
Latitude and rates of diversification in birds and butterflies

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Central to many explanations of latitudinal diversity gradients is the idea that rates of species diversification increase towards the equator. However, there have been few explicit tests of whether or not this pattern exists. Using sister-group analyses to compare 48 clades of passerine birds and swallowtail butterflies from different latitudes, I found evidence that relative rates of diversification per unit time are indeed higher towards the equator. This pattern is explicable in terms of abiotic factors which vary continuously with latitude, and may be further enhanced by diversity-dependent speciation and extinction processes.

Keywords: extinction; latitudinal gradients; sister groups; speciation; species richness

1. INTRODUCTION

Latitudinal gradients in the numbers of species are among the most general patterns in the natural world. However, the causes are still not fully understood, although numerous explanations have been proposed (see Rohde (1992) for a summary). In recent years opinion has begun moving away from equilibrium explanations, based largely on current ecological conditions (e.g. interactions among coexisting species), towards non-equilibrium, or historical, explanations (Ricklefs & Schluter 1993). Equilibrium hypotheses assume communities are saturated with species and that latitudinal diversity gradients result from an increase in the upper limit to diversity towards the equator. Non-equilibrium explanations assume the number of species in most communities is below saturation and that species richness is still increasing through evolutionary time. Under the non-equilibrium view, latitudinal diversity gradients are caused by either or both of two mechanisms: (i) tropical lineages tend to be older, so have had more time to accumulate species (Farrell & Mitter 1993; Ricklefs & Schluter 1993)—under this scenario, most of the major clades have roots in the tropics and the temperate members of these clades are derived from more recent invasions of the temperate zone; (ii) the tropics have higher rates of species diversification (i.e. speciation minus extinction) than higher latitudes (Rohde 1992; Rosenzweig 1975, 1995)—under this scenario more species should have accumulated in lower versus higher latitudes, even if the time available has been the same.

It has been predicted from theory that diversification should be faster in the tropics than higher latitudes. Rohde (1992) suggested that higher mean temperatures at lower latitudes lead to faster growth rates, selection and speciation. Rosenzweig (1975, 1995) argued that the larger surface area of the tropics allows for larger geographic ranges, inhibiting extinction and increasing

opportunities for allopatric speciation. However, there have been very few explicit tests of whether or not diversification is indeed faster in the tropics. A few studies have used fossil data to show that average taxonomic duration in some groups is shorter in tropical versus temperate assemblages (Stehli *et al.* 1969; Durazzi & Stehli 1972; Hecht & Agan 1972). This was interpreted as the result of higher rates of species origination in the tropics, although it sheds little light on patterns of accumulation of taxonomic diversity, and it was subsequently asserted that evidence for faster diversification in the tropics is equivocal (Stanley 1979). Given the importance of this idea for understanding latitudinal diversity gradients there is a need to supplement these previous studies with additional explicit tests for latitudinal bias in diversification rates.

A complementary approach to using fossil data in comparing rates of diversification is by phylogenetic methods such as sister-group analysis (Barraclough *et al.* 1998). Sister clades are, by definition, the same age, so a clade with more species than its sister clade has diversified at a faster rate. Therefore, under the hypothesis of faster diversification at lower latitudes, a clade of predominantly tropical species should be more speciose than its predominantly temperate sister clade, despite the fact they have both had equal time to diversify. This method provides phylogenetically independent replicate comparisons, and restricting comparisons to closely related sister taxa means that much extraneous variation may be eliminated from the analyses (Barraclough *et al.* 1998). The sister-group method also allows us to distinguish between the two non-equilibrium hypotheses for latitudinal diversity gradients. By comparing clades of equal age, the method factors out the explanation that tropical lineages are older and have had more time to diversify, allowing a direct comparison of diversification rates per unit time. A similar approach was taken by Farrell & Mitter (1993), but with only five tropical–temperate sister-group comparisons, their result (showing no latitudinal effect)

was equivocal. In this study, I identified a larger number of comparisons by treating latitude as a more or less continuous variable, rather than restricting the analysis to tropical versus temperate clades. In addition, the analysis presented here is global in scale. As test groups I used passerine birds (order Passeriformes) and swallowtail butterflies (family Papilionidae), both globally distributed groups for which phylogeny and geographic distributions are relatively well-known.

2. METHODS

The phylogenies used were Sibley & Ahlquist's (1990) DNA hybridization phylogeny of birds, and Hancock's (1978, 1983) morphological phylogeny of swallowtail butterflies. From these, I identified all possible pairs of monophyletic sister clades at the levels of tribe, subfamily and family for the passerines, and species group, subgenus and genus for the swallowtails. The analyses were restricted to these relatively recent phylogenetic levels in order to obtain a sufficient number of sister-group comparisons; this may also have served to minimize potential confounding effects of variation in palaeoclimate and palaeolatitude, which may have arisen if older clades were used.

Comparisons in which the two sister clades were latitudinally differentiated were identified by the following method. The latitudinal midpoint of the geographic range of every species was determined using published range maps, or for some passerine species, from the descriptions of distributions in Sibley & Monroe (1993). For each clade, a mean latitudinal midpoint was then calculated. I selected all pairs of sister clades for which these two means were separated by at least 10° latitude; this figure was chosen to maximize latitudinal separation while still allowing a sufficient number of comparisons to be identified. Clades were thus assigned as higher latitude or lower latitude. The number of species in the more speciose clade was divided by the number of species in the less speciose clade to give a species richness comparison. Comparisons were labelled positive if the lower-latitude clade was more speciose, negative if the higher-latitude clade was more speciose.

Under a null hypothesis of no latitudinal effect, the number of positive and negative species richness comparisons should be approximately equal. Sign tests were used to test for a significant departure from this expectation. I also considered the magnitudes of the species richness comparisons: under the null hypothesis, the differences in clade sizes should be approximately equal for both positive and negative comparisons. Wilcoxon's signed-ranks tests were used to test the significance of this pattern.

The possibility of the results being influenced by sampling artefact, arising from differences in clade size, should not be ignored. Clades with more species would be expected, simply by chance, to encompass a wider range of latitudinal midpoints. But whether this would bias mean latitudinal midpoints of larger clades towards the equator, away from the equator, or not all, is not obvious. To clarify this I carried out computer simulations where 'clades' of 5, 20, 50, 100 and 200 species were randomly selected from the entire list of species used in this study, with passerines and swallowtails being tested separately. For each random clade, the mean latitudinal midpoint was calculated. This was repeated 100 times to generate error around these means, which were then compared between the different clade sizes. This process was not intended to simulate the evolution of the geographic ranges of clades, but merely to test for a purely statistical effect of sample size on the latitudinal position of clades.

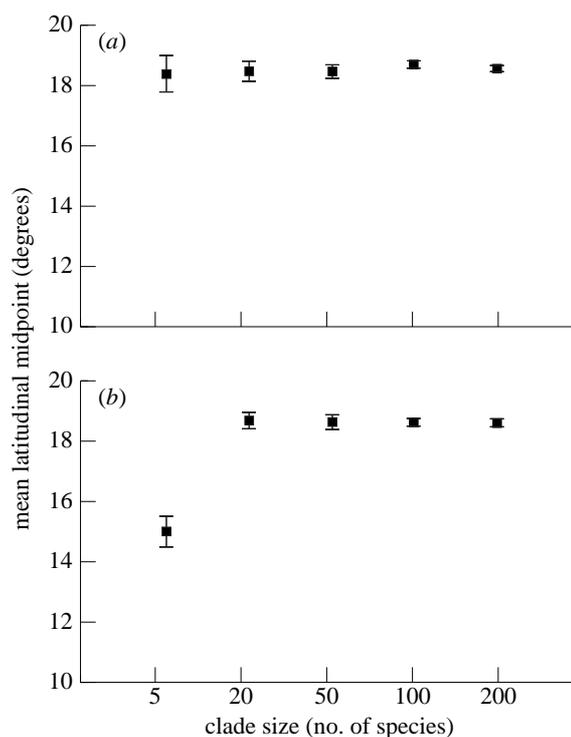


Figure 1. Results of simulation tests for effects of sampling artefact on mean latitudinal midpoints of clades. The points on the graphs represent the mean and s.e. (from 100 simulations) of the mean latitudinal midpoints for clades of 5, 20, 50, 100 and 200 species. Clades were selected at random from the complete list of species used in this study. (a) Passerines; (b) swallowtails.

3. RESULTS

Eleven passerine comparisons and 13 swallowtail comparisons which met the criterion of latitudinal separation were identified (table 1). For passerines, 10 out of 11 species richness comparisons were positive (i.e. the lower-latitude clade had more species than its higher-latitude sister clade), and for swallowtails, 10 out of 13 comparisons were positive. These results were significant at $p < 0.05$ under both sign tests and Wilcoxon's signed-ranks tests (table 2), supporting the hypothesis that diversification has been faster at lower latitudes within the period of time since divergence of the clades used. The simulation tests indicated that this pattern is not caused by sampling artefact (figure 1). The simulated 'clades' of all sizes had mean latitudinal midpoints of between 18° and 19°, with the exception of the smallest clade size (five species) for the swallowtails, which had a mean of 14.99°. This suggests that if any sampling effect does occur, it is likely to bias the latitude of the smallest swallowtail clades towards, not away from, the equator. Therefore, the result of the sister-group analysis was obtained despite, not because of, a possible sampling artefact.

4. DISCUSSION

This study has found a significant latitudinal effect on relative diversification rates between sister clades of passerines and swallowtails, which does not appear to be caused by sampling artefact. The method by which

Table 1. Sister groups used in the analyses: (a) passerines; (b) swallowtails

sister taxa	mean latitudinal midpoint (\pm s.d.)	number of species	species richness compar- ison
<i>(a)</i>			
Philepittidae	19 \pm 0.58	4	+3.5
Eurylaimidae	6 \pm 4.3	14	
Menuridae	31 \pm 2.88	4	+5
Ptilonorhynchidae	13 \pm 9.75	20	
Stipiturini	32 \pm 3.05	3	+5
Malurini	18 \pm 2.08	15	
Dasyornithinae	35 \pm 1.73	3	+20.33
Acanthizinae	21 \pm 12.57	61	
Mohouini	43 \pm 4.62	3	+18
Pachycephalini/ Falcunculini	12 \pm 10.14	54	
Bombacillini	52 \pm 5.51	3	+1.33
Ptilogonatin	17 \pm 8.72	4	
Certhiini	35 \pm 10.56	6	-6
Salpornithini	6	1	
Sylviini/Chamaeini	34 \pm 13.67	23	+10.13
Timaliini	17 \pm 23.97	233	
Artamini	18 \pm 11.61	24	+4.63
Oriolini	8 \pm 11.69	111	
Mimini	22 \pm 12.77	34	+3.35
Sturnini	1 \pm 19.86	114	
Fringillini	45 \pm 15.81	3	+55.33
Carduelini/ Drepanidini	23 \pm 20.1	166	
<i>(b)</i>			
<i>Parnassius tenedius</i> group	46	1	+4
<i>Parnassius charltonius</i> group	36 \pm 2.62	4	
<i>Luedorfa</i>	39 \pm 10.61	2	+2
<i>Bhutanitis</i>	27 \pm 2.88	4	
<i>Iphiclides</i>	38 \pm 6.36	2	+2
<i>Teinopalpus/Meandrusa</i>	18 \pm 8.26	4	
<i>Graphium pylades</i> group	17 \pm 6.66	4	-4
<i>Graphium ridleyanus</i> group	2	1	
<i>Graphium porthaon</i> group	14	1	+3
<i>Graphium illyris</i> group	3 \pm 2.3	3	
<i>Battus</i> group 1	24 \pm 6.25	3	+3.67
<i>Battus</i> group 2	11 \pm 8.59	11	
<i>Parides ascanius</i> group	21 \pm 7.89	11	+3.09
<i>Parides aeneas</i> group	9 \pm 7.58	34	
<i>Atrophaneura latreillei</i> group	25 \pm 3.59	14	-1.17
<i>Atrophaneura nox</i> group	10 \pm 8.52	12	
<i>Papilio glaucus/troilus</i> groups	34 \pm 8.23	8	+2.13
<i>Papilio scamander/homerus/</i> <i>zagreus</i> groups	12 \pm 9.73	17	
<i>Papilio bootes</i> group	25 \pm 3.51	5	+2.2
<i>Papilio memnon</i> group	8 \pm 5.41	11	
<i>Papilio</i> subgenus <i>Ellepone</i>	27	1	+11
<i>Papilio</i> subgenus <i>Chilasa</i>	9 \pm 5.77	11	
<i>Papilio delalandei</i> group	19 \pm 4.71	2	+2
<i>Papilio phorcas</i> group	8 \pm 7.9	4	
<i>Papilio palinurus/paris</i> groups	20 \pm 10.52	16	-2.67
<i>Papilio peranthus/ulysses</i> group	7 \pm 3.28	6	

Table 2. One-tailed *p*-values of statistical tests for latitudinal bias in species richness comparisons of sister clades

(All tests show that lower-latitude clades have significantly more species than their higher-latitude sister clades. $n = 11$ for passerines and 13 for swallowtails.)

	sign test	Wilcoxon's signed-ranks test
passerines	0.006	0.01
swallowtails	0.04	0.02

latitudinal positions of clades were determined means there will inevitably have been a certain degree of geographic range overlap among species from sister clades. Nonetheless, the criterion of at least 10° separation of mean latitudinal midpoints, and the relatively small ranges of most species (mean latitudinal span of 11.6° for passerines, 14.8° for swallowtails), means that despite overlap the sister groups chosen do largely inhabit different latitudes. Furthermore, it is clear that range overlap is more likely to have inflated type 2 rather than type 1 statistical error, so it should not alter the basic conclusion that there appears to be a latitudinal effect on rate of diversification in the two groups used here. Type 2 error may also have been inflated by the relatively small number of suitable comparisons identified, and by an undoubtedly high noise-to-signal ratio (due to the numerous determinants of diversification rates which do not vary latitudinally; see, for example, Owens *et al.* 1999).

The latitudinal effect on diversification rate also seems to be independent of the total area available to each clade. Among the passerines, there were two sister-group comparisons in which the less speciose clades were confined to relatively small islands which have been isolated for a long time (Philepittidae confined to Madagascar and Mohouini confined to New Zealand), so in these cases diversification may have been constrained by available area rather than latitude. However, the latitudinal effect was still significant after removal of these two comparisons from the analysis, despite the reduced degrees of freedom (sign test: $p = 0.019$; Wilcoxon's test: $p = 0.025$). Among the swallowtails, there were no clades whose ranges did not encompass parts of continents.

The result, therefore, seems to demonstrate a real pattern of latitudinal bias in diversification rates of passerines and swallowtails. This pattern is independent of the ages of clades, providing an explanation for latitudinal diversity gradients alternative to, or in addition to, the hypothesis that tropical lineages are older. It should be stressed that this is a preliminary study which has examined only two major taxa, and the generality of faster diversification at lower latitudes will need to be established by further studies which examine a wide range of additional taxa. The extent to which this is possible will, of course, be limited by the availability of adequate data on phylogenetic relationships and geographic distributions.

The treatment of latitude as a continuous variable in this analysis suggests that rates of diversification also approximate a continuous variation across latitudes, and

the global scale of the analysis augments this conclusion. Thus, whereas differences between clades in strictly tropical–temperate comparisons (particularly when limited to a single continent) might be explicable in terms of unique biogeographic histories, the result of this study suggests a causal mechanism which itself varies continuously with latitude. Therefore, this study is not entirely consistent with the idea that increasing land area towards the equator increases the rate of diversification, as land area does not increase towards the equator in a continuous fashion (Rosenzweig 1975). There are, however, a number of candidate abiotic explanations for continuously varying speciation and extinction rates across latitudes, which I briefly outline below, together with some counter arguments.

(a) *Temperature*

Mean ambient temperatures decrease continuously with latitude outside the tropical belt (Terborgh 1973). Rohde (1992) has argued that higher tropical temperatures cause faster growth and development of organisms, shorter generation times, and hence faster selection and speciation. Swallowtail generation times are shorter in the tropics (Tyler *et al.* 1994), but there is no evidence that the same applies to birds (Mayr 1976). However, generation time does not appear to affect speed of selection (Rosenheim & Tabashnik 1993; Mooers & Harvey 1994; Bromham *et al.* 1996), although it has been linked to the rate of neutral molecular evolution (Sibley & Ahlquist 1990; Martin & Palumbi 1993; Mooers & Harvey 1994; Bromham *et al.* 1996). Although rates of molecular evolution and species diversification may be correlated, the direction of causation is not clear (Barraclough *et al.* 1996, 1998).

(b) *Climatic variability*

Seasonality and unpredictability of climate increases away from the equator (Brown & Lomolino 1998) and may influence speciation and extinction rates by affecting the breadth of species' ecological tolerances. Species in more climatically variable regions tend to be eurytopic, or more widespread and generalist in their use of resources, while those in less variable regions tend to be stenotopic or more restricted and specialized (Pielou 1979). However, there is much debate over whether it is eurytopy or stenotopy that promotes faster diversification; indeed there is evidence to support either possibility (see Cracraft 1985; Owens *et al.* 1999).

(c) *Harshness*

Environmental harshness (expressed as a function of both the mean and annual dispersion of temperature and rainfall) has been claimed to cause latitudinal diversity gradients through control of extinction rates (Cracraft 1985). Regions of high harshness, such as high latitudes, lie outside the physiological tolerance ranges of a wide variety of species. In these regions, species require more energy to maintain homeostasis relative to their environments and fewer individuals can be supported, so the rate of extinction is higher. However, this argument has been dismissed as circular, on the grounds that the concept of harshness is itself defined by the number of species inhabiting an area (Terborgh 1973; Pielou 1979; Rohde 1992).

Each of the above explanations for faster diversification towards the equator has limitations, but in combination they may provide a plausible mechanism for an abiotic influence on speciation and extinction rates which vary continuously across latitudes. This mechanism would operate in the event of one species being split into two (whether through allopatric subdivision or dispersal), such that one daughter species is left occupying a more northerly range and the other a more southerly range. Once the more equatorial daughter clade has accumulated more species than its sister clade, differences in the rates of diversification may be further enhanced by a diversity-dependent positive feedback process. Both speciation and extinction rates per unit time should rise with the number of species present: the higher the diversity, the more species there are to split into additional species, and the more species there are to go extinct. If the speciation rate rises more steeply with increasing diversity than does the extinction rate (MacArthur 1969; Rosenzweig 1975), the speciation and extinction curves will diverge—and hence the observed rate of net diversification will increase—as one moves from a less diverse to a more diverse region. This is basically a spatial application of the model developed by MacArthur (1969) to describe speciation and extinction rates in a single community over time (see also Rosenzweig 1975). High species richness may also promote faster diversification if high species richness of some groups, such as primary producers, accelerates diversification of other groups dependent upon them. This probably applies to swallowtails and their angiosperm hosts (Tyler *et al.* 1994) and to a lesser extent to passerines and the plant groups on which they are directly or indirectly dependent.

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