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Sympatric Speciation in Birds Is Rare: Insights from Range Data and Simulations

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abstract: Sympatric speciation is now accepted as theoretically plausible and a likely explanation for divergence in a handful of taxa, but its contribution to large-scale patterns of speciation remains contentious. A major problem is that it is difficult to differentiate between alternate scenarios of geographic speciation when species ranges have shifted substantially in the past. Previous studies have searched for a signal of the geographic mode of speciation by testing for a correlation between time since speciation and range overlap. Here we use simulations to show that the proportion of species showing zero or complete range overlap are more reliable indicators of the geography of speciation than is the correlation between time since speciation and overlap. We then apply these findings to the distributions of 291 pairs of avian sister species. Although 49% of pairs show some overlap in their ranges, our simulations show that this is not surprising under allopatric models of speciation. More revealingly, less than 2% show complete range overlap. Our simulations demonstrate that the observed patterns are most consistent with a model in which allopatric speciation is dominant but in which sympatric speciation is also present and contributes 5% of speciation events.

Keywords: speciation, allopatric, sympatric, geographic range, birds, phylogeny.

Sympatric speciation has been at the center of one of the most protracted debates within evolutionary biology (Walsh 1864; Jordan 1905; Mayr 1942; Bush 1975; Futuyma and Mayer 1980; Berlocher and Feder 2002; Coyne and Orr 2004). Although sympatric speciation had been largely dismissed in many earlier reviews of speciation (e.g., Mayr 1942; Futuyma and Mayer 1980), recent theory has demonstrated that it is possible under certain conditions (e.g., Dieckmann and Doebeli 1999; Gavrilets and Waxman 2002), and empirical studies have provided examples for which a sympatric origin of species appears to be the most parsimonious explanation (e.g., Sorenson et al. 2003; Savolainen et al. 2006). The argument has therefore shifted from a debate on the plausibility of sympatric speciation to an examination of its frequency relative to other geographic modes of speciation (Jiggins 2005).

Biologists have long suspected that contemporary geographic distributions of closely related species offer a window into the historical processes that have generated those species (Jordan 1905, 1908; Jordan and Kellogg 1907; Mayr 1942). In many groups, recently diverged sister species tend to have allopatric rather than sympatric distributions, a classic pattern (sometimes referred to as Jordan's law) that has traditionally been interpreted as evidence for the predominance of allopatric speciation (Wagner 1873; Jordan 1905, 1908; Allen 1907; Jordan and Kellogg 1907; Mayr 1942; but see Anderson and Evensen 1978). However, one of the difficulties of using range overlap to study the geographic mode of speciation is that because of changes in distribution over time (e.g., Lessa et al. 2003), current

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patterns of range overlap may not be representative of range overlap at the time of speciation (Brown and Gibson 1983). Great caution must therefore be taken when attempting to use contemporary range information to infer past speciation processes (Chesser and Zink 1994; Losos and Glor 2003).

Using methods that allow for recent geographic range changes, several authors have suggested that under an allopatric model, the correlation between node age and range overlap after speciation should be positive, and the intercept should be close to 0. Conversely, under a sympatric model, a negative correlation and an intercept close to 1 are expected (Barraclough et al. 1998; Berlocher 1998; Barraclough and Vogler 2000; Ribera et al. 2001). The few studies that have applied this approach to contemporary distribution data have generally suggested that allopatric speciation is the predominant mode of speciation, but in situations where there may have been large changes in geographic ranges, it has typically proven difficult to reject the possibility that a substantial proportion of speciation events could have been sympatric (Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006; Perret et al. 2007).

The overall aims of this study were twofold: (i) to use spatial simulations to test the ability of several indices of range overlap to differentiate between alternate scenarios of speciation and (ii) to apply these indices to avian distribution data in order to reveal the relative contributions made by allopatric and sympatric speciation. One of the problems associated with phylogenetic tests is the low information content that can be derived from ancient phylogenetic nodes (Berlocher and Feder 2002; Fitzpatrick and Turelli 2006). To overcome this problem, we therefore restrict our analyses to recently diverged pairs of sister species (Stephens and Wiens 2003; Coyne and Orr 2004). We test whether the contemporary distributions of 291 avian species pairs depart from the null expectations generated under: (*a*) solely allopatric models of speciation or (*b*) models in which sympatric speciation constitutes (i) 5%, (ii) 10%, or (iii) 25% of speciation events. There are certain logistical advantages of conducting these analyses on birds, namely, the abundance of well-resolved genus-level phylogenetic information and a global database on geographical breeding ranges (Orme et al. 2005). While previous reviews of speciation in birds have tended to favor a predominantly allopatric mode of speciation (Mayr 1942, 1963; Cracraft 1982; Chesser and Zink 1994; Friesen and Anderson 1997; Barraclough and Vogler 2000; Coyne and Price 2000; Johnson and Cicero 2002; Price 2008), recent empirical evidence consistent with sympatric speciation is now emerging, notably in the brood-parasitic *Vidua* finches (Sorenson et al. 2003; Balakrishnan and Sorenson 2006) and band-rumped storm petrels (*Oceanodrama castro*; Harris 1969; Monteiro and Furness 1998; Smith and Friesen 2007). This suggests that a variety of geographic modes of speciation is plausible in birds. Birds also represent a challenging case because of their great mobility compared to that of other groups (Newton 2003), meaning range changes are likely to have been particularly extensive (Fitzpatrick and Turelli 2006). Consequently, if it is possible to reject a high incidence of sympatric speciation in birds, in spite of frequent range change, then our simulation approach is likely to be applicable to other less mobile taxa.

Methods

Simulations

In order to explore how different degrees of geographic range overlap between pairs of sister species can arise under different historical scenarios, we developed a series of simulations. Each simulation replicate was generated by randomly dividing an initial geographic range of known size into two "daughter" ranges, with the positions of these daughter ranges in relation to one another being dependent on the speciation model employed. These two daughter ranges, which represent the geographic ranges of a pair of sister species after a speciation event, were then allowed to move independently of each other for a number of time steps. For each replicate, there were four main parameters that could be varied: (i) the geographic mode of speciation, (ii) the number of time steps, (iii) the starting size of the ranges, and (iv) the rate at which ranges move. At the end of each replicate, we recorded the extent of range overlap between the two ranges and calculated a series of indices, with the aim of discovering whether any of these indices was able to recover the original mode of speciation under a wide range of conditions.

We simulated the spatial movements of ranges, including changes in both position and size, under several geographic and speciation scenarios. All simulations were performed on a square plane of 100 units × 100 units. Our simulation approach was similar in many ways to that of Barraclough and Vogler (2000), although there were several important differences, the most significant being that we modeled range change and overlap between just two species (for a simulation approach that shares several similarities with ours, see Waldron 2007), whereas Barraclough and Vogler modeled these processes through multiple successive speciation events.

The simulations were used to model vicariant (allopatric speciation via a barrier bisecting a range), peripatric (allopatric speciation via dispersal at the periphery of a range), parapatric (speciation in nonoverlapping space but abutting areas in the face of gene flow), and sympatric (speciation in completely overlapping space) modes of speciation. We simulated vicariant allopatric speciation by placing the larger of the two ranges randomly on the grid, subject to the constraint that there had to be a minimum of 2 units plus the square root of the smaller species range to the right of the larger species range. This was to allow room for the smaller species range, which was always placed 2 units to the right of the first, although its position on the vertical axis was permitted at any point along the vertical extent of the larger range. Under peripatric speciation, the larger of the two ranges was placed randomly on the grid by using two sets of random uniform coordinates, with the condition that the entire range had to fall within the confines of the grid. The second species range was then placed randomly on the grid, with the additional constraint that the two species ranges could not overlap. Parapatric speciation was simulated in a fashion identical to that of vicariant speciation, except for the omission of the 2-unit spatial separation of ranges. We simulated sympatric speciation by placing the larger range randomly on the grid and then placing the smaller species range randomly so that its range was completely overlapped by the species with the larger range.

Under the vicariant speciation model, the postspeciation range sizes of species were obtained by randomly breaking a stick of *r* units^2 (where *r* was one of 100, 1,000, or 2,000) into two parts (MacArthur 1957; Anderson and Evensen 1978; Barraclough and Vogler 2000; but for criticism of this approach, see Waldron 2007). On average, the smaller of the two ranges generated by stick breaking was one-third the size of the larger. To minimize the differences between alternative speciation models, we used stick breaking to simulate postspeciation range sizes under sympatric and parapatric speciation. Under peripatric speciation, the range size of the peripheral isolate is expected to be considerably smaller than that of its parent range. To simulate this scenario, we obtained the smaller range size by multiplying *r* by a value drawn from the γ distribution with shape and rate parameters of 0.1 and 10, respectively. The larger range size was obtained as *r* minus the smaller range. Under this peripatric speciation model, the smaller range was $<10\%$ of *r* in $>97\%$ of simulations. All the initial species ranges were square. Earlier simulations of range overlap through time conducted by Fitzpatrick and Turelli (2006) found that circular and square ranges returned qualitatively similar results.

We simulated range change by adding a different random normal deviate of a mean of 0 and standard deviation of 0.5 to vectors corresponding to the top, bottom, right, and left extents of each species range. This process was repeated at each time step and allowed each of the four sides of the species range to move in two directions independently of one another; this meant that unlike Barraclough and Vogler's (2000) simulations, range change was not related to range size. However, ranges were not allowed to expand beyond the limits of the grid and were always rectangular. We also explored a faster rate of range change with a mean of 0 and standard deviation of 2. We conducted simulations of varying average duration: short (obtained as rounded values from a random normal distribution with mean $=$ 100 and SD $=$ 25), medium (from a random normal distribution with mean $=$ 200 and SD $=$ 50), and long (from a random normal distribution with mean $=$ 1,000 and SD $=$ 250). If either of the species ranges contracted to 0 (or less) at any stage of the simulations (extinction), we started a new simulation with the same simulation duration as the failed one (although the starting range sizes and coordinates would be reallocated randomly). Most simulations were conducted with the vicariant speciation model (combined with varying frequencies of sympatric speciation), using a combined initial range size of 1,000 units^2, a range change rate with a random normal deviate of 0.5, and a simulation duration averaging 100 time steps. We make it clear when simulations depart from these default settings.

At the end of each simulation replicate, the proportion of overlap between the two species ranges was calculated as the area of overlap divided by the area of the smaller range, following Chesser and Zink (1994). The spatial similarity between the starting and the finishing position of each range was assessed for each simulation using Jaccard's similarity coefficient; that is, the area of overlap between the beginning and the ending range was divided by the sum of the area covered by the two ranges. We then calculated the average of the Jaccard similarity coefficients for the two species ranges for each simulation.

To explore the influence of the geographic mode of speciation, the proportion of speciation events that were allopatric (vicariant, peripatric, or parapatric) versus sympatric was varied from 0 to 1 in iterations of 0.1. For each selected combination of parameter values, we conducted 10,000 separate simulations, after which we estimated several range overlap parameters. Using Kendall's τ, we estimated the correlation between range overlap and (i) simulation duration and (ii) the smaller range size. Kendall's τ was preferred to parametric methods because of the very high incidences of 0s and/or 1s in the overlap data. We calculated the proportion of replicates that showed zero overlap and complete overlap and the degree to which simulations produced bimodal distributions, that is, high instances of zero and complete overlap cases. We quantified bimodality as $(z \times c)/(0.5 \times n)$, where z and c are the number of individual simulations that resulted in zero and complete overlap, respectively. The number of simulations (in this case 10,000) was denoted as n. The resulting value lies between 0 and 1, where a value of 0 indicates no bimodality and a value of 1 corresponds to complete bimodality; that is, the cases are divided evenly between those showing zero and complete overlap. Finally, we calculated the median Jaccard similarity between the range position at the outset and at the end of simulations across each set of replicates. R code for running the simulations is available from A.B.P. on request.

Speciation in Birds

We identified 568 pairs of avian sister species, defined here as the two most closely related extant descendants of a common ancestor, by using two approaches. The first approach involved identifying monophyletic sister species from published molecular phylogenies that included more than 80% of the species in a clade. An 80% completeness threshold was selected as a compromise between identifying true sister taxa and maximizing the number of available pairs. The second approach was taxonomy based; two species were recognized as sisters if their genus included just two species. We used the taxonomy of Sibley and Monroe (1990, 1993). A corollary of using this taxonomy is that our species delimitation should generally correspond to the biological species concept. Where the phylogeny and taxonomy conflicted, we adopted the phylogenetically identified sister pairs. Our expectation was that although it is likely that a small fraction of the pairs of species we identify in this manner may not be true sister species, they would be close relatives. Furthermore, all species-pair comparisons will be phylogenetically independent of one another (Harvey and Pagel 1991).

Information on the geographical distribution of the pairs of sister species was obtained from a database of breeding range extent ArcGIS shapefiles (Orme et al. 2005, 2006). The range sizes of the focal species and the extent of range overlap between sister species (both in km^2) were estimated from these data by using ArcGIS code written by C.D.L.O. Across all 568 pairs of sister species, we also calculated the incidences of both zero and complete overlap.

We conducted more thorough range overlap analyses on a smaller sister pair data set that was designed to minimize the problem of major recent range shifts (as recommended by Coyne and Orr [2004]). We excluded species found in the Holarctic, where major vegetation shifts and concomitant avian range shifts occurred during the past 22,000 years following the last ice age (Rand 1948; Pianka 1966; Pielou 1991; Lessa et al. 2003). We also excluded pairs where at least one member was restricted to islands smaller than 500,000 km^2 because in such cases our unconstrained range change simulations would be inappropriate.

For pairs of species in the reduced data set, we estimated the genetic distance between sister species from mitochondrial sequence data stored in GenBank. The program Geneious (Drummond et al. 2006) was used to search for sequence data from two frequently sequenced mitochondrial protein coding genes, cytochrome *b* (cyt *b*) and NADH dehydrogenase subunit II (ND2). Each species was represented by a maximum of six sequences, and efforts were made to sample from multiple subspecies if available. Sequences were aligned using CLUSTAL W (Thompson et al. 1994) in MEGA3.1 (Kumar et al. 2004) and checked by eye. For each pair of species, the maximum overlapping region of nucleotide base pairs was calculated, and sequences that spanned more than 75% of this region were included in the analysis of genetic distance. For both cyt *b* and ND2, the mean proportional pairwise differences in sequence bases were estimated between species. We estimated relative time since divergence of sister species by using the proportional distances and made the assumption that the rates of nucleotide substitution in cyt *b* and ND2 were similar and clocklike. The mean genetic distance estimates across the two genes were calculated from the proportional distances after arcsine transformation.

Across the pairs of avian sister species, we calculated the range overlap indices described for the simulations above; these were (i) the correlation between time since speciation (estimated using genetic distance) and proportion of range overlap, (ii) the correlation between the smaller range size and the proportion of range overlap, (iii) the proportion of cases showing zero overlap, (iv) the proportion of cases showing complete overlap, and (v) the degree to which the range overlap data are bimodal. To allow for mapping and rounding error, we defined complete overlap as those cases where overlap was >0.9999.

Sympatric species that hybridize can be misidentified as sister species on the basis of their mitochondrial gene trees (Funk and Omland 2003). To minimize the potential for hybridization inflating the frequency of apparent sympatry (Fitzpatrick and Turelli 2006), we identified those species pairs known from phylogenetic sources for which natural hybridization has been inferred or reported (McCarthy 2006). We conducted analyses both including and excluding phylogenetic sister species that are known to hybridize. A related problem is that hybridization may reduce the estimated genetic distance between sister species that are in parapatry or sympatry. Consequently, we excluded hybridizing pairs from the analysis of the relationship between genetic distance and range overlap.

To identify the most likely mode of speciation in birds, we examined whether the observed value for each of the five indices lay within the expected distributions generated for (i) a high incidence of sympatric speciation (25% of all speciation events), (ii) a low incidence of sympatric speciation (10% of all speciation events), (iii) a low incidence of sympatric speciation (5% of all speciation events), and (iv) a zero incidence of sympatric speciation (i.e., a solely allopatric model). To allow for sampling error in our collection of species pairs, each single range change simulation had $1 - s$ probability of being allopatric and s probability of being sympatric (where s was 0.25, 0.10, 0.05, or 0). We adopted parameter values that we considered to be biologically plausible and conservative with respect to the null hypotheses involving sympatric speciation. The null hypotheses were generated via 1,000 simulations, keeping the sample size equal to that in the observed data sets. All tests were two tailed.

Results

Simulations

Our simulations showed that when speciation was solely allopatric, approximately half of the cases showed zero range overlap (under the vicariant mode of speciation and default parameters), with most of the remainder showing intermediate range overlap and very few cases showing complete overlap (fig. 1*A*, 1*D*). Alternatively, when speciation was an equal mixture of allopatric and sympatric, the distribution of overlap was bimodal, with many cases of zero and complete overlap and fewer intermediate cases (fig. 1*B*, 1*E*). Finally, under a purely sympatric speciation model, there were many cases of complete or high overlap (overlap >0.5) and very few cases of zero overlap (fig. 1*C*, 1*F*). In all speciation scenarios, however, the relationships between the degree of range overlap and time since speciation (fig. 1*A*–1*C*) or smaller range size were noisy (fig. 1*D*–1*F*).

In general, the simulations demonstrated that the correlation between time since speciation and the degree of range overlap tends to be very weak ($-0.11 <$ Kendall's $\tau < 0.08$; fig. 2*A*; table A1 in the online edition of the *American Naturalist*). There was relatively little variation in the estimated correlation coefficient when we considered different simulation durations, starting range sizes, or range change rates. Under some speciation scenarios, the analyses conducted on the simulations returned the positive and negative correlations predicted under predominantly allopatric and sympatric modes, respectively. However, given small initial range sizes, rapid range change, or long simulation durations, the simulations showed little evidence for the predicted negative correlation under the solely sympatric model (Kendall's $\tau > -0.04$ in all cases). When the modes of speciation were 50% allopatric and 50% sympatric, both positive and negative correlations between time since speciation and range overlap were obtained, depending on the simulation conditions employed (fig. 2*A*; table A1). Therefore, although a correlation as high as >0.1 would indicate allopatric speciation and a correlation as low as −0.04 would indicate sympatric speciation, intermediate correlation values could arise from several different geographic speciation scenarios. Peripatric and parapatric speciation models returned age range correlations that were qualitatively very similar to those of the vicariant model (table A1).

Under the default simulation parameters (vicariant speciation, medium range size, slow range change, and short simulation duration), the size of the smaller range possessed useful properties as a correlate of range overlap (fig. 2*B*), with allopatric and sympatric models of speciation returning positive and negative correlations, respectively. However, when range changes were more pronounced (because of a faster rate of range change, a smaller starting range size, or a longer simulation duration), the correlation tended to be positive or only weakly negative, even under the solely sympatric speciation scenario. Although the parapatric model returned results similar to those of the vicariant model, the correlations produced by the peripatric model were highest at intermediate frequencies of sympatric speciation and produced negative correlations only when the frequency of sympatric speciation was very high. This pattern can be explained by the different starting range sizes generated under the two speciation scenarios; the smaller of the two postspeciation ranges will be larger under the sympatric mode, thus explaining the correlation between sympatry and range size. A combination of these factors implies that a positive correlation is not reliable evidence for a primarily allopatric mode of speciation. Conversely, a negative correlation may still be a useful indication of the presence of substantial sympatric speciation, but this approach will lack power if range change has been extensive.

As the proportion of sympatric speciation events increased, the proportion of cases showing zero overlap tended to decline (fig. 2*C*). Under the default and medium-duration conditions, an increase in the frequency of sympatry resulted in a consistent decrease in the proportion of cases showing zero overlap, from more than 0.55 to less than 0.05. A smaller starting range size resulted in qualitatively similar proportions when allopatric speciation predominated, but when all speciation was sympatric, a considerable proportion of species pairs still showed zero range overlap (approximately 20%). Furthermore, when the rate of range change was increased, there was a corresponding decrease in the proportion of cases that showed zero overlap when sympatry was rare and an increase in the frequency of zero overlap when sympatry was common. The parapatric model again returned results similar to those of the vicariant model, except for a slight decline in the proportion of cases showing

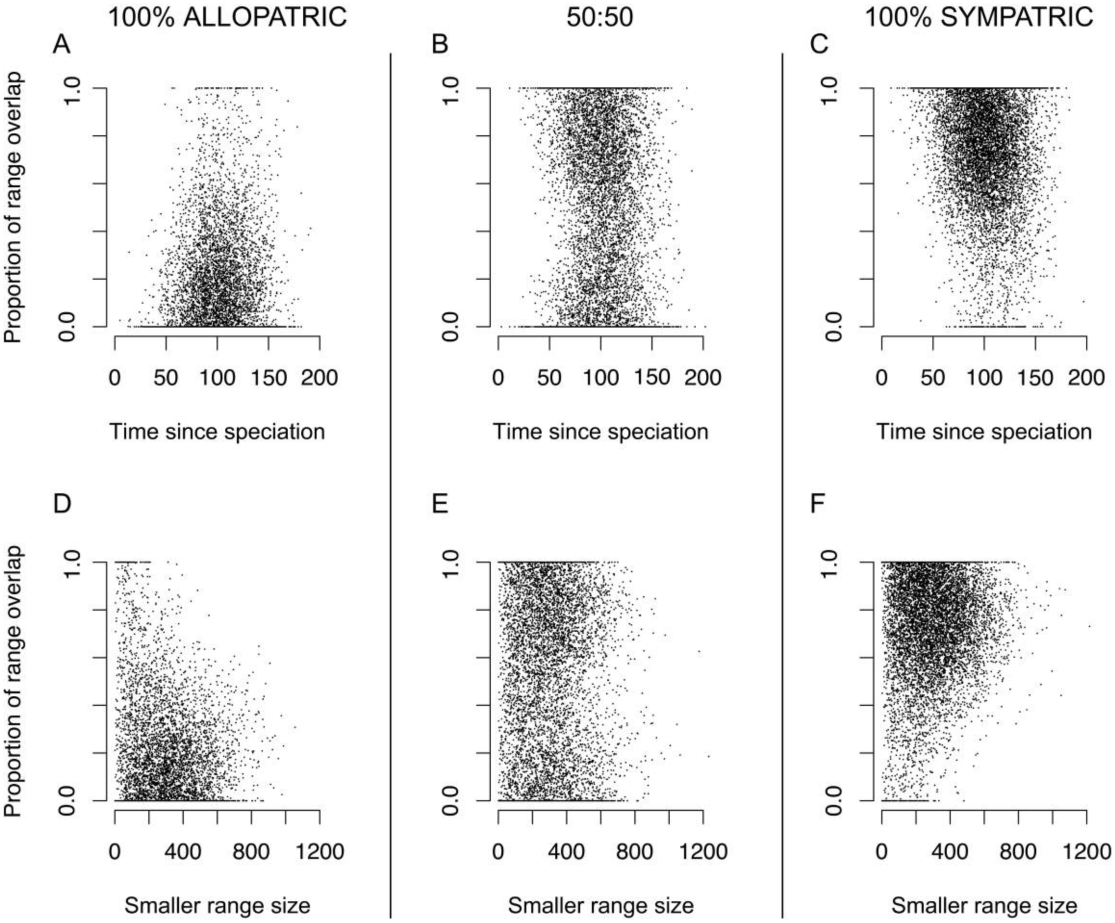

Figure 1: Relationship between the extent of overlap in the geographic ranges of sister species and time since speciation (*A*–*C*) and range size (*D*–*F*) under different geographical speciation scenarios. Plots illustrate the results obtained from 10,000 simulations. *A* and *D* represent 100% allopatric speciation (vicariant model), *B* and *E* represent 50% allopatric and 50% sympatric, and *C* and *F* represent 100% sympatric speciation. Simulations were run for an average of 100 time units (short duration), the combined starting range size was 1,000 units^2, and the standard deviation used for simulating rate of range change was 0.5. Time since speciation represents the duration for which each single speciation and range change simulation was run. Smaller range size is the size in arbitrary square units of the smaller of the two sister species ranges at the end of a simulation. For each pair of species, proportion of range overlap was estimated as the proportion of the smaller range that overlapped with the larger range.

zero overlap when sympatric speciation was infrequent. The peripatric model also departed from the vicariant model when sympatric speciation was rare, but under this mode of speciation the proportion of cases showing zero overlap was much higher (approximately 0.9 when peripatric speciation was ubiquitous; table A1). Thus, low proportions (<0.1) of zero overlap are robust indicators that sympatric speciation is frequent. Depending on the dominant forms of allopatric speciation, either high (>0.5) or very high (>0.8) incidences of zero overlap may be required to provide robust evidence to reject frequent sympatric speciation. Again, intermediate proportions of cases showing zero overlap arise under several speciation and range change scenarios.

A large proportion of cases showing complete sympatry were a robust indicator of frequent sympatric speciation under a variety of speciation models and simulation parameters (fig. 2*D*; table A1). When initial range size was small, range change was fast, or simulation duration was long, the proportion of cases showing complete overlap was low. This means that a low proportion of complete sympatry (often considered indicative of allopatric speciation) can arise under a range of scenarios and is likely to have low power to reject hypotheses postulating a role for sympatric speciation.

A low bimodality score arose from a prevalence of either allopatric or sympatric speciation or as a result of erosion of the geographic signal of speciation, such as may occur

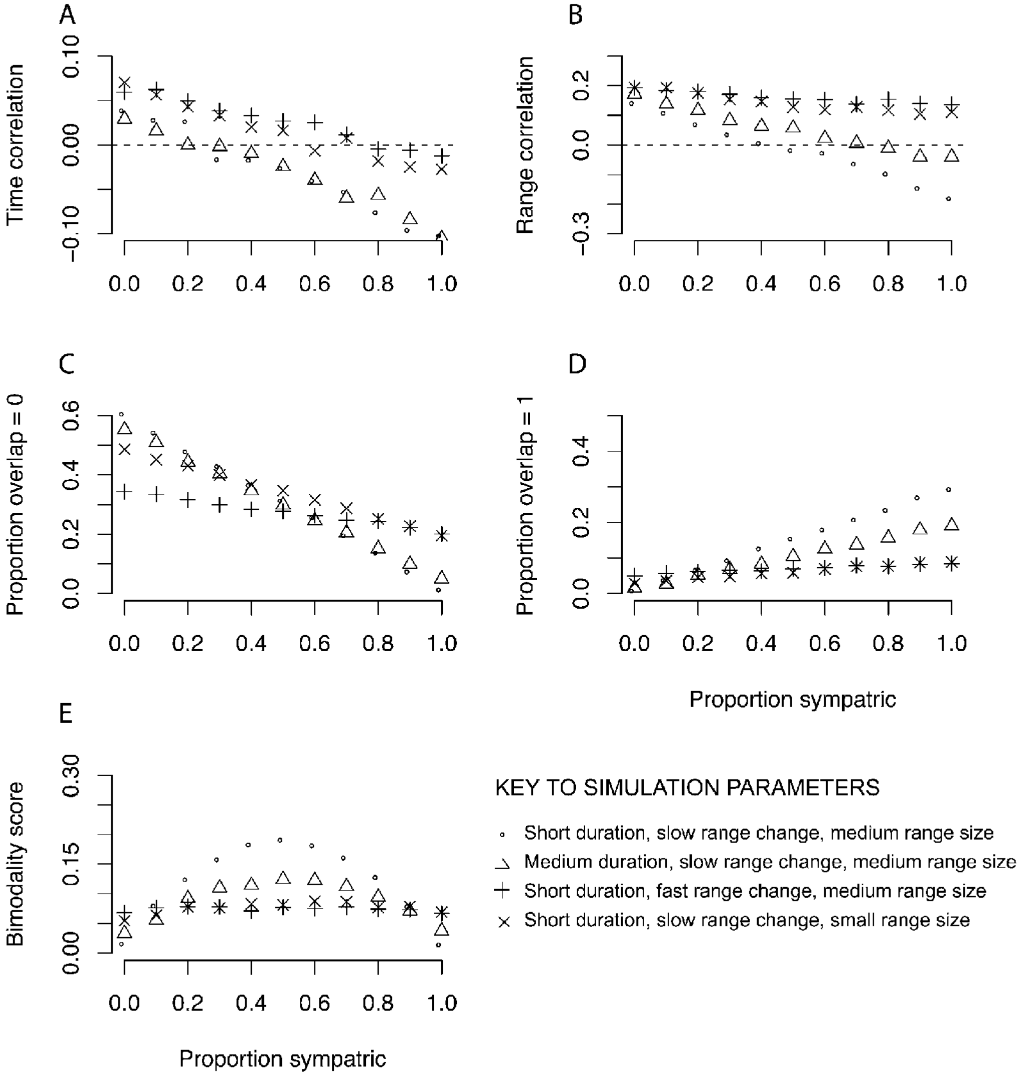

Figure 2: Relationships between the proportion of speciation events that are sympatric rather than allopatric and five indices of range overlap under different model parameters. Points represent values obtained from 10,000 simulations. *A*, Kendall's τ correlation statistics between time since speciation and the proportion of range overlap at different frequencies of sympatric speciation. *B*, Kendall's τ correlation between the smaller range size and the proportion of range overlap. *C*, Proportion of cases where range overlap was 0. *D*, Proportion of cases where range overlap was complete. *E*, Median bimodality score. Circles represent the results of simulations using the default parameters, that is, short simulation duration (100 time units), a combined range size of 1,000 units^2, and slow rate of range change (SD = 0.5). Triangles differ from the default only in simulation duration (200 time units). Plus signs differ from the default in the rate of range change (SD = 2.0). Crosses differ from the default in the use of a smaller combined range size (100 units^2).

through rapid range change or long simulation duration (fig. 2*E*). A high bimodality score (>0.15) will arise only if speciation is a mixture of allopatric and sympatric and the geographic signature of speciation is relatively well preserved. At intermediate frequencies of sympatric speciation, the peripatric and parapatric models resulted in higher and lower bimodality scores, respectively (table A1).

As expected, the similarity between the starting post-speciation range position and the range position at the end of simulations was eroded when the simulation duration was increased, the rate of range change was increased, or the starting range size was reduced (table A1). Similarity was also lower under the peripatric model of range splitting, as a result of small ranges being more likely to differ in position between the start and the end of the simulation. Ideally, an observed similarity estimate could

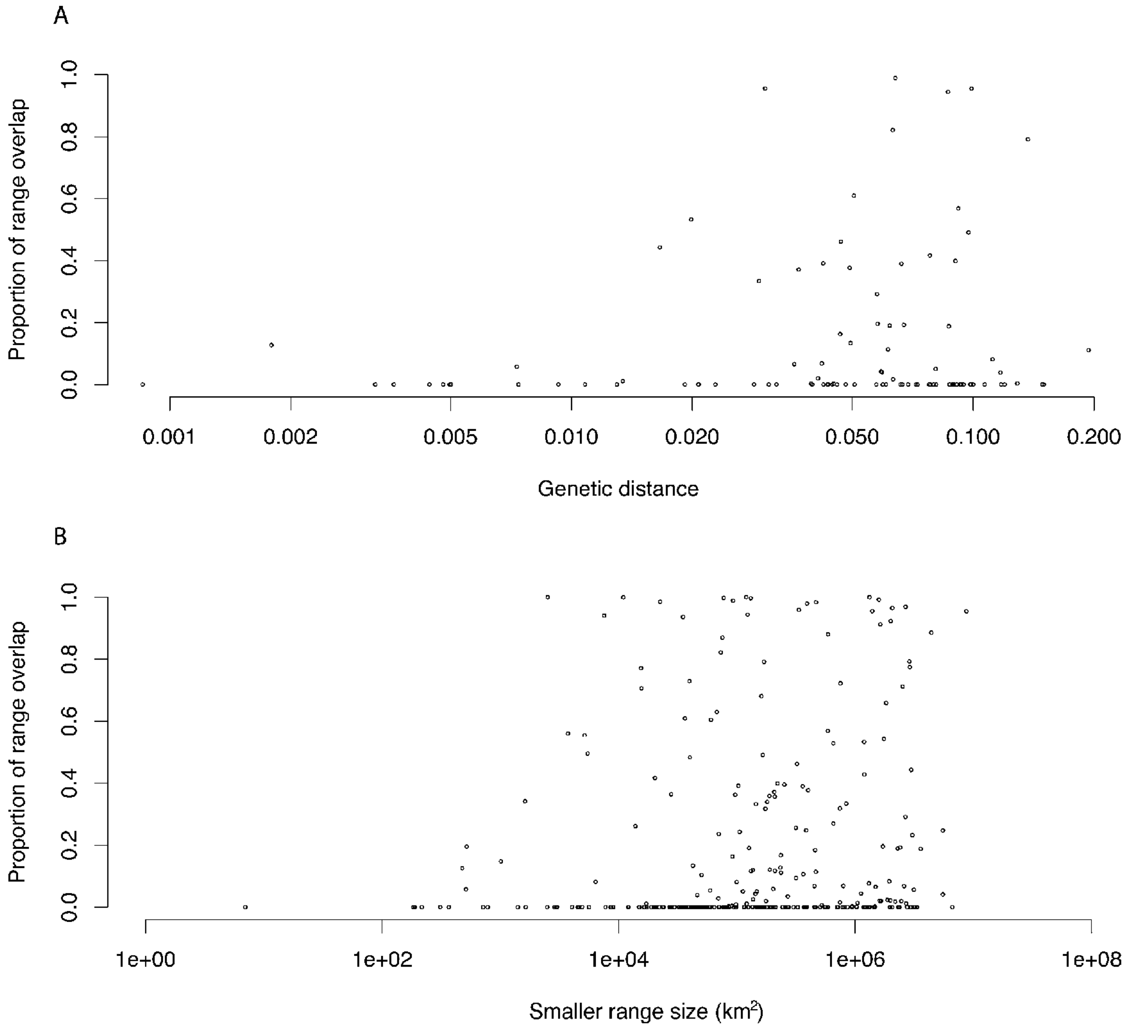

Figure 3: Correlation between range overlap in continental non-Holarctic sister species and genetic distance (*A*) and smaller range size (*B*). Genetic distance is the back-transformed mean of the arcsine-transformed proportional distances obtained from cyt *b* and ND2 sequences.

be calculated by incorporating paleontological information to compare the distribution of species at two time slices; this could then be used to inform a study of the actual rate of range change and suitable simulation parameters.

Speciation in Birds

We identified a total of 568 avian sister pairs (table A2 in the online edition of the *American Naturalist*), of which 295 (51.9%) showed no range overlap and just eight pairs (1.4%) showed complete range overlap. The low incidence of complete overlap was reflected in a low bimodality score of 0.029. The exclusion of 53 species pairs that had been identified using phylogenies and that were known to hybridize did not qualitatively change these patterns (results not shown).

After restricting our database to continental species not inhabiting the Holarctic, we were left with 291 species pairs. Of these, 149 (51.2%) showed zero range overlap, and four (1.4%) showed complete range overlap. Again, the rarity of cases of complete sympatry resulted in a low bimodality score (0.028). The correlation between genetic distance and overlap was not significantly different from 0 ($\tau = 0.053$, $P = .48$, $n = 98$; fig. 3*A*), but the correlation between smaller range size and range overlap was positive and significant ($\tau = 0.187$, $P < .001$, $n = 291$; fig. 3*B*).

We then tested whether our results for the reduced data set of species pairs not found in the Holarctic were significantly different from the expectation under (i) a solely allopatric, (ii) a 5% sympatric, (iii) a 10% sympatric, or (iv) a 25% sympatric mode of speciation. We did this by simulating the null expectation for a set of chosen parameter values. In the absence of substantial fossil evidence regarding range change parameters, we compared the observed parameter values to those expected under several null hypotheses, including both vicariant and peripatric modes of allopatric speciation.

The observed values from the pairs of avian sister species were most similar to those generated under the short-duration vicariant/sympatric null model, with sympatric speciation comprising 5% of events (table 1). The observed data showed fewer cases of zero overlap than expected under the solely allopatric scenario but also showed fewer cases of complete overlap and a lower bimodality score than expected under the 10%–25% sympatric simulations. The peripatric/sympatric simulations showed very little agreement with the observed data as a result of the observed frequency of zero range overlaps being considerably lower than that expected. Moreover, when the contribution of sympatric speciation was high (25%), then the observed bimodality and the incidence of zero overlap were both significantly lower than expected. The observed results differ substantially from those expected under a vicariant/sympatric model run for 1,000 time steps, as the incidence of zero overlap and the bimodality score were consistently greater and lower than the null expectation, respectively.

Discussion

Our simulations suggest that the most reliable indicators of the geographic mode of speciation are the proportions of cases showing zero overlap and complete overlap. If speciation tends to be allopatric, a high proportion of cases will show zero overlap, and a low proportion will show complete overlap, while the reverse is true if speciation tends to be sympatric. These two indices are less sensitive to changes in range size or rate of range change than the other indices we explored. When used in conjunction with other indices, the simple bimodality score that we have introduced represents a robust means of examining whether the geographic mode of speciation varies or whether a single mode predominates. Across a large data set of the geographic ranges of avian sister species, we found that the incidence of zero overlap is high while the incidence of complete overlap is very low. Although almost half the sister species show some range overlap, this does not depart from the expectation under several allopatric speciation models. Rather, we find that the rarity of cases of complete overlap and the low bimodality of the data provide the strongest evidence for the low frequency of sympatric speciation. Under the short-duration vicariant/sympatric simulations, we can robustly reject a hypothesis under which sympatric speciation comprises 25% or 10% of speciation events. However, we also rejected the solely allopatric model, and it was in fact the 5% sympatric model

Table 1: Tests of agreement between the values of five indices of the geographic mode of speciation observed in analyses of avian sister species and the values expected under different geographic scenarios

			Indices of geographic mode of speciation				
Allopatric mode of speciation	Proportion of sympatric speciation events	Simulation duration	Proportion of cases with overlap = 0	Proportion of cases with overlap = 1	Age range correlation	Correlation with smaller range size	Bimodality score
Vicariant	0	100	−.089**	.007	.017	.065	.011
Vicariant	.05	100	−.062*	−.007	.017	.082	−.020
Vicariant	.1	100	−.029	−.020*	.025	.094*	−.050*
Vicariant	.25	100	.058	−.065**	.044	.135**	−.115**
Peripatric	0	100	−.426**	.011*	.030	.119**	.015
Peripatric	.05	100	−.381**	−.003	.029	.019	−.034
Peripatric	.1	100	−.333**	−.017	.040	−.037	−.080**
Peripatric	.25	100	−.196**	−.062**	.058	−.122**	−.187**
Vicariant	0	1,000	.131**	−.027**	−.010	−.005	−.037*
Vicariant	.05	1,000	.144**	−.031*	−.005	.001	−.037*
Vicariant	.1	1,000	.151**	−.034**	.004	.008	−.039*
Vicariant	.25	1,000	.182**	−.041**	.013	.022	−.043**

Note: All statistics represent the observed value minus the median expected value obtained from 1,000 simulations. For details regarding the calculation of different statistics, see "Methods."

* Two-tailed significance at $P < .05$.

** Two-tailed significance at $P < .01$.

that exhibited the fewest significant departures from the null expectation.

Our estimate that approximately 49% of pairs of avian sister species show some range overlap may be, however, an overestimate of the frequency of syntopy. This is because species distribution maps reflect the extent of occurrence, a measure that is likely to overestimate the area of occupancy (Orme et al. 2005, 2006). This does not affect the main conclusion that sympatric speciation is rare. However, it may serve to reduce the disagreement between the null expectation under the 100% vicariant scenario and the observed frequency of zero overlap.

In light of the results of our analyses of avian sister species, we suggest that recent high-profile studies reporting potential instances of sympatric speciation in birds (Sorenson et al. 2003; Smith and Friesen 2007) are unlikely to represent a commonplace mechanism of avian speciation (Price 2008). Given that a combination of peripatric, vicariant, or parapatric speciation is likely to explain the vast majority of avian speciation events, both species-level studies (e.g., Irwin et al. 2005; Seddon and Tobias 2007) and broader comparative analyses (Lynch 1989; Chesser and Zink 1994; Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006) should make distinguishing among the relative contributions a priority. However, the results of a recent simulation study suggest that recovering the true contribution of each mode is likely to be challenging (Waldron 2007).

Our simulations suggest that the correlation between species age and the degree of range overlap, the index employed in a number of earlier studies (e.g., Barraclough et al. 1998; Berlocher 1998; Barraclough and Vogler 2000), lacks power to distinguish between alternative speciation scenarios, meaning that the approach is likely to be of limited utility in highly mobile species. This is largely in agreement with earlier studies that observed that the age range overlap correlation approach had low power to distinguish between alternative scenarios (Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006). An additional issue with the age range correlation approach is that the genetic distances estimated between sister species may capture different stages of the speciation process, depending on the geography of speciation. If speciation takes place in allopatry, genetic distance should relate to the timing of geographical isolation, whereas if speciation takes place in sympatry or parapatry, genetic distance should relate to the point when reproductive isolation declined to zero. The bias introduced here will depend on the time taken for sympatric/parapatric speciation to be completed and will be minimized if sympatric speciation occurs on very short timescales. When range change was limited, the correlation between the degree of range overlap and the size of the smaller range showed useful properties as an indicator of the mode of speciation. However, this index is likely to be of limited practical value because if geographical distributions change substantially over time or if the dominant mode of allopatric speciation is peripatry, the correlation will always tend to be positive. A negative correlation between range size and overlap nonetheless constitutes strong evidence for substantial sympatric speciation.

One consequence of using a simulation approach to study speciation scenarios is that it requires assumptions regarding the properties of ranges, the space available to species, and range change over time. Fortunately, several of the indices explored here, such as the proportion of cases showing complete range overlap, appeared to be relatively robust to changes in many of the parameters included in the models. Biological scenarios exist that may render the simple simulations presented here unrealistic. For example, while we assume that, postspeciation, the ranges of species move independently of one another, competition and adaptation to particular environments and niches are likely to be major determinants of species distributions. If competition between species that have originated in sympatry is strong, then this may lead to the rapid transition to allopatric distributions (Barraclough and Vogler 2000). Alternatively, species may originate in allopatry, in which case, because of phylogenetic niche conservatism, they are likely to be adapted to similar niches (Harvey and Pagel 1991). Thus, if one species' range moves such that it comes into contact with its sister species, then the environment occupied by the sister species may be more suitable and more likely to be invaded than surrounding areas containing different environments. Although these scenarios are possible, we have no reason to believe that they are commonplace or that they undermine our results.

The simulations presented in this article suggest that under a wide range of situations, contemporary range information can be used to infer generalities regarding the geography of speciation. Moreover, when this method was applied to birds, an exceptionally mobile group of animals, we were able to reject the hypothesis that sympatric speciation is commonplace. Instead, our analyses suggest that allopatric speciation is the dominant geographic mode of speciation in birds, with sympatric speciation being limited to 5% of cases.

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