta, T. The nearly neutral theory of molecular evolution. *Annu. Rev. Ecol. Systemat.* **1992**, *23*, 263–286.
67. Ohta, T.; Gillespie, J.H. Development of neutral and nearly neutral theories. *Theor. Popul. Biol.* **1996**, *49*, 128–142.
68. Woolfit, M.; Bromham, L. Population size and molecular evolution on islands. *Proc. Biol. Sci.* **2005**, *272*, 2277–2282.

69. Bromham, L.; Leys, R. Sociality and the rate of molecular evolution. *Mol. Biol. Evol.* **2005**, *22*, 1393–1402.
70. Woolfit, M.; Bromham, L. Increased rates of sequence evolution in endosymbiotic bacteria and fungi with small effective population size. *Mol. Biol. Evol.* **2003**, *20*, 1545–1555.
71. Hawks, J.; Wang, E.T.; Cochran, G.M.; Harpending, H.C.; Moyzis, R.K. Recent acceleration of human adaptive evolution. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 20753–20758.
72. McBride, P.; Wright, S.D.; Gillman, L.N. The effect of population size on rates and patterns of molecular evolution in New World passerines. Auckland University of Technology, Auckland, New Zealand. Unpublished work, 2013.
73. Bazin, E.; Glemin, S.; Galtier, N. Population size does not influence mitochondrial genetic diversity in animals. *Science* **2006**, *312*, 570–572.
74. Hughes, A.L. Reduced microsatellite heterozygosity in island endemics supports the role of long-term effective population size in avian microsatellite diversity. *Genetica* **2010**, *138*, 1271–1276.
75. Stevens, M.H.H.; Sanchez, M.; Lee, J.; Finkel, S.E. Diversification rates increase with population size and resource concentration in an unstructured habitat. *Genetics* **2007**, *177*, 2243–2250.
76. Gossmann, T.I.; Keightley, P.D.; Eyre-Walker, A. The effect of variation in the effective population size on the rate of adaptive molecular evolution in eukaryotes. *Genome Biol. Evol.* **2012**, *4*, 658–667.