link between selection and the ecological consequences of evolutionary change has been apparent since Lande's pioneering work (14). Our results are a useful step toward extending stochastic evolutionary demography toward a theoretical framework that describes population dynamics in terms of the quantitative traits on which selection operates. Such a theory would describe the feedback between ecological and evolutionary processes in a stochastic environment and would illuminate the mechanisms shaping additive genetic variation and phenotypic variation.

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The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals

Jason T. Weir* and Dolph Schluter

Although the tropics harbor greater numbers of species than do temperate zones, it is not known whether the rates of speciation and extinction also follow a latitudinal gradient. By sampling birds and mammals, we found that the distribution of the evolutionary ages of sister species—pairs of species in which each is the other's closest relative—adheres to a latitudinal gradient. The time to divergence for sister species is shorter at high latitudes and longer in the tropics. Birth-death models fitting these data estimate that the highest recent speciation and extinction rates occur at high latitudes and decline toward the tropics. These results conflict with the prevailing view that links high tropical diversity to elevated tropical speciation rates. Instead, our findings suggest that faster turnover at high latitudes contributes to the latitudinal diversity gradient.

The tropics possess many more species than temperate regions, yet the underlying causes of this latitudinal gradient in species diversity are poorly understood (1–3). A number of authors have estimated net diversification rates (speciation minus extinction) across a latitudinal gradient and concluded that more species accumulate per unit time at tropical latitudes [including birds (4–7), primates (8), marine bivalves (9), foraminifera (10), and butterflies (4)]. By examining the age distributions of the youngest species of birds and mammals, and how they change with latitude, we examined the contributions of recent speciation and extinction to the latitudinal gradient in net diversification.

We studied a large data set comprising the ages and midpoint latitudes of breeding range for 309 sister species pairs of New World birds and mammals. We defined sister species as the most closely related pair of extant species descended from an immediate common ancestor. Their ages were estimated from genetic distances of mitochondrial DNA from the cytochrome b gene. The rate of evolution in this gene is approximately constant with time within birds and mammals (11–13) and has been used widely to date phylogenetic events in these groups. The average of the absolute value of midpoint breeding latitude for a sister-species pair was used to approximate the latitude at which speciation occurred. This approach is reasonable for sister-species pairs that have narrow latitudinal ranges, but greater uncertainty exists when latitudinal ranges are broad. Excluding all species pairs with a combined latitudinal range (defined by the northern and southern limits for the pair) of greater than 40° did not affect the relationship between age and midpoint latitude. Latitudinal ranges of species at high latitudes have shifted in response to glacial cycles. However, using the presumed latitudes of species ranges during past glacial maxima, when many temperate species were forced southward, would only steepen the gradients estimated here.

Near the equator, the ages of sister-species pairs spanned the past 10 million years, with a mean age of 3.4 million years ago (Ma) (Fig. 1A). As distance from the equator increased, the upper limit and mean ages of sister species declined significantly [slope = -0.043 ± 0.007 Ma/degree latitude ($\pm$ SEM), student's t test = -6.5, $P <$ 0.0001, intercept = 3.37, degrees of freedom (df) = 307]. At the highest latitudes, all of the sister species diverged less than 1.0 Ma. This pattern of declining age with latitude is opposite to the pattern that would occur if faster rates of speciation had driven the buildup of Neotropical diversity, because the ages of sister species should be youngest where speciation rates are highest.

The differences in species ages between low and high latitudes is partly the result of a longer lag time in tropical faunas between population splitting, as measured by genetic markers, and species designation (Fig. 1, B and C). The evidence for this lies in the coincident latitudinal gradient in the ages of the oldest haplotype splits within 154 currently defined species of birds and mammals (Fig. 1B) and in the oldest phylogroup splits within 130 species (Fig. 1C). Avise (14, 15) defined a phylogroup as a reciprocally monophyletic geographic subdivision

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within a species. By examining sets of closely linked alleles (haplotypes), we were able to use maximum haplotype divergence as well as the age of the deepest phylogroup splits to compare the lag time to species formation, because species at high latitudes are so young that most lack phylogroups. Both haplotype and phylogroup splits are older in the tropics than in temperate zones, on average, implying that the process of speciation takes longer at low latitudes. This may be in part an artifact of the greater taxonomic uncertainty at lower latitudes, because a higher proportion of tropical species are currently undescribed and thus considered together in our analysis. Nevertheless, taxonomic uncertainty is unlikely to be the sole cause of the gradient.

This is because the latitudinal gradient in the ages of sister species is present even within the Nearctic fauna of North America, which is well defined taxonomically north of approximately 30°N (slope = −0.041 ± 0.017, $t = -2.44$, $P = 0.017$, intercept = 3.3, df = 99). Reproductive isolation, marking the completion of the speciation process, usually takes time to evolve after population splitting, and our data suggest that this process might take a longer period of time at lower latitudes, although we are not sure why this is the case.

There are differences in the age distributions of sister species across the latitudinal gradient apart from the lag-time difference. Therefore, it may be possible to extract information about

speciation (rate of cladogenesis) and extinction rates from the distribution of sister-species ages after correcting for the lag-time, because speciation and extinction can be inferred by the shape of the age distributions of sister species. In phylogenetic simulations using a pure birth model, in which speciation rates are constant through time and no extinction occurs (16), ages of sister species approximate an exponential distribution for which the mean is proportional to the speciation rate; adding a lag time shifts the mode in the distribution toward the mean lag time. Extinction changes the shape of these distributions by increasing the breadth of the tails (17).

We used maximum likelihood to fit a birth-death (18) model in which speciation (λ) and extinction (μ) rates changed linearly across the latitudinal gradient:

$$\lambda = b_\lambda L + c_\lambda \qquad (1)$$
$$\mu = b_\mu L + c_\mu \qquad (2)$$

where L is the absolute value of latitude, b is the slope, and c is the rate at 0° latitude. The model estimated the slopes (b_λ, b_μ) and intercepts (c_λ, c_μ) for the linear relationships between λ, μ, and L (Fig. 2) by fitting data points at each latitude to simulated probability distributions of sister species ages corresponding to different values of speciation and extinction in a reconstructed birth-death process (17). We generated probability distributions of sister-species ages by simulating a large number of phylogenetic trees under a birth-death process and recording the resulting distribution of sister-species ages for a range of parameter values. Simulated trees were corrected for the lag time to species recognition assuming that lag times had an exponential distribution with mean equal either to the average age of the oldest known haplotype splits, or to the average age of phylogroup splits within species at that latitude (17).
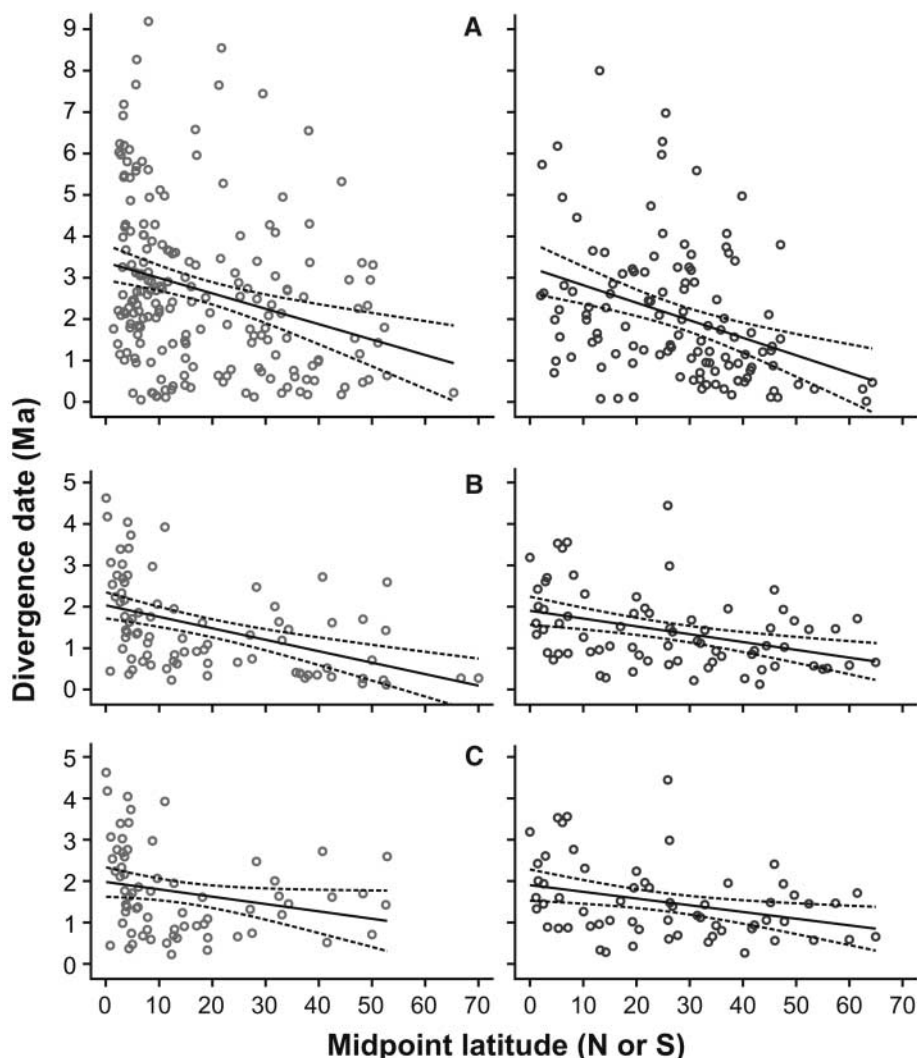
Fig. 1. Relationship between time since splitting and average absolute midpoint latitude for sister taxa of New World birds and mammals. (**A**) Ages of 309 sister-species pairs of New World birds (left; n = 191) and mammals (right; n = 118). Linear regression lines are shown for birds (slope = −0.040, t = −4.368, P < 0.0001, intercept = 3.38 Ma) and mammals (slope = −0.042, t = −4.258, P < 0.0001, intercept = 3.26 Ma). (**B**) Ages of 154 maximum coalescent dates for intraspecific haplotype variation within bird (n = 81) and mammal (n = 73) species. Linear regression lines are shown for birds (slope = −0.028, t = −4.58, P < 0.0001, intercept = 2.03 Ma) and mammals (slope = −0.019, t = −3.62, P < 0.0006, intercept = 1.91 Ma). (**C**) 130 phylogroup splits for birds (n = 68) and mammals (n = 62). Linear regression lines are shown for birds (slope = −0.018, t = −2.00, P = 0.049, intercept = 1.98 Ma) and mammals (slope = −0.016, t = −2.67, P < 0.01, intercept = 1.91 Ma).
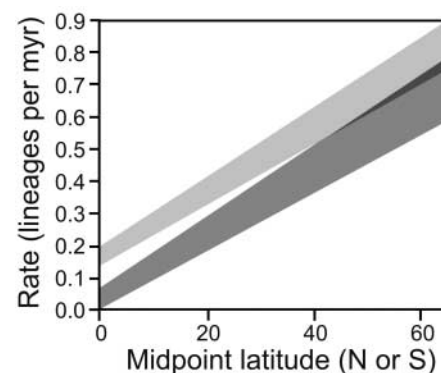
Fig. 2. Estimates of speciation (light gray) and extinction (medium gray) rates in millions of years (myr) across latitude (L) for New World birds and mammals. All rate estimates within 1 log likelihood unit of the maximum likelihood estimate are shown. Region of overlap shown in dark gray.

The maximum likelihood model estimated significantly positive slopes for the relationship between λ (support interval, 0.0076 to 0.0117), μ (support interval, 0.0046 to 0.0135), and latitude for the combined data set of bird and mammal sister species (Fig. 2). Results were similar when maximum haplotype or oldest phylogroup splits were used to correct for lag times, and only the correction with haplotypes is reported here. Estimated speciation and extinction rates were lowest at the equator and increased significantly toward the poles (Fig. 2). The same trends were obtained when excluding sister-species pairs with combined latitudinal ranges greater than 40° and when bird and mammal data sets were fit separately, but results were not significant in the mammal data set. These results hold true even when correcting for the latitudinal gradient in lag time to speciation. We expect that better knowledge of species-level taxonomy in the tropics will revise the lag time and sister-species age gradients. This revision should have minimal influence on the estimates of speciation and extinction, given that they are adjusted for lag time.

These results are surprising because the latitudinal gradient in estimated speciation rate is opposite to the gradient in net rate of diversification estimated by many studies to be highest in tropical taxa (4–10). For our data on sister species, the gradient in net diversification is not significantly different from zero ($b_λ = b_μ$). Still, the range of estimates for the net diversification gradient supported by this study is consistent with estimates obtained elsewhere for birds (5). If the gradient is real, as other studies encompassing longer time periods indicate (4–10), our findings would support the classic views of Wallace (19), Fisher (20), and others (12, 21, 22), who reported that reduced extinction risks at tropical latitudes promoted the gradual buildup of high species diversity there.

These quantitative estimates are based on the assumption that speciation and extinction can be approximated by a continuous birth-death process as latitude becomes higher or lower. Yet, we know that there have been fluctuations in the opportunities for speciation and extinction over the past few million years (12, 23). For example, extensive climatic fluctuations that occurred at high latitudes during the late Pliocene and Pleistocene (2.5 Ma to present) may have concentrated speciation and extinction events in time, resulting in episodic species turnover. In contrast, the bursts of diversification in tropical faunas may predate the late Pliocene and Pleistocene, and the patterns observed today may be the result of a subsequent decline in diversification either because the geological processes that promoted diversification (e.g., formation of Isthmus of Panama, marine incursions, orogeny, and river formation) have slowed or because diversification rates declined as the number of tropical species approached a "carrying capacity" (7, 12).

Given such variability, our estimates are best regarded as averages over the periods studied.

Despite these uncertainties, our results suggest that elevated speciation and extinction rates in the temperate zone can drive high turnover of species, whereas rates of species turnover at tropical latitudes are reduced. A recent study of fossil marine bivalves also showed higher per capita rates of genus extinction at high latitudes, suggesting higher species extinction rates as well (24) (estimates of per capita speciation rates are still lacking). Together, these results suggest that extinction rates are greatest where species diversity is lowest. Whereas most efforts have aimed at identifying the geological, climatic, and ecological factors that might have elevated tropical speciation rates, our results suggest that both speciation and extinction vary with latitude and contributed importantly to the latitudinal diversity gradient.

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Disrupting the Pairing Between *let-7* and *Hmga2* Enhances Oncogenic Transformation

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MicroRNAs (miRNAs) are ~22-nucleotide RNAs that can pair to sites within messenger RNAs to specify posttranscriptional repression of these messages. Aberrant miRNA expression can contribute to tumorigenesis, but which of the many miRNA-target relationships are relevant to this process has been unclear. Here, we report that chromosomal translocations previously associated with human tumors disrupt repression of High Mobility Group A2 (*Hmga2*) by *let-7* miRNA. This disrupted repression promotes anchorage-independent growth, a characteristic of oncogenic transformation. Thus, losing miRNA-directed repression of an oncogene provides a mechanism for tumorigenesis, and disrupting a single miRNA-target interaction can produce an observable phenotype in mammalian cells.

*H*mga2 codes for a small, nonhistone, chromatin-associated protein that has no intrinsic transcriptional activity but can modulate transcription by altering the chromatin architecture (1, 2). *Hmga2* is primarily expressed in undifferentiated proliferating cells during embryogenesis and in a wide variety of

benign and malignant tumors (3–6). In many of these tumors, a chromosomal translocation at 12q15 truncates the human *HMGA2* open reading frame (ORF), typically retaining the three DNA-binding domains of HMGA2 while replacing the spacer and the acidic domain at the C terminus by any of a wide variety of ectopic

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