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Limits to Speciation Inferred from Times to Secondary Sympatry and Ages of Hybridizing Species along a Latitudinal Gradient

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ABSTRACT: Range expansions are critical to renewed bouts of allopatric or parapatric speciation. Limits on range expansions—and, by implication, speciation—include dispersal ability and permeability of geographical barriers. In addition, recently diverged taxa may interfere with each other, preventing mutual expansion of each other's range into sympatry, because reproductive isolation is incomplete and/or ecological competition particularly strong. On the basis of geographical distributions and mitochondrial DNA phylogenetic information for 418 recently diverged species of New World birds, we estimate that secondary sympatry takes on the order of millions of years following population splitting and hence could impose an important limit on the rate of range expansion, thereby limiting further rounds of species formation. Average rates of achievement of sympatry have been faster in the temperate region (we estimate 1.7 million years to sympatry at 60°) than in the tropics (3.2 million years to sympatry at the equator). Evidence from the ages of species with hybrid zones implies that one factor associated with the slowed sympatry in the tropics is the rate of accumulation of reproductive isolation.

Keywords: hybrid zones, latitudinal diversity gradient, birds, reproductive isolation, sympatry, speciation rates.

Introduction

Species that form in allopatry (or parapatry) must have smaller ranges than their ancestors. By implication, and given the predominance of allopatric modes of speciation (Coyne and Orr 2004; Phillimore et al. 2008), speciation rates are limited by the ease of range expansions: species with very small ranges will not produce daughters (Rosenzweig 1995). Range expansions are limited by the permeability of physical barriers as well as features of the environment beyond the current range, including abiotic and biotic factors such as competition and disease (Ricklefs 2009, 2010). An important biotic limit on range expansions is set by mutual interactions of sister taxa, which inhibit each other's spread into sympatry (Price 2008; Ricklefs 2009). Closely related parapatric species with abutting ranges, which may or may not include hybrid zones, are widespread (Ricklefs 2009; Rundell and Price 2009). Establishment of sympatry between such taxa clearly requires development of reproductive isolation and may also be slowed because closely related species are ecologically similar (e.g., Peterson et al. 1999) and competitively exclude one another from each other's range.

The difficulty of achieving sympatry between sister species (so-called secondary sympatry) may ultimately slow speciation rates (fig. 1). To illustrate, consider the speciation process, which in birds typically begins when an ancestral species expands its geographic range across preexisting barriers (fig. 1*b*) or is bisected by new barriers. Barriers allow formation of new sister species on either side. When species have formed on opposite sides of all barriers in a continent, further rounds of speciation can occur only if sister species are able to expand their ranges into sympatry (fig. 1*c*). The ability of each species to become sympatric provides an important limit on further rounds of speciation and the buildup of diversity within each region. If sympatry is retarded, further rounds of speciation will be delayed and speciation rates will slow. To determine the importance of secondary sympatry as a limit to speciation, we set out to estimate the timescale over which secondary sympatry arises. Long waiting times to achievement of secondary sympatry—for example, involving millions of years—would suggest that secondary sympatry provides an important rate-limiting step to the diversification process.

We consider the rate at which newly formed taxa become sympatric along the latitudinal gradient of New

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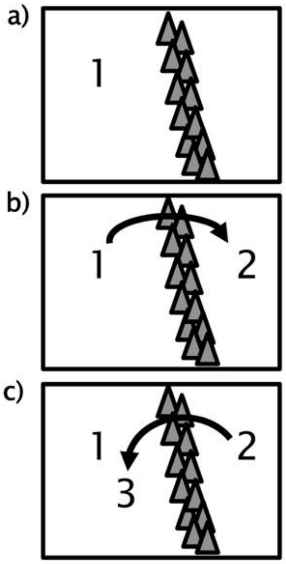

Figure 1: Progressive buildup of regional species diversity; ultimate limits to speciation are set by the ability of species to expand ranges (*b*), which often involves achievement of secondary sympatry (*c*). Three species shown are labeled 1–3 and are distributed on either side of a barrier.

World birds for which detailed range maps and extensive genetic data are available. By studying the rate of formation of sympatry throughout the New World, we are able to ask how sympatry may limit speciation in regions that differ in both climate and recent history and also evaluate factors that may limit sympatry. We compare molecular divergence times of sister taxa that are sympatric, parapatric, or allopatric in order to address the following specific questions: (1) How long does it take to achieve secondary sympatry? Although we find a few examples of very young sympatric species, we show that secondary sympatry generally requires millions of years to achieve. (2) Are there differences in the rate of secondary sympatry along the latitudinal gradient? We find that high latitudes have younger sympatric species than the tropics. In the "Discussion" we consider explanations for this finding (i.e., possible differences in barriers, ecological opportunity, and reproductive isolation) and consequences for the latitudinal gradient in diversity. (3) Is the rate of achievement of secondary sympatry associated with more rapid gain of reproductive isolation? We use ages of divergence for species pairs forming hybrid zones to show that the rate of acquisition of reproductive isolation is indeed slower in the tropics, although this is conceivably an effect, rather than a cause, of delayed achievement of sympatry in the tropics.

Methods

Our approach follows the methods introduced by Avise and Walker (1998; see also Avise et al. 1998) in a more general analysis of timing of speciation. We use the average age of sister taxa in sympatry to place an upper bound on the rate at which sympatry is formed and the average age of the deepest (allopatric or parapatric) divergences within these sisters to place a lower bound on this rate (fig. 2).

We generated a large data set, using molecular phylogenetic trees for New World birds at the genus level with complete or nearly complete species-level sampling, provided mitochondrial cytochrome b sequences were available (in some cases, the trees themselves were based on other genes, but cytochrome b sequences are always used for distance estimation). We excluded marine and aquatic bird orders and species endemic to oceanic islands (continental island species were included). At northern latitudes, a small number of groups possess a species with both Holarctic and Palearctic distributions. Less than 7% of all comparisons were of taxa pairs with midpoint latitudes in the southern latitude temperate region.

Each node along a phylogenetic tree was classified as allopatric if the geographic ranges of the descendant lin-

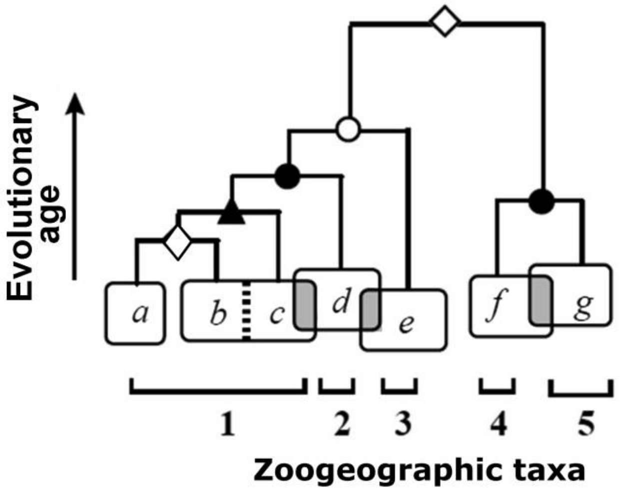

Figure 2: Example phylogenetic tree with five zoogeographic taxa. Nodes are labeled as allopatric (*diamonds*), parapatric (*triangles*), or sympatric (*circles*) on the basis of geographic ranges at the present. Taxa at the tree tips are labeled *a*–*g*, and their geographic ranges are plotted. Sympatric range overlap is illustrated by gray areas. Parapatric contact zones are shown by dashed line (between *b* and *c*). Solid symbols represent node ages analyzed in this study. These include sister zoogeographic taxa (*solid circles*) and the oldest allopatric or parapatric nodes within these (*solid triangle*). Zoogeographic taxa 1 and 2 form a sympatric sister zoogeographic pair, as do taxa 4 and 5. However, taxa 2 and 3, though sympatric, do not represent sister zoogeographic taxa because 2 is more closely related to 1 than it is to 3.

eages had no geographic contact, parapatric if ranges abutted and came into geographic contact but did not overlap (local coexistence along parapatric contact zones does not here qualify as sympatry), or sympatric if ranges overlapped, typically by hundreds of kilometers or more. Sympatry includes partial sympatry, in which a portion of one lineage's range overlaps a portion of the other, as well as complete sympatry, in which the smaller range is completely included within the range of the larger. We do not make a distinction between partial and complete sympatry in our analysis because even partial sympatry generally indicates the ability of both species to maintain their identities while coexisting. Along elevational slopes of the Andes, taxa are considered sympatric if they overlap broadly in altitude but parapatric if their ranges come in altitudinal contact without altitudinal overlap. Only breeding geographic ranges were analyzed (migration routes and wintering range were excluded). Species geographic ranges were obtained from digitized range maps for all New World Birds (Ridgely et al. 2003) and from maps in the Birds of North America Online database (http://bna.birds.cornell.edu/BNA/) and field guides (Hilty and Brown 1986; Howell and Webb 1995; Ridgely and Greenfield 2001; Schulenberg et al. 2007).

We estimated approximate dates of splitting for nodes of interest by applying a molecular clock of 2.1% per million years (1.05% per lineage per million years) to GTR-γ genetic distances of the mitochondrial cytochrome b sequences, obtained using PAUP (ver. 4.0b10; Swofford 2002). The 2.1% clock is based on 74 avian calibrations spanning 12 taxonomic orders (Weir and Schluter 2008) using the same gene and model of sequence evolution as used here. The clock appears consistent over the past 12 million years and across most avian orders, supporting its general usefulness for molecular dating for the timescales relevant to this analysis. We averaged over many pairs of taxa, with the expectation that errors in dating would not result in any consistent biases. Importantly, for birds all lines of evidence point to similar rates of sequence evolution across the latitudinal gradient in mitochondrial protein coding genes (Bromham and Cardillo 2003; Weir and Schluter 2008).

We used empirical base pair frequencies ($A = 0.275$, $C = 0.344$, $G = 0.132$, $T = 0.250$) and estimated other parameters of the GTR-γ model using maximum likelihood for the entire data set of 543 sequences ($\gamma = 0.429$; reversible substitution rates: A to C = 1.883, A to G = 12, A to T = 1.117, C to G = 0.354, C to T = 13.160, G to T = 1). Although models simpler than GTR-γ might suffice for smaller data sets, to be consistent, we use the GTR-γ model throughout. DNA sequences were generated using standard sequencing methods (Weir and Schluter 2007) or were obtained from GenBank (data available in Dryad; http://dx.doi.org/10.5061/dryad.8098).

Sequences diverge prior to population splitting, because ancestral populations are polymorphic when splitting occurs (Edwards and Beerli 2000). For birds, best estimates indicate that coalescent dates for mitochondrial sequences at both low and high latitudes generally precede population splitting by 0.2–0.3 million years, on average (Moore 1995; Weir 2006). Because the discrepancy between coalescent times and population splitting appears relatively small and similar in temperate and tropical regions (comparing data in Moore 1995 with those in Weir 2006), we approximate the date of population splitting with the coalescent date.

Phylogenetic trees were used to define clades that consist of allopatric and parapatric lineages, but not sympatric ones. These clades of allopatric and parapatric taxa, referred to as zoogeographic taxa hereafter, may contain either a single monotypic species or else multiple taxa (species or subspecies; fig. 2). Zoogeographic taxa are generally equivalent to zoogeographic species (Mayr and Short 1970; Fjeldså and Krabbe 1990; Mayr and Diamond 2001; Weir 2009), except that they do not condition on taxonomy and in rare cases may even contain members of different genera. We studied the most closely related pairs of zoogeographic taxa (referred to as sister zoogeographic taxa hereafter) that show some sympatry with each other (by definition, sister zoogeographic taxa have some sympatric overlap). Sister zoogeographic taxa represent the youngest taxa that have achieved sympatry (solid circles in fig. 2). Note that the definition of these taxa is unambiguous because sympatry, rather than taxonomy, is used to circumscribe them.

Times to Sympatry

We use the average age of sister zoogeographic taxa to provide an upper-bound estimate of the time at which sympatry is achieved, and we use the average evolutionary ages of the deepest phylogenetic splits within these taxa (solid triangle in fig. 2) to provide a lower-bound estimate on the time required for sympatry. On average, time to sympatry lies somewhere between the age of sympatric zoogeographic taxa and the age of the oldest allopatric or parapatric taxa within these taxa; we use the midpoint as an approximate estimate for comparing differences in times to sympatry across the latitudinal gradient. We estimated averages across the latitudinal gradient using a least squares regression of age versus midpoint latitude. Using quantile regression of the median value of age, as opposed to least squares regression, gave similar results, and we report only the least squares regression results.

Hybrid Zone Data

To evaluate rates of development of premating reproductive isolation, we estimated the ages of taxa that meet in hybrid zones. We analyzed hybrid zones both between species and between phylogroups (defined as geographically separated populations that are reciprocally monophyletic in mitochondrial DNA) but did not include zones of introgression between subspecies that do not represent separate phylogroups. We obtained information on hybrid zones primarily from McCarthy (2006), corroborated from a number of other sources. We excluded parapatric and sympatric taxa that are known to have hybridized but do not form hybrid zones. We also excluded parapatric taxa with insufficient information on hybridization. It is probable that many potential hybrid zones from the tropics and a few from northern temperate latitudes remain to be described because populations along their zones of contact have yet to be studied.

Latitudinal Comparisons

For both of our comparisons—times to sympatry and ages of hybridizing taxa—we evaluated variation along the latitudinal gradient. We defined latitudinal position of sympatric sister zoogeographic taxa as the midpoint latitude of the region of sympatric overlap, and we used the same midpoint latitude for the deepest phylogenetic splits within sister zoogeographic taxa. The midpoint latitude of the region of sympatry is appropriate for contrasts with relatively small latitudinal extents, but uncertainty is introduced when latitudinal extents are large. As such, we excluded all sister zoogeographic taxa with sympatric regions exceeding 30° (eight contrasts were excluded, though results were very similar when they were included). We compared ages of taxa forming hybrid zones at different latitudes using the midpoint latitude of the hybrid zone. In all cases, we took absolute values of midpoint latitudes from the Southern Hemisphere.

Results

Ages and midpoint latitudes for the entire data set are available in Dryad (http://dx.doi.org/10.5061/dryad.8098).

Establishment of Sympatry

Age of sympatric sister zoogeographic taxa show a significant decline with increasing latitude ($\beta = -0.0166 \pm 0.0083$ [SE], $t = -2.0$, $N = 137$, $P = 0.048$, y-intercept $= 3.57$), though the relationship is only marginally significant; sympatric sister zoogeographic taxa near the equator (mean 3.57 ± 0.42 million years, 95% confidence interval) are estimated to be 1 million years older on average than pairs at high latitudes (mean 2.58 ± 0.73 million years, 95% confidence interval at 60° latitude; fig. 3). The ages of the deepest phylogenetic splits within each pair of sympatric sister zoogeographic taxa decrease significantly with latitude ($\beta = -0.0311 \pm 0.0095$ [SE], $t = -3.26$, $N = 75$, $P < 0.0017$, y-intercept $= 2.78$), from an average of 2.78 ± 0.43 million years (95% confidence interval) near the equator to 0.91 ± 0.86 million years (95% confidence interval) at 60° latitude (fig. 3). The actual time to sympatry at each latitude lies, on average, somewhere in the interval between these upper and lower bounds, and we use the midpoint as a rough approximation. This midpoint line has a slope of -0.0238 and ages of 3.18 million years at the equator and 1.74 million years at 60° latitude (fig. 3). We infer that time to sympatry is about 1.44 million years longer at the equator than at 60°.

Reproductive Isolation

The presence of hybrid zones at all latitudes (fig. 4) implies that geographic contact is achieved prior to the completion of premating reproductive isolation in at least some cases. Differences in the relative rate of achievement of reproductive isolation across the latitudinal gradient can be directly assessed from the age of taxa in these hybrid zones. All latitudes possessed young hybrid zones, but the oldest

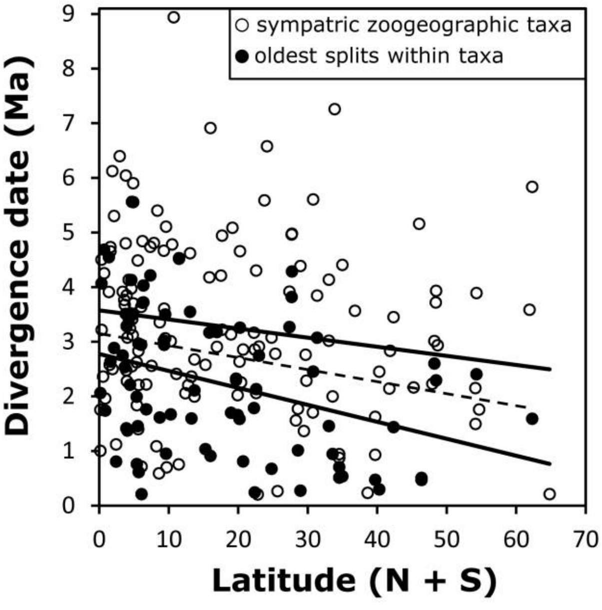

Figure 3: Latitudinal gradients in the average age of sympatric sister zoogeographic taxa and the deepest phylogenetic splits within these taxa. Least squares linear regression lines are plotted. Dashed line gives the midpoint between these two regression lines.

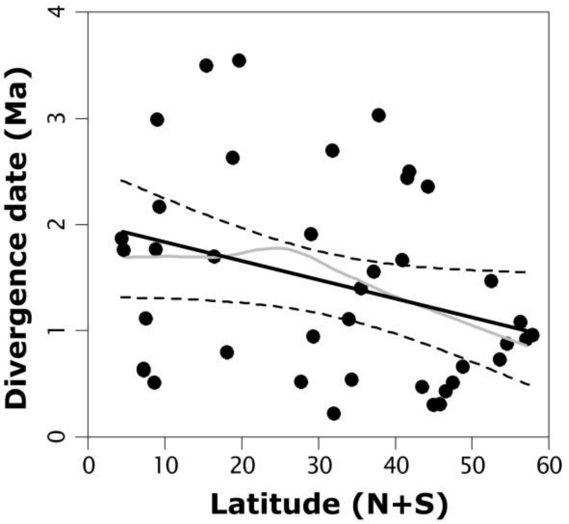

Figure 4: Divergence dates for New World species and phylogroup pairs that form hybrid zones. Least squares regression slope (±95% confidence limits) and loess curve (*gray line*) are shown.

hybrid zones occurred at lower latitudes, with hybridizing species pairs as old as 3.6 million years. In contrast, the oldest pair of species forming a hybrid zone above 45° latitude was <1.5 million years (fig. 4). Species pairs forming hybrid zones have an average age of 1.9 million years at the equator and 0.98 million years at 60° latitude, and the relationship between age of species and latitude was close to significance (fig. 4; $\beta = -0.0159 \pm 0.0085$ [SE], $t = -1.88$, $N = 40$, $P = 0.069$, y-intercept $= 1.93$). This difference is likely underestimated because we excluded many potential hybrid zones from the tropics, often involving very old species pairs, as a result of limited information on the extent of hybridization. The absence of old species pairs with hybrid zones at high latitudes implies that high-latitude species achieve premating reproductive isolation at an earlier age than do those in the tropics.

Discussion

We report two main findings. First, sympatric sister zoogeographic taxa are typically separated by millions of years. This places a constraint on the rates of allopatric and parapatric speciation, which depend on range expansions. Second, although the data show much scatter (fig. 3), we estimate that sympatry took almost twice as long to achieve at low latitudes than at high latitudes (on average 3.2 million years at the equator; cf. 1.7 million years at 60°N).

These findings are robust to the vagaries of taxonomy (Tobias et al. 2008), being based on comparisons of sympatric taxa. They do depend on a rough calibrated molecular clock, relatively small contributions of ancestral polymorphism to divergence times, and the fact that rates of molecular evolution are not strongly correlated with latitude. Given current understanding, previous analyses imply that our results are robust to these assumptions (Weir and Schluter 2008). The ages of some pairs may also be affected by mitochondrial DNA introgression, but this can only mean that we have underestimated what are already long times to secondary sympatry.

With few exceptions, the evidence that speciation in birds involves an initial allopatric phase is overwhelming (Coyne and Price 2000; Coyne and Orr 2004; Phillimore et al. 2008). We therefore interpret the younger ages of sympatric zoogeographic sister pairs at high latitudes as evidence for faster rates of secondary sympatry following allopatry, rather than evidence for a greater contribution of rapid sympatric speciation away from the equator. At least three factors may lead to the tropics having a slower rate of secondary sympatry than temperate regions: (1) stronger barriers to range expansion, (2) differences in the strength of competitive exclusion, and (3) slower rates of development of reproductive isolation. We briefly consider each in turn.

Barriers

Barriers in the tropics may function for longer periods of time or may be less permeable and may thereby limit rates of secondary sympatry. Key Neotropical barriers for lowland tropical forest species—for example, the Andean cordilleras and wide Amazonian rivers—have operated as barriers to birds for millions of years (Sick 1967; Capparela 1991; Marks et al. 2002; Aleixo 2004; Rossetti et al. 2005; Burney and Brumfield 2009). In contrast, key barriers at high latitudes, such as the Pliocene and Pleistocene ice sheets, repeatedly bisected temperate birds and other groups into multiple refugia (e.g., Weir and Schluter 2004). Species ranges presumably have had more opportunity to come back into secondary contact, given the shorter time periods during which high-latitude barriers operated. In support of this, we find that a higher proportion of the deepest splits within zoogeographic sister taxa are parapatric at high latitudes (58%) than in the tropics (34%).

Dispersal propensity also appears to differ with latitude and may affect the ease of range expansion across barriers. Many tropical species show low dispersal propensity (Moore et al. 2008; Weir et al. 2009) consistent with the longer times to secondary sympatry, whereas many temperate species are highly dispersive, as evidenced by their ability to annually migrate great distances to escape low ambient winter temperatures (Paradis et al. 1998). Dispersal propensity is a double-edged sword. Low dispersal across barriers promotes differentiation, whereas high dispersal promotes range expansion necessary for further rounds of speciation. In a general survey by Phillimore et al. (2006), families containing highly dispersive species are more species rich, suggesting that limits on range expansions ultimately limit speciation rates (fig. 1).

Competitive Exclusion

Given that parapatry is common at all latitudes (33 of the 75 deepest splits within sister zoogeographic taxa are parapatric; see data available in Dryad; http://dx.doi.org/10.5061/dryad.8098), dispersal across barriers seems unlikely to be the only factor affecting secondary sympatry. Competitive exclusion is especially likely between closely related species, which are expected to be ecologically similar. As environments are filled with species, they should become more difficult to invade, making competitive exclusion between sisters more powerful. A steeper regional rather than local latitudinal diversity gradient (about five times steeper in New World birds across the northern latitudes; Hillebrand 2004) implies that a relatively high proportion of species in the tropics fails to establish in any one local community. Climatic disturbance (and associated extinctions) in high latitudes may have resulted in relatively undersaturated ecological communities, facilitating range expansions in the recent past. It is becoming more generally accepted that ecological space places an upper limit on local species diversity (Rabosky 2009; Ricklefs 2010), and to the extent that communities approach that limit, range expansions and hence ongoing speciation should become slowed (Weir 2006; Phillimore and Price 2008, 2009).

Reproductive Isolation

A final factor affecting range expansions, the development of reproductive isolation, is unique to recently diverged taxa. Although there are a few examples of very young sympatric continental species in birds (Benkman 1993) as well as more generally (Mallet 2008), it remains unclear how taxonomically widespread these species are (many of the youngest sympatric bird species are finch-billed forms; Price 2010) and whether they persist over long time periods (Price 2010). Instead, the evidence here implies that premating reproductive isolation regularly takes millions of years to complete. In consequence, even taxa divergent for long time periods may, on recontact, form stable hybrid zones (fig. 4) or completely merge back into one species, rather than spreading into sympatry. On the basis of the hybrid zone data, premating reproductive isolation appears to arise more quickly in the temperate region than in the tropics (<1.5 million years above 45°N vs. up to 3 or 4 million years at the equator). Avian song and plumage coloration also evolve faster at high versus tropical latitudes (Martin et al. 2010; Weir and Wheatcroft 2011), which implies, when combined with hybrid zone data, that premating isolation has accumulated more slowly in the tropics over the recent past.

A possible reason for the relatively fast rate of accumulation of reproductive isolation at high latitudes is that climatic disturbance has created more diversifying selection pressures (involving either ecological or secondary sexual traits), with reproductive isolation evolving as a correlated response (Weir and Wheatcroft 2011). In addition, or alternatively, rapid establishment of sympatry between partially reproductively isolated taxa—for reasons such as ease of dispersal across barriers at high latitudes and reduced ecological competition—may drive increased reproductive isolation (Noor 1999; Price 2008, chap. 14; Martin et al. 2010). Selection pressures to increase reproductive isolation in sympatry include ecological character displacement (with reproductive isolation evolving as a correlated response), reinforcement (strengthening of premating isolation as a result of selection against hybrids), and social competition (e.g., trait divergence driven by competition of males for territories; Noor 1999; Price 2008, chap. 14).

Local Species Diversity

Our results, together with those reported by Weir and Schluter (2007), point to slower recent speciation in tropical versus temperate regions. Many workers have posited faster speciation in the tropics, specifically to account for the high species diversity in these regions (Dobzhansky 1950; Fischer 1960; Rohde 1978, 1992; Davies et al. 2004; Allen et al. 2006; Wright et al. 2006; Mittelbach et al. 2007). However, if diversity is capped in any one region, it makes little sense to talk about speciation rate, which is expected to slow as diversity accumulates (Rabosky 2009). A decline in speciation rate has been observed in molecular phylogenies (Weir 2006; McPeek 2008; Phillimore and Price 2008). We suggest that as communities become more saturated with species, range expansions into secondary sympatry become more difficult and speciation slows (Phillimore and Price 2009).

In this view, our findings of faster rates of reproductive isolation and sympatry at high latitudes are consistent with temperate communities being further from saturation than tropical communities. One likely cause is extinction. High extinction rates at high latitudes would drive diversity below its saturation level, and ecological opportunity afforded by extinction would promote rapid episodes of reproductive isolation and sympatry. In support of this scenario, climatically disturbed higher latitudes do seem to have experienced higher extinction rates than lower latitudes, as demonstrated from marine fossils (Goldberg et al. 2005; Jablonski et al. 2006) and analyses of molecular relationships among birds and mammals (Weir and Schluter 2007). The latitudinal gradient in local species diversity, then, may arise because species diversity is further from saturation at high latitudes as a result of ongoing episodes of extinction but approaches saturation in less disturbed tropical regions. Whether, in the absence of high extinction rates, levels of temperate diversity would catch up to tropical levels ultimately depends on whether any cap on diversity in tropical and temperate regions is comparable (Pianka 1966; Wright 1983; Hawkins et al. 2003; Mönkkönen et al. 2006; Davies et al. 2007).

In conclusion, the long time spans it takes for sympatry to be achieved among divergent taxa place a severe limit on the rate of ongoing speciation, on the assumption that speciation is largely allopatric or parapatric. We suggest that secondary sympatry is limited by geographic barriers, ecological factors affecting interspecific coexistence, the rate of development of reproductive isolation, and their interaction and that these factors have been relatively less constraining in the recent past at higher latitudes.

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