

# DIVERSIFICATION OF RAINFOREST FAUNAS: An Integrated Molecular Approach

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■ **Abstract** Understanding the evolutionary processes that generate and sustain diversity in tropical faunas has challenged biologists for over a century and should underpin conservation strategies. Molecular studies of diversity within species and relationships among species, when integrated with more traditional approaches of biogeography and paleoecology, have much to contribute to this challenge. Here we outline the current major hypotheses, develop predictions relevant to integrated molecular approaches, and evaluate the current evidence, focusing on central African, Australian, and South American systems. The available data are sparse relative to the scale of the questions. However, the following conclusions can be drawn: (a) in most cases, the divergence of extant sister taxa predates the Pleistocene; (b) areas with high habitat heterogeneity and recent climatic or geological instability appear to harbor more species of recent origin; (c) there is support for both allopatric and gradient models of diversification and more attention should be given to the role of diversifying selection regardless of geographic context; and (d) conservation strategies should seek to protect heterogeneous landscapes within and adjacent to large rainforest areas, rather than rainforests alone.

## SCOPE AND ISSUES

The search for the basis of high species diversity in tropical forests has occupied biologists for over a century (91, 115, 143, 151). What biologists seek to understand is how there come to be so many species in a single place (alpha diversity) and so much turnover of species between habitats (beta diversity) and

regions (gamma diversity; 27). Traditionally, this question has been subdivided into defining processes that maintain high species diversity, primarily within areas (ecological processes), and those that generate high diversity through time and across regions (historical evolutionary and biogeographical processes). However, this dichotomy between ecological and evolutionary processes is being blurred through the recognition that history has played a substantial role in shaping both regional and local species diversity (71, 118, 154) and that ecological factors can influence or drive speciation (83, 102, 121, 122).

Here we focus on the processes, both ecological and geographic, that have generated species diversity in tropical forests and affected the balance between the origin and extinction of species. In so doing, we need to be clear about what we mean by "species." There is a plethora of species definitions in the literature (70, 88, 103). Our approach is shaped by the phenomenon that we seek to explain—functional diversity in complex ecosystems. Thus, we recognize as species geographically bounded sets of populations that are distinct for morphological traits or are reproductively isolated from congeners, with or without corresponding molecular divergence. This definition encompasses situations in which there are concordant molecular and phenotypic differences, but allows for circumstances in which the progenitor of a recently evolved, phenotypically distinct lineage is paraphyletic with respect to the derived species (105). This definition excludes allopatric populations that are divergent for presumed neutral molecular genetic characters but not clearly distinguishable using behavioral or morphological traits. While such populations represent independent evolutionary lineages and would qualify as species under an Evolutionary or Phylogenetic Species Concept (31), they do not represent the type of diversity typically considered by ecologists.

The purpose of this review is to explore the contribution that analyses of molecular phylogenetics and population genetics are making to the understanding of the origin of faunal diversity in tropical forests. Examining patterns of molecular diversity provides the potential to link anagenetic evolution and speciation, to shed light on historical biogeography, and to test alternative hypotheses about mechanisms of diversification (40, 41). One finding that emerges from this and previous reviews (3) is the need to integrate molecular systematics with analyses of phenotypic variation and reproductive isolation and, where possible, with independent evidence of landscape history such as that derived from geology or paleoclimatology.

The importance of testing alternative hypotheses about speciation mechanisms was emphasized by Endler (40, 41), who demonstrated that the same geographic pattern of species abundance and congruence of subspecies and species boundaries can be explained by both parapatric (gradient) and allopatric (refuge) mechanisms. We review major current hypotheses about the cause of high species diversity in tropical faunas and develop contrasting predictions about patterns of molecular and phenotypic variation for alternative speciation models. We then evaluate molecular evidence from recent studies spanning three continents, starting with ages of rain-forest species inferred from interspecific comparisons and proceeding through case

studies that illustrate the use of molecular and, where available, morphological and ecological information to test predictions of specific hypotheses about mechanisms of diversification. We conclude that while geographic context is important, the role of ecology and divergent selection in determining functional diversity within and among species in rainforests deserves greater attention. This has important implications for conservation.

The molecular analysis of rainforest faunas is in its infancy, yet already it is clear that it will contribute to understanding the history of species diversification (52) and historical biogeography of particular regions. This, in turn, should inform the study of community ecology (118) by providing the historical framework with which to interpret patterns of species distribution and community composition (124) and, perhaps, by estimating critical variables such as rates of speciation, extinction and immigration (71, 98).

Insights from molecular systematics and population genetics, when combined with analyses of species distributions, phenotypic variation, and landscape history should also lead to improved strategies for conservation. Given that we should seek to maintain evolutionary processes (7, 42, 94, 140), including the requisite ecological viability of systems, it is important to understand how historical processes have shaped genetic and species diversity in whole communities of organisms (2, 95) and how current evolutionary processes are maintaining phenotypic diversity. While the details of these processes will differ among systems, it should be possible to devise conservation strategies that protect both the (irreplaceable) genetic diversity attributable to historical isolation and the landscape features that promote phenotypic diversity through a balance between gene flow and selection (94). Such process-oriented strategies for conservation are likely to be more effective in a changing world than those that assume a static distribution of diversity (20).

## CURRENT HYPOTHESES OF DIVERSIFICATION

The major hypotheses concerning high species diversity in tropical systems can be placed into two nonexclusive categories: those that invoke low rates of extinction versus those focused on high rates of speciation. The former argue that tropical biotas have accumulated large numbers of species over long time periods because, relative to temperate or boreal systems, the tropics are old and have been stable climatically (143). An extension is that ecologically stable rainforest areas either accumulate paleoendemics or combine low extinction rates with high speciation rates to accumulate both paleo- and neoendemic species (44, 45). In principle, the hypothesis that high species richness is partly attributable to low extinction and/or high speciation rates is testable by comparing sister groups between tropics and temperate zones (24, 43) or between tropical areas of different stability (e.g. stable lowland tropics versus volatile Andes; see below).

Hypotheses concerning factors that promote speciation in tropical faunas are too numerous to review in detail here (for recent reviews, see 19, 62). By and large,

**TABLE 1** Brief description of major models of evolutionary processes that promote diversification of rainforest faunas<sup>a</sup>

Name—Geographic Mode <sup>b</sup>	Isolating Barrier	Evolutionary Mechanisms	Key Reference(s)
Refugia model—allopatric	Dry forests, savanna	Isolation, drift, selection	37, 57, 62, 148
Riverine model—allopatric	Major rivers	Isolation, drift? <sup>c</sup> , selection? <sup>c</sup>	6, 151
Vanishing refuges—allopatric	Dry forests, savanna	Isolation, drift, directional selection	148
Disturbance—vicariance—allopatric	Heterogeneous forest structure	Competition, directional selection? <sup>c</sup>	19, 28
Gradient model—parapatric or allopatric	None necessary	Divergent selection, with or without gene flow	39, 117, 141

<sup>a</sup>See Figure 1 and text for further description.

<sup>b</sup>Several variations on these themes are reviewed by Haffer (62). These include a river-refuge model that combines major rivers and dry biomes between rainforest refugia as agents promoting geographic isolation within Amazonia and various paleogeography models that invoke tectonic and mountain-building events barriers.

<sup>c</sup>?, Refers to processes for which operation is uncertain.

these hypotheses have been preoccupied with the geographic context of speciation and, for allopatric models, the physical cause of isolation (Table 1). The refugia model has been the most widely discussed (85, 115, 153) and rests on the premise that climatic change caused rainforests to contract to refugia separated by dry forests and savanna and that this isolation promoted speciation. Initial discussions focused on Pleistocene events, particularly those for the last glacial cycle or two (37, 57), although more recently the model has been extended to Tertiary events on the assumption that climatic oscillations driven by Milankovitch cycles through this period were of sufficient amplitude and duration to promote speciation (61, 62).

Criticisms of the refuge model include uncertainty about whether Amazonian rainforests contracted or just changed in composition (29), concerns about sampling bias in identifying locations of refugia (100), debate over whether contact zones between presumed sister-taxa are appropriately located (40, 92), increased complexity (and reduced testability) as additional refugia are proposed (85), and the argument that alternative speciation mechanisms provide equally good explanations for the biogeographic patterns observed (40, 41, 87). Moreover, with few exceptions, the evolutionary mechanisms supposed to promote morphological or reproductive divergence among the isolated populations are rarely explicit. Finally, only rarely can the paleoecological and biogeographic evidence specify either the size or ecological characteristics of putative refugia.

One interesting variation on this theme is the vanishing refuge model (148), which posits that some populations differentiated to species through directional

selection toward tolerance of ecotones or dry habitats as rainforest patches became too small to retain viable populations. This idea was prompted by the impression that sister taxa commonly occur in geographically adjacent but distinct habitats, a pattern that is also predicted by gradient models (see below). Another refuge-based model that explicitly discussed the mechanisms involved in population divergence was developed to account for the extraordinary diversity of mimetic forms of butterflies in the neotropics (17, 18, 89). Turner (146; but see also 15, 87) proposed that random loss of model species among refugia was a major selective agent that resulted in diversification of mimetic species.

The second major class of allopatric model (Table 1) invokes substantial river systems as barriers to gene flow, such that populations on either side gradually diverge to form separate species (151). Empirical support for this “riverine barrier” model comes from observation that the boundaries of closely related species or subspecies often coincide with the major rivers of Amazonia [e.g. tamarins and marmosets (64); various birds (30, 58–60, 63); Amazonian lizards (1)]. Difficulties with this model arise because the strength of the barrier to gene flow in widely distributed species diminishes toward the upper reaches of a river (6, 114), and the location of many rivers is highly dynamic on both short and long time scales (84). A problem shared with the refuge model is that distributional data alone do not distinguish between the rivers as current meeting points for species that diverged elsewhere versus locations of primary diversification (60, 62, 128).

Models based on divergent selection across strong environmental gradients (gradient model, Table 1) differ fundamentally from allopatric models in that complete suppression of gene flow is not a prerequisite for phenotypic divergence and speciation (39, 102, 117). For rainforests, the gradient model suggests that strong environmental (e.g. habitat) gradients resulted in adaptive divergence and speciation. This is expected to result in sister species adapted to adjacent but distinct environments (e.g. rainforest—dry forest). Evidence consistent with this model in rainforest faunas comes from the frequent location of hybrid zones in ecotones (41, 42) and observations of species-level phenotypic differentiation between populations in rainforest and adjacent habitats (126, 141). Recent emphasis on current (145) and, possibly, historical (28) heterogeneity of vegetation structure within Amazonia suggests additional possibilities for this mechanism to operate. However, once again, distributional data alone are open to multiple interpretations (e.g. 85, 92).

Aside from the inherent ambiguity of current distribution patterns, a further difficulty with all of the above models is the spatio-temporal dynamics of key variables such as the structure, location, and contiguity of rainforests and the concomitant strength and location of selection gradients. These are poorly resolved or contentious for the late Pleistocene, let alone earlier periods. Any discussion of refuge or other models should bear this in mind and critically evaluate evidence from paleopalynology or climate modeling to confirm that such habitat mosaics did, in fact, exist (18).

## PREDICTIONS FROM MOLECULAR SYSTEMATICS

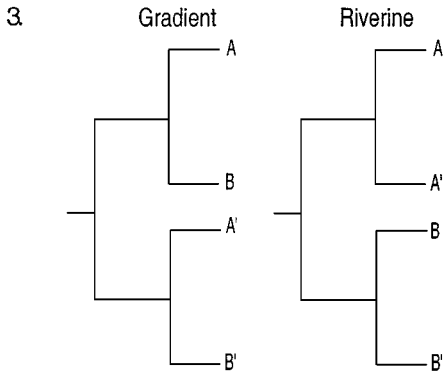
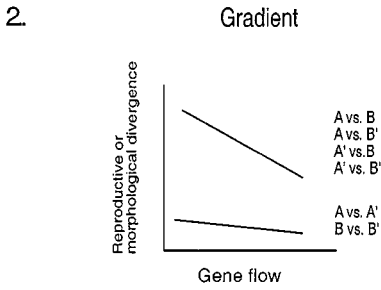
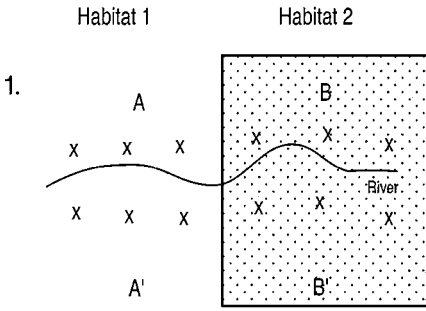
Molecular data, when combined with information on phenotypic variation, species distributions, and landscape ecology and history can provide four types of information relevant to hypotheses about speciation in rainforests:

1. Relationships among species and historical (phylogeographic) lineages within species, in particular identification of sister groups in relation to geography and habitat/ecological attributes (32, 85) although nonmolecular data are also informative.
2. Approximate estimates of the timing of divergence events (4, 5, 14, 35, 66, 124) and, potentially, examination of the long-term balance between speciation and extinction within monophyletic lineages (98);
3. Estimates of current and historical gene flow rates among populations (129), against which patterns of morphological variation or reproductive isolation can be compared (39, 102);
4. Tests for historical founder events and range expansions (130, 144), especially in relation to the location of putative refugia and expansion zones.

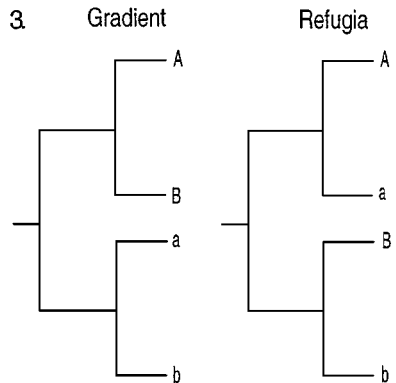
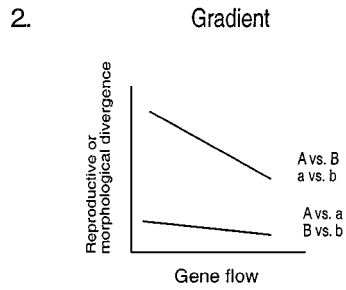
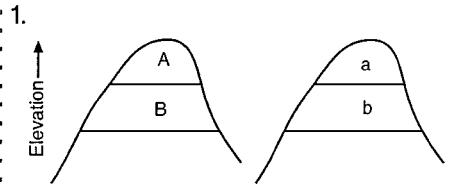
The predictions of three major hypotheses, the refugia, riverine, and gradient models, are illustrated in Figure 1 and Table 1. Briefly, the refugia model predicts that recently evolved sister taxa occur in adjacent refugia (as defined a priori by substantial paleoecological evidence) and that there should be evidence from intraspecific gene trees for range expansions and secondary contact between refugia and, if drift is invoked, for population restriction within refugia. These patterns should be broadly congruent among species with similar ecological requirements and vagility (3). An important caveat is that a rainforest refugium itself may be

**Figure 1** Complementary approaches to discriminating among major hypotheses concerning mechanisms that promote diversity in rainforest faunas (see Table 1). For both Riverine (allopatric) vs Gradient (panel *A1*) and Refugia (allopatric) vs Gradient (panel *B1*) comparisons, expected outcomes in relation to phenotypic divergence vs gene flow in multipopulation comparisons (panels *A2*, *B2*), and phylogeny of taxa (panels *A3*, *B3*). In the Riverine vs Gradient test, populations are distributed among habitats (*A* vs *B* and *A'* vs *B'*) that may result in divergent selection pressures and, on either side of a river, are hypothesized to suppress gene flow (*A* and *B* vs *A'* and *B'*). The Refugia vs Gradient test is illustrated for populations occupying adjacent elevational zones (*A* and *a* vs *B* and *b*) across which a selection gradient is hypothesized and geographically disjunct habitats (*A* and *B* vs *a* and *b*) are hypothesized to represent separate historical refugia (e.g. 104). In both cases, the Gradient model predicts an inverse relationship between phenotypic divergence and gene flow across habitats but not within habitats, and that recently derived sister-taxa should occupy distinct environments. Conversely, the allopatric (riverine or refugia) models predict that sister taxa should be separated by the barrier to gene flow. For further discussion and predictions, see text.

# A. Riverine vs. Gradient



# B. Refugia vs. Gradient



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dissected by dry habitats (68), in which case the refugial population may retain multiple genetic lineages within a metapopulation structure, potentially confounding tests for population bottlenecks and range expansion. Another limitation is that refuge hypotheses do not predict a unique phylogenetic structure for sister species (36) unless the putative refugia are linearly arrayed (124) or the sequence of isolation can be predicted with confidence from independent paleoecological or geological evidence (85).

The riverine model predicts that sister species, and distinct phylogeographic clades within species, should occur across major rivers rather than being segregated within fluvial areas or across gradients (Figure 1). In contrast to the refugia model, there is no expectation for genetic signatures of range expansion. Again, the vicariant pattern should be congruent among species with similar ecological requirements and capacity to disperse across rivers. Importantly, phylogenies within and among closely related species can distinguish between primary divergence across rivers versus secondary contact between nonsister lineages that diversified elsewhere (110). Complications arise for species that occupy flood plains across which the actual location of the river channel varies in time, potentially relocating populations of the adjacent lineages onto opposite banks due to meander cutoffs. As a consequence, specialists of floodplain forest are less likely to exhibit riverine diversification than are upland ("terra firma") forest specialists (109, 110).

For both of the above "allopatric" models (and the river-refugia combination; 62), the insights into historical biogeography provided by intra- and interspecific gene trees provide an opportunity to ask what happens when vicariant populations come into secondary contact. Is there evidence for reproductive isolation, for example, linkage disequilibrium or pre- or postmating isolation (9, 10)? In the context of determining whether geographic isolation alone is sufficient to promote speciation, these are important questions regardless of the level of phenotypic differentiation between the sister lineages.

The gradient (or "divergence with gene flow") model makes unique predictions about the relationship between gene flow and morphological or reproductive divergence within species and also predicts that sister taxa should occupy distinct but adjacent habitats (Figure 1). Within species, this model predicts that, for a given level of gene flow, phenotypic and reproductive divergence among populations should be much greater among habitats than within habitats. Morphological divergence should be strongly inversely correlated with gene flow because of contrasting selection pressures in different habitats (Figure 1; 102). Divergence for neutral quantitative traits should also be inversely correlated with gene flow due to drift, but no difference is expected for comparisons among versus within habitats (Figure 1; 86, 102). The prediction that sister species should occupy distinct habitats is shared with the vanishing refugia model (148), but the latter also requires severe population bottlenecks and range expansion, whereas the gradient model does not.

Tests of speciation models will be most informative for recent to middle-aged taxa. Lineages resulting from ancient divergences are likely to have undergone species extinctions, diverged in ecology, or changed distributions to the point where



the original geographic/ecological context of speciation is obscured. On the other hand, very recent lineages may not have achieved a genetic signature sufficient to pinpoint their mode of origin. This issue is relevant to both phylogenetic and biogeographic approaches. Although analytical methods to distinguish between allopatric and sympatric speciation mechanisms from species phylogenies have been proposed (8), it seems unlikely that they can distinguish parapatric models (e.g. gradient model) from other alternatives.

## TEMPO OF SPECIATION

Molecular phylogenies of extant taxa offer the opportunity to examine the tempo and mode of speciation for groups in which fossil data are lacking (99) as is the case for most tropical rainforest taxa. Several questions regarding the evolution of the high species diversity of tropical regions may be addressed as comprehensive molecular phylogenies for diverse groups become available. First, is there evidence for recent bursts of speciation consistent with Pleistocene Refuge models? Second, how do the relative divergence times of tropical and temperate lineages compare—are tropical taxa older than temperate taxa? Third, how do estimates of extinction and speciation rates in tropical clades compare to those of nontropical sister groups—does the high species diversity in tropical groups result from higher speciation rates, lower extinction rates, or a combination of the two? Fourth, how does the tempo of speciation, inferred from molecular divergence, differ among rainforest regions with different ecological and/or geological histories?

Is there evidence for recent Pleistocene speciation? Given uncertainties about rates of molecular evolution and the typically low precision of most estimates (67), the following compilation of genetic divergence among sister species of rainforest vertebrates seeks only to examine broad patterns. Comparisons of relative divergence estimates among sister taxa in tropical and temperate regions involve few assumptions, other than that of similar rates of substitution across taxa and among groups. Bearing the above caveats in mind, molecular phylogenies of birds, mammals, lizards, frogs, and salamanders from tropical regions of Central and South America, Australia, and Africa suggest that most speciation events in tropical rainforests predate the Pleistocene (Table 2). For example, only 7 of 125 speciation events in 22 genera of tropical South American small mammals occurred in a time frame consistent with Pleistocene divergence (<about 4% sequence divergence for mtDNA cytochrome b sequences; Figure 2) and most of those occurred in a single rodent genus, *Oecomys*. In birds, 18 of 64 speciation events show sister groups differing by >4% in mitochondrial protein coding genes (cyt-b and/or ND2). Most of these (10) are concentrated in a single genus of Spinetails (*Craniioleuca*; 48). In total, the available data indicate that Pleistocene climate oscillations played little role in generating vertebrate species diversity in tropical rainforests.

Are tropical taxa older than temperate taxa? We do not know of any studies that directly compare ages of species from temperate and tropical regions. However, a

**TABLE 1** Summary of genetic distance among sister species and/or sister groups from molecular systematic studies of tropical vertebrate taxa<sup>a</sup>

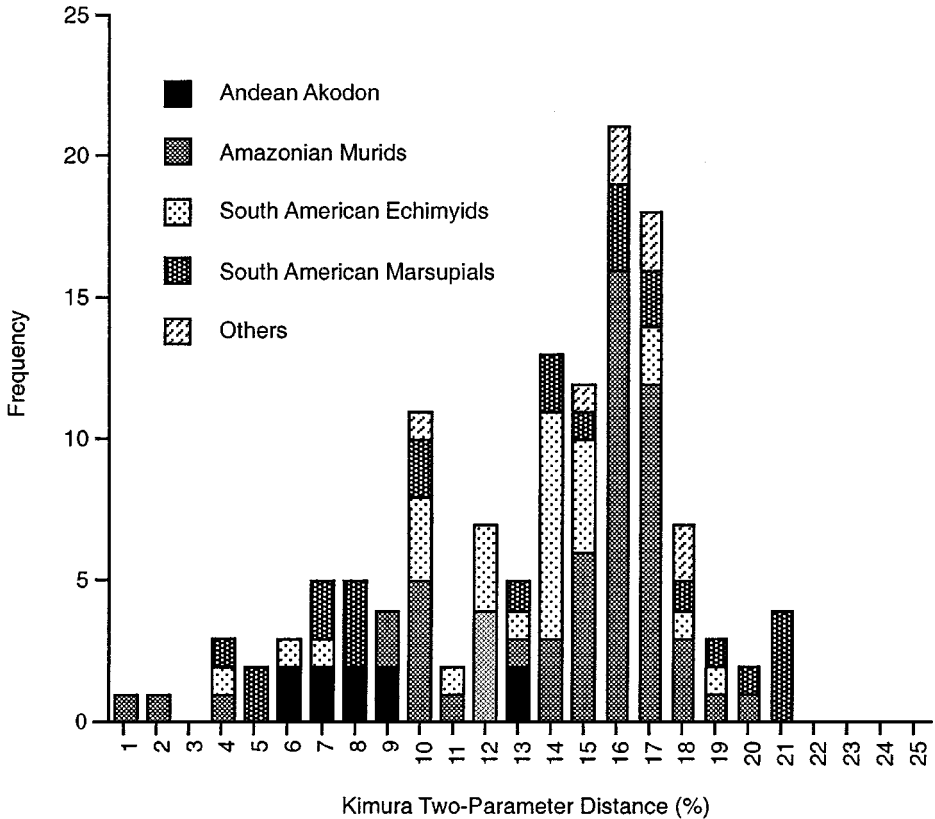
<b>Taxon</b>	<b>Data Type</b>	<b>Mean (range)</b>	<b>Time (My)</b>	<b>Reference(s)</b>
Caudata				
<i>Oedipina</i>	Allozymes Nei's D	0.73 (0.35–1.60)	4.87 (2.3–10.7)	53
Anura				
<i>Physalaemus</i>	12S rRNA	10.12 (2.24–18.71)	10.12 (2.24–18.71)	21
<i>Bufo</i> (neotropical species)	16S rRNA	15.14 (6.17–24.89)	15.14 (6.17–24.89)	55
<i>Cophixalis</i>	16S rRNA	9.66 (4.82–14.47)	9.66 (4.82–14.47)	C Hoskins & C Moritz, unpublished data
<i>Cyclorhamphus</i>	MCF <sup>b</sup>	33.95 (3.0–102.0)	16.98 (1.5–61.0)	66
Squamata				
Australian carphodactyline geckos ( <i>Carphodactylus</i> , <i>Saltuarius</i> , and <i>Phyllurus</i> )	12SrRNA	8.55 (3.7–14.35)	8.55 (3.7–14.35)	CJ Schneider, unpublished data
Mammalia				
Australasian ring-tail possums	ND2, Cyt-b	15.24 (4.11–23.29)	7.62 (2.06–12.65)	96, MC Lara & C Moritz, unpublished data
Amazonian possums	Cyt-b	9.36 (2.30–19.90)	4.68 (1.65–9.95)	36, 97, 106
Amazonian rodents	Cyt-b	12.51 (0.90–19.63)	6.75 (0.45–9.82)	35, 36, 79, 108–110, 131, 132

Andean Akodon	Cyt-b	7.95 (5.40–12.20)	3.98 (2.70–6.10)	104, 111
Atlantic Forest marsupials	Cyt-b	13.99 (5.80–19.30)	7.00 (2.90–9.65)	97
Atlantic Forest rodents	Cyt-b	13.30 (5.84–17.40)	6.65 (2.92–8.70)	78, 79
<i>Saguinus monkeys</i>	308bp Cyt-b, 600bp control region.	11.85 (6.79–13.90) <sup>c</sup>	5.93 (3.40–7.95)	72
Aves				
Tanagers ( <i>Rhamphocelus</i> )	Cyt-b	4.69 (1.60–8.32)	2.35 (0.80–4.16)	56
Nyctibiid Potoos	Cyt-b	14.41 (11.10–16.20)	7.21 (5.55–8.10)	90
Bul-buls ( <i>Andropadus</i> )	Cyt-b	10.60 (4.59–18.24)	5.30 (2.30–9.12)	119
Scrubwrens ( <i>Sericornis</i> )	Cyt-b	8.27 (5.1–13.1)	4.18 (2.55–6.51)	73
Chat tyrants ( <i>Silycultrix</i> )	ND2	7.40 (5.80–9.70)	3.7 (2.90–4.85)	47
Spinetails ( <i>Cranioleuca</i> )	ND2, Cyt-b	1.9 (0.50–4.00)	0.95 (0.25–2.00)	48
Tit-tyrants ( <i>Anairetes</i> )	ND2, Cyt-b	3.3 (1.10–5.30)	1.65 (0.50–2.65)	120

<sup>a</sup>Studies were selected based on their relatively complete representation of known species and use of mitochondrial DNA in most cases. In all cases, Kitch trees were produced from a distance matrix as listed under Data Type, using PhyIip version 3.5. Divergence values represent the branch length between phylogenetically independent pairs of species or sister groups on the Kitch tree and, with the exception of the *Saguinus* monkeys (uncorrected p distance) are based on Kimura 2-parameter estimates. Approximate divergence times were estimated by using 0.15 D/My for allozyme data and 1% and 2%/My sequence divergence for mitochondrial 12S and 16S rDNA and protein-coding genes (ND2 and Cyt-b), respectively (see text for caveats).

<sup>b</sup>MCF, Micro-Complement Fixation.

<sup>c</sup>Sequence unavailable in Genbank.



**Figure 2** Histogram of Kimura two-parameter distances between mammalian sister species, as shown in Table 2, grouped by taxonomic affiliation and geographic distribution.

limited sampling of tropical bird taxa (Table 2) allows a preliminary comparison. Klicka & Zink (77) found the mean sequence divergence among temperate zone sister species to be  $5.1\% \pm 3.00\%$ . Among the tropical bird species listed in Table 2, the average divergence is  $7.2\% \pm 4.37\%$ . This difference is not statistically significant (*t*-test,  $p = 0.12$ ) but additional data are needed for a robust analysis. Avian tribes at low latitudes tend to be older (as estimated from DNA hybridization data) than those at high latitudes (51). Further, avian sister taxa (tribes to families) at low latitudes are also more species rich, implying a higher rate of diversification (speciation less extinction; 24). As molecular phylogenies accumulate for species-rich genera and families, it should be possible to analyze more precisely the tempo of diversification in tropical vs temperate clades.

Does the tempo of speciation differ among rainforest regions with different ecological and/or geological histories? Again, data are lacking for most taxa and regions but evidence for two groups from South America (birds and mammals)

is informative. Based on the DNA hybridization data of Sibley & Alquist (127), Fjelds  (44) suggested that the tropical Andes contain a greater proportion of young bird species than do the Amazonian lowlands. This view is supported by low levels of mtDNA sequence divergence among species within genera that have a primarily Andean distribution (48, 49, 120; but see 47). For South American mammals, there are sufficient data for murid rodents (104, 113, 131, 132) to examine the relative depth of divergence among species from the Andes and lowland Amazonian rainforests. For species in the genus *Akodon* and closely related genera, mitochondrial cytochrome-b sequence divergence indicates that species in the Andes are significantly younger than those in the Amazonian lowlands. The mean distance between sister taxa in Andean genera is  $7.9\% \pm 2.45\%$ , whereas the mean distance between sister taxa within Amazonia is  $13.8\% \pm 3.76\%$  (t-test,  $p < 0.001$ ).

Although these comparisons are based on few taxa, the pattern of relatively old species in tropical rainforests may reflect a general pattern worldwide. Roy (119) found that lowland species of a widespread African rainforest bird genus (*Andropadus*) were older than species in the Rift Mountains of East Africa. In Australia, species of rainforest-endemic vertebrates appear to be extremely old, as inferred from the large genetic distance among them (Table 2; 96), and may represent the remnants of an ancient, previously more widespread rainforest fauna. In addition, mtDNA divergence of small mammal species from the Amazon basin and the Atlantic Forest of eastern Brazil reveal similarly ancient speciation events in many taxa (see below and 78, 97, 132), consistent with earlier indications of pre-Pleistocene divergence of Amazonian and Atlantic forest amphibians (66). As better calibrations of molecular evolutionary rates become available and paleoecological reconstructions of habitat distributions are extended further back in time, comparisons of absolute time of divergence among species may allow us to infer the geographic and climatic context of speciation in these ancient lineages.

## MOLECULAR PERSPECTIVES ON SPECIATION MECHANISMS

### Refugia Models

While rainforest refugia have been postulated for most rainforest areas of the world, the molecular data necessary to test whether such refugia existed and, if so, whether their existence is associated with speciation have begun to be collected for only a few systems. We summarize findings from analyses of low-moderate elevation areas in Africa, South America, and eastern Australia as a series of case studies. We exclude the high Andes because, while the fauna of these paramo and grassland communities were likely the subject of vicariance (150), they are not germane to the rainforest refuge model.

**Africa** Molecular analyses have been applied to avian fauna of montane rainforests of east Africa. Using published DNA hybridization data (127), Fjelds  and colleagues (44, 46) demonstrated that these, along with other mountains and the forest/savanna ecotone surrounding the Guineo-Congolian lowland forest, contain concentrations of both recent and old species, whereas the lowland area is dominated by old species. The mountains of east Africa have been proposed as refugia that provided relatively stable montane forest environments during the Quaternary and as a site of recent diversification (37). Phylogenetic analyses of mtDNA sequences from various species and subspecies of bulbuls (*Andropadus*) indicated that the montane taxa were a monophyletic group relative to those in the lowlands and that some of the former had diverged recently (<3 million years (My), 119), whereas the latter were mid-early Miocene in age. These observations were interpreted as supporting a montane refuge model of speciation through genetic drift in populations of reduced size (119).

**South America** The forested Andean slopes, the western Amazon Basin, and the Atlantic Forest of coastal Brazil are all major areas of biotic endemism, with refugia proposed for each (17, 18). Despite the extraordinarily rich biota of these regions, however, few molecular data are available, and phylogeographic tests of proposed refuges have yet to be developed (15, 36).

Using the DNA hybridization data of Sibley & Ahlquist (127), Fjelds  (44) identified the tropical Andes and the lower eastern Andean fringe as areas with the highest concentration of recently evolved endemic bird species. In contrast, phyletic relics and medium-old taxa characterize the forests of lowland Amazonia. Fjelds  (45) described those areas with concentrations of old lineages as "ecologically extremely stable" (EESA) regions, ones that remained stable through the shifting climatic periods in the Pleistocene. "Stability" here refers to ecological conditions that maintained species pools despite local habitat shifts and changing community compositions, rather than constancy of specific extant communities over long time periods.

Fjelds  (44, 45) related the high proportion of young species in the Andes (by a factor of three or more relative to Amazonia) to the topographic and climatic complexity created by uplift of the central and northern Andes since the Miocene. These analyses also suggested that most young species within the Atlantic Forest of coastal Brazil occur in the central region in the states of Rio de Janeiro and Espirito Santo, another area where faulting has generated relatively recent escarpments and coastal ranges. Importantly, this region is actually located between postulated Pleistocene refuges.

These conclusions accord with the few available phylogeographic studies of bird lineages distributed from Amazonian lowlands to Andean highlands. For example, the Amazonian species of the flycatcher genus *Leptopogon* is basal to all others in the complex, and the altitudinally zoned Andean species become increasingly younger from low to high elevations (11). Hence, speciation in this genus is consistent with old lowland forest taxa diversifying into habitats of successively

higher elevation in the Andes as the mountains rose. Creighton (33) had proposed a similar model for lowland and Andean taxa of mouse opossums of the genera *Marmosops*, *Marmosa*, and *Gracilinanus*, although without molecular data.

The same pattern of older lowland and younger high-elevation species is apparent in small-bodied mammals for which molecular data are available (35, 36, 104, 132). As noted above, sister-species of lowland forest mice are significantly more divergent than are those of Andean taxa. Moreover, divergences among species within lowland lineages of both rodents and marsupials are not only deep but relatively uniform (mtDNA distances  $13.7\% \pm 0.16\%$ ). These data suggest that speciation episodes in each were approximately concordant at some time in the late Tertiary (assuming similar rates of molecular divergence).

In coastal Brazil, those few mammalian taxa for which molecular data are available (78, 97) exhibit distribution patterns inconsistent with diversification between the proposed refuges along the Atlantic escarpment. For example, the two species of the slender mouse opossum *Marmosops* in the Atlantic Forest are elevationally segregated in the mountains of southern coastal Brazil, rather than replacing one another between proposed refuges.

Replacement, with possible contact at a midpoint between refuges, would be expected if refugial isolation had promoted their divergence. The substantial molecular difference between these two species (mtDNA distance of 16.7%) also supports ancient differentiation. Finally, this pair of species cannot be confirmed as phyletic sisters in relation to the five lowland Amazonian species, as would be required if their divergence within the Atlantic Forest were refuge-related. The combination of distribution pattern, depth of molecular divergence, and nonsister relationship all point to differentiation at a time earlier than, and by a process different from, Pleistocene refuge formation. The distribution pattern of elevational segregation, with a geographically limited higher-elevation species in the southern Atlantic Forest and much more broadly distributed lower-elevation one also characterizes other mammals [e.g. rodents of the genera *Delomys* (149) and *Akodon* (26)] as well as some birds [ant wrens of the genus *Drymophila* (155)]. Although molecular estimates of divergence in these taxa have not been published, the shared distribution pattern with *Marmosops* suggests the possibility of a common history.

The association between recent diversification and areas of tectonic, as well as climatic, activity is supported by recent reconstructions of the geological history of the central and northern Andes and adjacent Amazonia. The last (and continuing) major episode of Andean uplift began in early to mid-Miocene (10–12 MYA). By the end of the Pliocene, the eastern cordillera was sufficiently high to alter the flow of the proto-Amazon from north into the Caribbean to its present exit into the Atlantic Ocean to the east (82, 84). Andean uplift also generated substantial subsidence of foreland basins and forebulge formation in western Amazonia, producing a series of subbasins now filled with sediments of Andean origin. Phylogeographic signatures concordant with these underlying paleogeophysical features remain evident in the small mammal fauna of that region today (36, 81, 107, 110).

A general conclusion reached from the molecular studies is that species diversification in the lowland tropical forests is older than previously thought, with a substantial proportion of the extant fauna initiating divergence prior to the Pleistocene. In the case of Amazonia, the high species richness and endemism of the proposed refugia may have resulted from greater age and, perhaps, longer-term stability. These regions have thus served as reservoirs for speciation in the geologically active areas around the periphery of Amazonia, but not as centers of active and recent speciation.

**Australian Wet Tropics** The rainforests of the Australian wet tropics occupy a small (<1 million hectare) area in northeast Queensland but have the high species diversity and endemism (relative to temperate/arid regions in Australia) typical of rainforests elsewhere. Geologically, the major topographic features—peaks of the Great Dividing Range—are ancient eroded remains of an uplift that is perhaps >150 Mya in age; superimposed on this has been localized volcanic activity in the late Cenozoic to as recently as 10 kya. From paleopalynology, there is strong evidence for contractions of complex angiosperm rainforests during glacial cycles, so that the forests were restricted to mesic (mostly high elevation) areas for much of the Quaternary and perhaps earlier (76). High-elevation Pleistocene refugia have been proposed by plant biogeographers (152) although analyses of charcoal indicate that these were extensively dissected by dry forests (68). Paleoclimate modeling (101) infers a major disjunction of the cool complex rainforests, which harbored the majority of endemic vertebrates, to either side of a relatively low, dry saddle termed the Black Mountain Corridor (BMC) during the last glacial maximum. This was followed by a rapid expansion of these forests at 8 thousand years ago (kya) (68, 101) reaching a maximum extent in a cool wet phase between 7.5 and 6 kya, which would have facilitated migration between areas of upland rainforest, even those that are now isolated.

Molecular comparisons of endemic species indicate that very few are likely to have arisen within the Pleistocene, with most probably representing Miocene divergences (see above). This, together with evidence from geographic patterns of species richness (154), indicates that the major effect of mid-late Pleistocene climate fluctuations has been local extinction rather than speciation. In the absence of recent radiations within genera so far examined, we focus on the patterns of molecular and morphological variation within widely distributed endemic species.

Phylogeography of mtDNA has been examined for 13 species of vertebrate (five birds, four frogs, four lizards): all but three birds (two of which are not rainforest specialists) show a congruent phylogeographic break located at or adjacent to the BMC (74, 124, 126; M Cunningham, unpublished data). Levels of sequence divergence across the BMC range from <1% to 12%, with a mean of 0.84% for birds, 7.58% for frogs, and 7.35% for lizards. For the herpetofauna, most (7/8) divergence values across the BMC are >4%, indicating largely pre-Pleistocene isolation of these high-elevation communities. Within areas, there is evidence from the gene trees for recent population reductions followed by (presumably



Holocene) range expansions (124, 125) as required by the refuge model (Table 1). Notably, it appears that the community of rainforest-dependent vertebrates from the southernmost block has been largely or wholly reconstituted by migration from the north during the Holocene expansion events (124). Two rainforest species examined, a high-elevation bird (*Sericornis keri*, 74) and a low-mid elevation *Drosophila* (*D. birchii*, 75), showed exceptionally low diversity and no geographic structure across the wet tropics, suggestive of recent restriction to a single region.

The evidence for both refugial isolation, in some cases extending back millions of years, and recent range expansions provides an unusual opportunity to evaluate critically the effect of isolation combined with population bottlenecks on morphological differentiation within species. The result is straightforward—little or no differentiation in ecomorphological traits was observed in the lizards (125, 126) or frogs (M Cunningham, unpublished data). Detailed morphometric comparisons have not yet been made for the birds, but it is notable that there are no pairs of subspecies separated by the BMC. Experimental tests for reproductive isolation between the isolated populations have not been carried out. However, genetic analyses of secondary contact zones in three taxa (a frog, skink, and mammal; M Cunningham, B Phillips, L Pope, respectively, unpublished data) did not reveal linkage disequilibrium or consistent heterozygote deficiency, as would be expected with strong reproductive isolation.

The Wet Tropics system provides an ideal test case for the refuge model, even allowing for pre-Pleistocene events. The paleoecological and molecular evidence for long-term isolation combined with late Pleistocene contractions and subsequent range expansions is compelling, yet there is little detectable effect on morphological or reproductive divergence where this has been examined. While not all species are expected to diversify in response to refugial isolation and drift (85), the consistency of these observations across taxa must cast doubt on the general validity of the refugia hypothesis. More detailed studies of zones of secondary contact between the northern and southern lineages are needed to substantiate our conclusion.

## Riverine Barrier Model

Few studies have used molecular approaches to investigate the role of rivers as boundaries demarcating diversified taxa within Amazonia, and none, to our knowledge, have been concerned with such a role in other lowland tropical forest regions of the globe. Results of the few molecular studies designed to test explicitly for riverine isolation (22, 23, 50, 56, 81, 108, 110) tend to be equivocal, as might be expected, since the question must be asked for each individual taxon for each of the major river systems of Amazonia. Capparella's research on birds (22, 23) shows a riverine effect, although its extent is unknown given the short section of the Rio Amazonas examined. Broad-scale phylogeographic (mtDNA) analyses of felids (ocelots, margays) revealed a congruent division across the Rio Amazonas (38), although sample sizes were small.

Divergence patterns for both frogs (50, 81) and small mammals (108–110) have been examined for the Rio Juruá, western Brazil, with the same sampling design, using allozymes and/or mtDNA sequences. Of the 29 species or species pairs of small mammals (7 marsupials, 1 primate, and 21 rodents), a clear riverine effect was observed only for subspecies of the saddle-back tamarin (*Saguinus fuscicollis*; 114). However, phylogenetic analyses of the entire species complex (72) suggest that the Rio Juruá is only a point of secondary contact and was not involved in primary divergence (107). A riverine effect is plausible for two other species (*Oecomys* sp. and *Proechimys echirothrix*, but the geographic extent of sampling for these is inadequate. In all other cases, no riverine effect is apparent. In 15 of these taxa, little molecular divergence is present, and individual haplotypes are broadly distributed on both banks and along the entire length. In the remaining 11 taxa, deep divergences between sister lineages are concordant with their geographic placements along the river. The turnover point is perpendicular to the river, not along its bank, and is coincident with both paleogeographic features and a transition between present forest formations (110). The Rio Juruá also fails to form a barrier among any of the frog taxa examined to date, although the same phylogeographic break related to paleogeography and/or forest type is apparent (50, 81).

## Gradient Models

In Central Africa, Smith et al (141, 142) evaluated the Gradient (divergence with gene flow) model in several species of birds found both in central rainforest and the vast (often greater than 1,000 km wide) forest-savanna mosaic that surrounds it. Central African rainforest contrasts sharply with ecotone habitats in both climate and ecology (93). Ecotonal forest patches experience both lower annual rainfall and greater annual variation in rainfall than the main rainforest (80). In addition to these climatic differences, there are also large differences in community structure, involving both fauna and flora. For example, mosaic habitats include fewer numbers of forest species in addition to savanna species absent from the forest. These physical and ecological differences have resulted in contrasting selective environments and corresponding differences in morphology (25) of the organisms that live in them. Endler (40) estimated that 52% of the contact zones between sister species in Africa occurred between forest and savanna, not between historical refugia as predicted by the forest refugia hypothesis. More recently, Fjeldså (44) concluded that newly evolved species were concentrated in the transitional ecotones and montane environments that surround the main central African rainforest.

Smith and colleagues (139, 141, 142) compared morphological divergence within and between habitats for three widely distributed and phylogenetically distinct species of birds in Central Africa. These include the little greenbul (*Andropadus virens*), black-bellied seedcracker (*Pyrenestes ostrinus*), and olive sunbird (*Nectarinia olivacea*). Genetic divergence as a measure of gene flow was also examined within two of the species (cf Figure 1). In the little greenbul (141), the relationship between gene flow and morphologic divergence in heritable

characters was found to support a central prediction of the Gradient model (39, 117). Ecotone and forest populations diverged more morphologically per unit gene flow than did populations from the same habitat. Finally, the magnitude of morphological differences between ecotone and forest populations were similar to that seen between species, suggesting that differential selection was resulting in species level differences in morphology.

The agent of selection causing the morphological differences between the two habitats was not identified. However, the direction of morphological change, particularly the finding that ecotone populations of little greenbuls have longer wings, is consistent with the need for greater aerodynamic efficiency in more open habitats (141) because of increased predation by aerial predators (12, 123).

Causes of habitat-associated morphological shifts in the black-bellied seed-cracker are clearer. Seedcrackers show a polymorphism in bill size (133, 138). Small- and large-billed morphs interbreed throughout their range. However, they differ in feeding ecologies (134, 136, 137), in diet, and in feeding efficiencies on sedges, which results in disruptive selection on bill width (138). In contrast to rainforest populations in which only small- and large-billed morphs occur (135), a "mega-billed" morph is found in ecotones (139). Mega-billed morphs specialize on a species of sedge found only in ecotonal areas that has seeds too hard for either small- or large-billed morphs to crack (139). Despite high levels of gene flow with central rainforest populations (mtDNA control region  $N_m = 7$ ), the mega-billed morph is maintained because of its selective advantage for feeding on these extremely hard seeds (139).

Examination of morphological and geographic distance in populations of the olive sunbird revealed a similar pattern of divergence between forest and ecotones (142). As in both other species, morphological divergence is greater between than within habitats, regardless of the geographic distance separating populations. Although estimates of gene flow are unavailable, populations of ecotones and forests separated by only 200 km are more morphologically divergent than forest populations separated by more than 600 km.

None of these studies examined levels of reproductive isolation, but Orr & Smith (102) suggested substituting morphological divergence with an index of reproductive divergence and comparing levels of gene flow within and between habitats to examine whether reproductive divergence is higher for between-habitat comparisons per unit gene flow than within-habitat comparison. Indices of reproductive divergence could be obtained from mate choice experiments or analyses of genetically based signaling characters important in mate recognition (102).

A similar pattern of morphological divergence between habitats was found in a species of ground-dwelling rainforest skink (*Carlia*) in the Wet Tropics of Australia (126). Despite substantial gene flow, adult males and females were found to be about 15% smaller in body size in open (wet sclerophyll) forests than in adjacent rainforest and also to differ in head and limb proportions independent of size. Although this variation could partially result from phenotypic plasticity, it is notable that life history also differs, with adults reproducing at an earlier age in open

habitats. Like other endemic rainforest vertebrates in the Wet Tropics (see above), *C. rubrigularis* shows a major phylogeographic break in mtDNA variation across the BMC (>12% sequence divergence). Differences in ecomorphological traits across the BMC were trivial relative to those between habitats, despite the long period of isolation between regions. These observations of intraspecific variation appear more consistent with the gradient model than the refuge model. Furthermore, using model lizards in the two habitats, Schneider et al (126) identified increased predation by birds as a possible agent of selection for smaller body size in the open forest habitat.

Explicit tests of the role of elevational gradients in speciation are scarce. Patton and colleagues (104, 111) applied the phylogenetic approach (Figure 1) to species of akodontine and oryzomyine rodents distributed across geographically adjacent elevational transects. The results rejected the gradient model and supported a vicariance hypothesis, as sister-species were distributed between geographically adjacent areas of similar altitude rather than among different elevations along each montane transect.

For African greenbul, Smith et al (142) found that morphological divergence per unit geographic distance was as high between central lowland rainforest and mountain populations as it was between lowland forest and ecotone populations. In contrast, other comparisons between habitats, and those among mountain populations, showed much less morphological divergence. Therefore, isolation on mountains alone, at least for greenbul, does not appear to cause morphological divergence. These results suggest that elevational gradients may be an important factor leading to morphological divergence.

## SYNTHESIS

### Tempo and Causes of Speciation

Molecular data, when appropriately integrated with paleoecology, biogeography, and studies of phenotypic variation and reproductive divergence (13), have great potential to inform theories about the factors that generate species diversity in tropical rainforest faunas and how these faunas have changed through time. Given that such investigations have only recently begun in earnest, it is no surprise that this potential has not yet been realized. Despite their limitations, the results to date have sharpened the questions and suggested improved ways of addressing previously intractable problems.

The analyses of intraspecific diversity described above provide general support for the effectiveness of selection gradients in generating phenotypic diversity and are consistent with several requirements of the gradient (divergence with gene flow) model. Further, they suggest that geographic isolation per se, even when combined with population bottlenecks and subsequent range expansions, does not generate substantial diversity in phenotypes. There are few cases where the gradient and refuge models have been contrasted directly for the same system.

However, juxtaposition of the first two observations above suggests that differential selection, such as that occurring among populations inhabiting different forest types, is a primary determinant of phenotypic variation within species of rainforest fauna, with its effectiveness depending on the balance between selection pressure and gene flow. This conclusion is hardly novel (39) but is worth stating given the prominence accorded to genetic drift in many recent discussions (119). Given that selection-driven divergence can occur without complete suppression of gene flow, we suggest that greater attention should be given to ecological factors that promote selection gradients, with less attention on whether the geographic context is allopatric, parapatric, or sympatric (102, 121, 141). The role of sexual selection in promoting speciation (116) in rainforest faunas has yet to be explored.

The link between factors driving intraspecific diversity and those causing speciation is still to be established. While the divergence with gene flow model underlying the gradient hypothesis has a sound theoretical basis (39) and is supported by experimental studies of *Drosophila* (39, 117), it remains to be demonstrated unequivocally that selection across ecological gradients is a major cause of speciation in tropical faunas. Whereas the intraspecific analyses tend to support the gradient model, the few tests employing interspecific phylogeny did not (104). Data from both approaches are too sparse to warrant further speculation, but one thing is clear—we need to integrate studies of intraspecific molecular, phenotypic, and reproductive variation with those of interspecies phylogenies in order to rigorously distinguish between the alternative hypotheses about speciation mechanisms (Table 1). Such studies need to be extended to taxa that can be manipulated experimentally.

The foregoing review does provide one clear result—the great majority of vertebrate species so far examined appear to have diverged from their extant sister species well before the onset of the climatic perturbations of the Pleistocene. Further, there is tantalizing evidence that relatively young taxa are geographically concentrated, occurring predominantly in areas that have been recently active geologically and in ecotonal regions. Whether these patterns reflect geographic differences in rates of extinction, speciation, or both remains to be seen, but we note that higher speciation rates in areas with strong habitat heterogeneity is consistent with the potential for speciation via diversifying selection. That species within most genera examined to date tend to be very old has limited the inferences that can be made about speciation mechanisms. In this context, it would be rewarding to focus more attention on species-rich lineages occupying geographic regions with concentrations of young species.

The substantial age of most species examined raises one intriguing question—given that any one of the mechanisms suggested has the potential to cause rapid speciation, particularly if connected with shifts in mate choice, why are there not more young species? We expect that the rapid shifts in the composition and distribution of vegetation and associated climates during the last two glacial cycles would have generated abundant opportunity for speciation via selection gradients or differential selection among isolates, but there is little evidence for this in tropical

systems. By contrast, there are numerous examples of recent adaptive radiations or speciation events in postglacial temperate environments, on islands, or in recently formed lakes (52, 54, 65). There are several possible, nonexclusive reasons why this might be so. First, it may be that late Pleistocene fluctuations did cause numerous speciation events, but that the derived taxa were subject to a high extinction rate relative to ancestral or unaffected taxa. Second, it may be that most rainforest (and adjacent) environments lacked the ecological opportunity for survival of new species that is characteristic of islands, recently formed lakes, etc. Third, perhaps species responded to rapid climate change predominantly by migration rather than adaptive differentiation (112), so that populations remained in structurally similar environments with morphology under stabilizing selection. Further progress on this question will require close integration of molecular and morphological information with information from the fossil record and paleoecology.

While some progress is being made with rainforest vertebrates, comparable studies of invertebrates and plants are mostly lacking. Given the prominence of tropical arthropods and plants in accounts of global and tropical species diversity, this is clearly a major omission. Neotropical butterflies are an exception (reviewed by 15, 18, 89). Almost no attention has been paid by to the evolutionary dynamics of species interactions in tropical systems, a dominant theme in ecological perspectives on tropical rainforest diversity. Molecular analyses of interacting species [e.g. host plants and phytophagous arthropods (43), host-parasite systems, mutualisms, etc.] would be extremely rewarding in this respect and are becoming more plausible as taxonomic and biogeographic data are improving for some groups.

## Implications for Conservation Planning

That tropical rainforests and the species they sustain are under threat from habitat destruction and degradation has been emphasized repeatedly, although not all accounts are uniformly negative (16). In response to this and the recommendations of the 1992 International Convention on Biological Diversity, there is an effort by global and national agencies to prioritize and set aside areas for conservation (e.g. reserves) and sustainable development. How can a better understanding of the tempo and causes of diversification of rainforest taxa inform this process?

One important contribution is to identify geographic areas that represent concentrations of old endemic species versus those where recently derived species are concentrated. The work of Fjeldså and colleagues (44, 46) is notable in this respect. While areas of both types might be rich in endemic species (i.e. hotspots), the reasons for conserving them and the optimal strategies differ. The former are important as reservoirs of phylogenetic diversity (34, 147) and their protection should focus on maintaining sufficiently large tracts of intact rainforest to preserve the endemics. Areas with concentrations of young species are important from the context of maintaining the evolutionary processes that generate species and phenotypic diversity (42, 94, 140, 141). Several such areas, for example, the central African ecotones, East African rift mountains, Andean slopes, and their

parallels elsewhere warrant increased attention from conservation agencies, with particular attention to maintaining the viability, representation, and connectedness of habitats that contribute to these heterogeneous landscapes.

Protection of intraspecific genetic diversity is also prominent in conventions and conservation policies. In this context, we can distinguish between historical and adaptive components of diversity (94)—the former focusing on representation of historically isolated areas, which can be identified by comparative molecular phylogeography combined with paleoecology (2, 95), and the latter focusing on maintaining viable populations within heterogeneous landscapes (141). Conservation priorities based on complementarity of species distributions do not necessarily predict those based on identification of congruent genetic divisions within species (95; T Smith, unpublished data). Moritz (94, 95) suggested an iterative approach whereby areas of high values from species irreplaceability and historical isolation within species are combined. Within such areas, it is essential to maintain the integrity and heterogeneity of habitats in order to protect the adaptive component of intraspecific diversity.

Finally, along with other evidence, comparative molecular phylogeography can reveal how historical fluctuations have shaped the current distribution and composition of communities (124). These studies, along with paleoecological data (68, 69), are providing unambiguous evidence that individual species and ecological communities are highly dynamic in space in time. By contrast, most conservation assessments are essentially static, seeking to identify areas that maximize the representation of species, community, and environmental diversity under present conditions. While these efforts are important and must continue, planners need to ensure that such areas are extensive enough to permit natural dynamic processes to continue. Again, maintaining heterogeneous landscapes on the margins as well as interior of rainforests is essential. Further, as the necessary geographic scale will often be greater than can be reasonably be accommodated within conservation reserves and there is extensive human pressure on landscapes adjacent to rainforests, there is urgent need to focus on conservation strategies and sustainable development outside of protected areas.

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