

MONKEYS AND TOADS DEFINE AREAS OF ENDEMISM ON SULAWESI

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Abstract.—Ecological or geological phenomena can impose limits on geographic diversification that cause biogeographical patterns of distantly related but sympatrically occurring taxa to be similar. Concordant patterns of diversity facilitate conservation management because strategic designation of protected areas can capture complementary rather than redundant components of variation. Here we demonstrate that on the biodiverse Indonesian island of Sulawesi, seemingly idiosyncratic distributions of diversity in endemic monkeys (*Macaca* species) and toads (*Bufo celebensis*) are actually virtually identical on a fine geographic scale. It appears that range fragmentation has generated seven multi-taxon areas of genetic endemism, each of which should be targeted for conservation. Joint consideration of molecular phylogeography, morphology, and demography helps resolve apparent contradictions in paraphyletic macaque mitochondrial DNA and in undifferentiated toad morphology, and facilitates an understanding of biogeography and conservation genetics of Sulawesi fauna.

Key words.—Biogeography, conservation genetics, Indonesia, phylogeography, vicariance.

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Preventing rapid biodiversity loss requires efficient allocation of conservation efforts (Pimm et al. 2001) within biodiversity hotspots—those areas where concentrations of endemic species clash with high levels of human activity (Myers et al. 2000). One hotspot, Wallacea, encompasses Sulawesi, the Lesser Sunda Islands, and the Moluccas. As with many large islands, the biota of Sulawesi is highly distinctive, but this island is too large to protect in its entirety. Therefore, designation of conservation areas requires a detailed understanding of patterns of endemism on it. Macaque monkeys, for example, diversified into seven endemic allopatric species (Fooden 1969), and the central Sulawesi species *Macaca tonkeana* is further divided into two populations (Fig. 1A, 2A; Evans et al. 2001). In contrast, the Celebes toad (*Bufo celebensis*) has remained morphologically undifferentiated throughout the island. Because monkeys and toads differ markedly in their demography and ecology, evolutionary processes including dispersal, selection, and genetic drift are expected to lead to different distributions of variation in each taxon. Persistent barriers to dispersal, however, could produce concordant patterns of variation in distantly related sympatric taxa (Avice 2000).

To test the hypothesis that Sulawesi was an archipelago in the past (actually or effectively due to multiple terrestrial barriers to dispersal), we generated an intraspecific molecular phylogeny of *B. celebensis* and compared it to contact zones of species and populations of macaque monkeys. Herein we describe seven highly concordant areas of endemism shared by Sulawesi monkeys and toads that support this hypothesis.

MATERIALS AND METHODS

Phylogenetic Estimation

Bufo celebensis specimens were collected throughout Sulawesi and outgroup specimens from the Sunda Shelf (Table

1; Fig. 1A). DNA was extracted from alcohol-preserved muscle, amplified by polymerase chain reaction (PCR; Goebel et al. 1999), and 859 base pairs spanning most of the 12S ribosomal gene were sequenced for 29 individuals from Sulawesi. Alignment was straightforward and done by eye; sequences have been deposited in the Genbank database (Table 1).

Data were analyzed using maximum parsimony and Bayesian methods. We performed a heuristic search for the most parsimonious tree with 100 replications of random taxon addition using PAUP* Version 4.0 (Swofford 1998), with outgroup taxa from Borneo, Sumatra, and Java, and treating gaps as a fifth character state. For Bayesian analyses we used a model of evolution (GTR + Γ + I) that was selected with a hierarchical likelihood ratio test (Goldman 1993). We performed three independent Markov Chain Monte Carlo runs starting with randomly chosen trees for each of four simultaneous chains under the GTR + Γ + I model of evolution, using MrBayes version 2.01 (Huelsenbeck and Ronquist 2001), with chains of 4,000,000 total generations, a burn-in of 1,500,000 generations, default prior distributions for model parameters, and the differential heating parameter set to 0.2. The joint posterior probability distributions of each run were congruent, suggesting that the chains were run for a sufficient number of generations to adequately sample the posterior probability landscape.

For comparative purposes we reanalyzed a subset of macaque mitochondrial DNA (mtDNA) sequences from Evans et al. (1999) with maximum parsimony and Bayesian methods. We used *M. fascicularis* as an outgroup because mtDNA monophyly of this taxon relative to the Sulawesi macaques is well supported (Evans et al. 1999). Procedures were similar to those above with the exception that the Bayesian analyses used a shorter burn-in (100,000 generations) and a shorter total chain (1,000,000 generations).

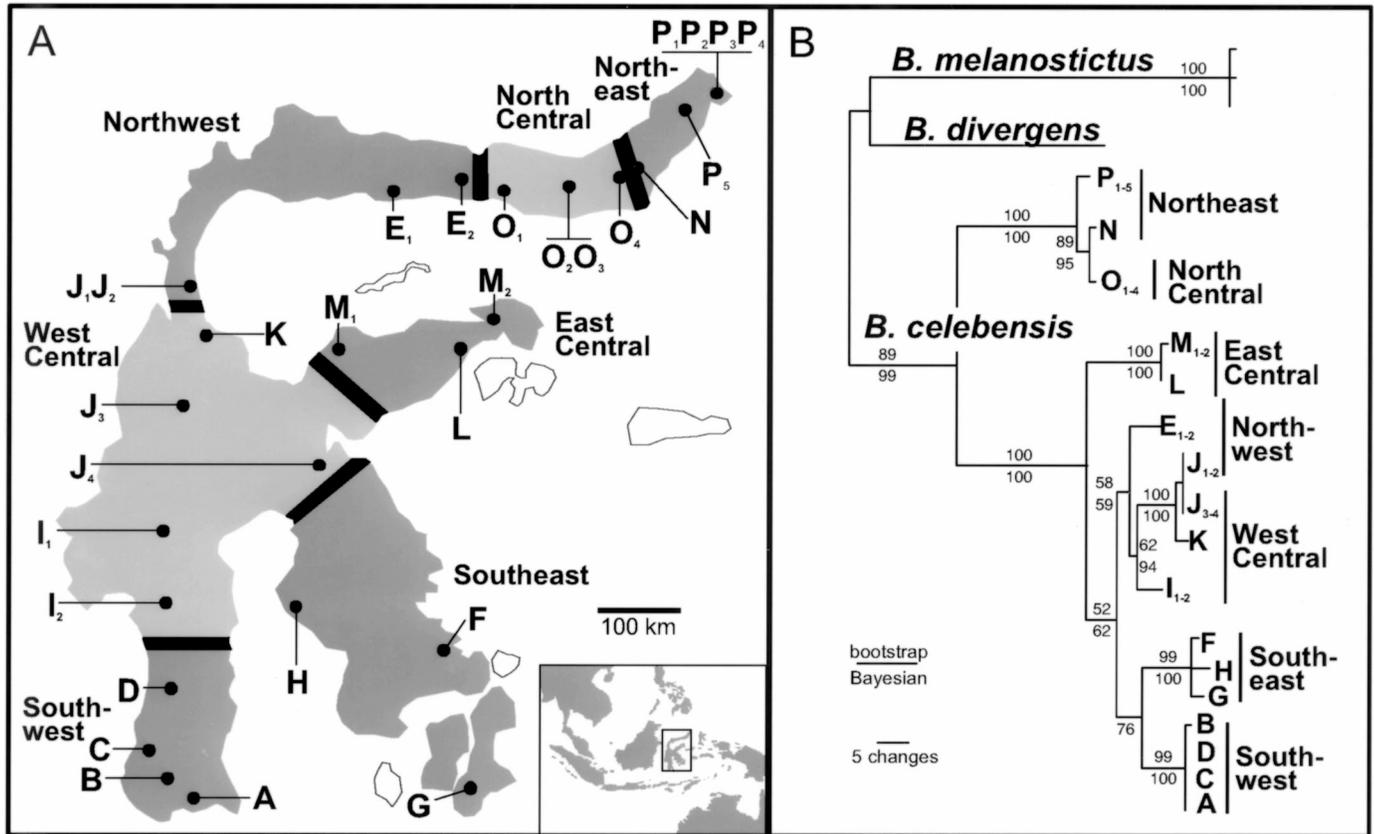


FIG. 1. Toad mitochondrial DNA (mtDNA) phylogeography and monkey areas of endemism on Sulawesi. Uppercase letters signify unique toad mtDNA sequences; for sequences present in more than one toad, individual toads are denoted with numbered subscripts after the letter. (A) Locations of *Bufo celebensis* mtDNA sequences and macaque areas of endemism. Shaded areas of endemism are each occupied by an endemic macaque species as depicted in Figure 2. Macaque contact zones are indicated with a thick line. (B) Intraspecific phylogeny of *B. celebensis*. Branch lengths are proportional to the number of evolutionary changes. Percentages of 2000 bootstrap replicates greater than 50 are above branches and Bayesian posterior probabilities (shown as percentages) are below branches. Labels on the right refer to areas of endemism on Sulawesi.

Hypothesis Testing

We used a parametric bootstrap procedure (Hillis et al. 1996; Huelsenbeck and Rannala 1997; Goldman et al. 2000) to test the null hypotheses of monophyly of toad and of monkey mtDNA in each area of endemism. For each test we simulated data with Seq-Gen version 1.2.5 (Rambaut and Grassly 1997) under the most parsimonious tree consistent with the null hypothesis using a model of evolution that was selected with a likelihood ratio test. We obtained a *P*-value by comparing the observed length difference of trees constrained and unconstrained for the null hypothesis to the distribution of length differences from 1000 simulated datasets.

Nested Clade Analysis

To explain patterns of endemism in toad and monkey mtDNA, we used nested clade analysis (NCA; Templeton et al. 1987; Templeton 1998) to test the null hypothesis of no geographical association among mtDNA sequences and to explain significant associations with hypotheses of gene flow and population history. Nested Clade Analysis uses information about space (the geographic distribution of nucleotide sequences) and time (the hierarchy of nested clades) to test

whether a phylogeographic pattern is consistent with hypotheses of range fragmentation, isolation by distance, or range expansion (Templeton 2002). In this analysis, unrooted statistical parsimony networks of mtDNA sequences of *B. celebensis* and the Sulawesi macaques were constructed (Templeton et al. 1992) using TCS version 1.13 (Clement et al. 2000). One-step clades were grouped starting at terminal branches and proceeding inwards, then two-step clades were grouped, again starting from terminal branches and treating one-step clades as single entities. This procedure was repeated until a single multi-step clade encompassed the entire network. For each clade, the average distance of a clade from the geographic center of its distribution (D_c) and the average distance of a clade from the geographic center of its evolutionary sister clades (D_n) was calculated using Geodis version 2.0 (Posada et al. 2000) from overland distances in kilometers. For nested clades with significant values, biogeographical interpretations were based on the inference key in Templeton (1998).

RESULTS

Parsimony analysis of 16 unique mtDNA sequences from *B. celebensis* samples collected throughout Sulawesi recov-

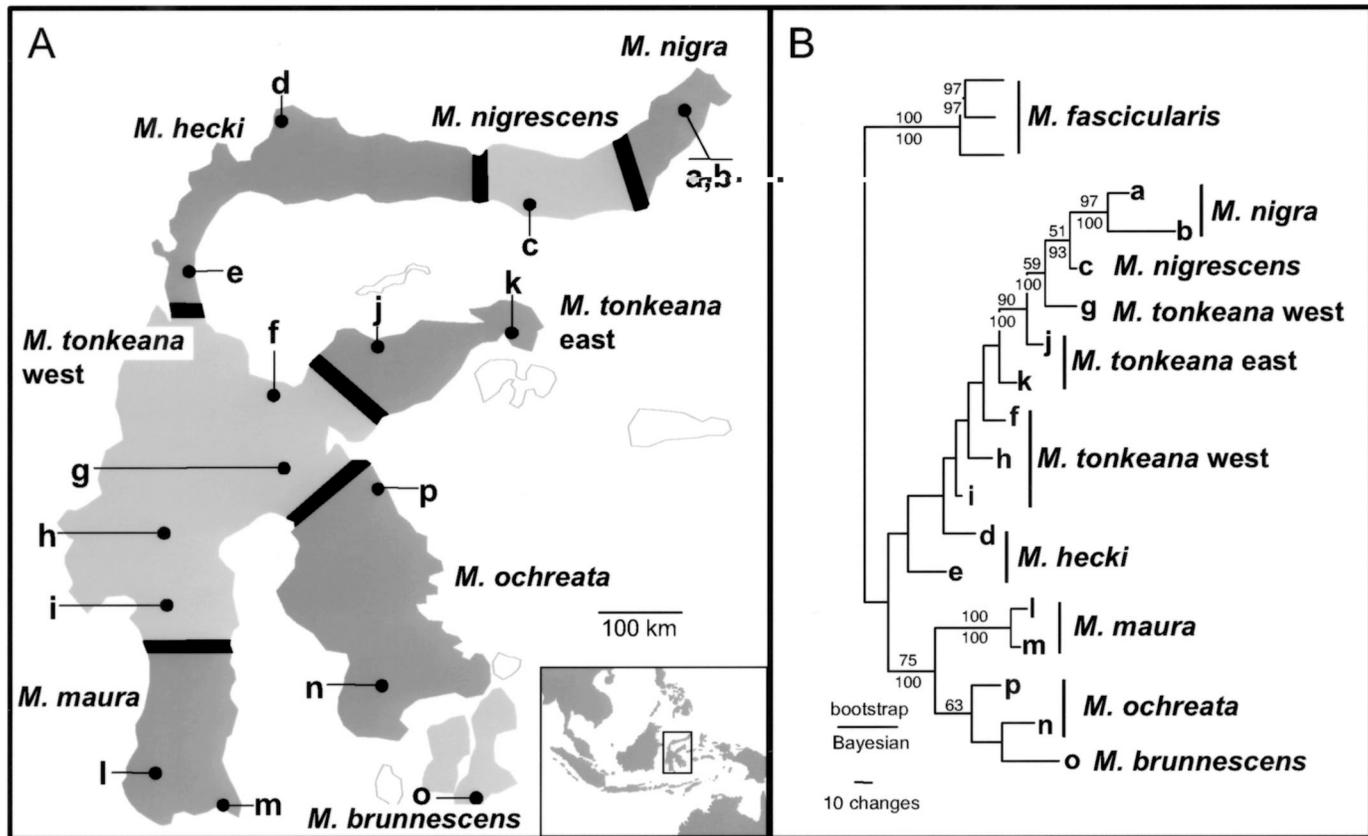


FIG. 2. Macaque mitochondrial DNA (mtDNA) phylogeography on Sulawesi; reanalysis of a subset of sequences from Evans et al. (1999). (A) Locations of *Macaca* mtDNA sequences, areas of endemism, and contact zones labeled as in Figure 1. Macaque contact zones are indicated with a thick line. (B) Mitochondrial DNA parsimony phylogeny of Sulawesi macaques. This is one of two most parsimonious trees that differ in the placement of the root; the other tree is rooted on the branch between sequences d and e. The topology of the Bayesian tree differs from the parsimony analysis in that sequence e instead of sequence f is sister to sequences a, b, c, g, j, and k and that sequences l, m, n, o, and p have the following topology: (o(n(p(l,m))))).

ered one most parsimonious tree (Fig. 1); the topology of this tree is identical to that obtained from Bayesian analyses. Endemic toad clades are present within the ranges of each of the seven areas of monkey endemism on Sulawesi. Geographic boundaries of these clades correspond exactly to four of six macaque contact zones as defined by morphology (Ciani et al. 1989; Watanabe and Matsumura 1991; Watanabe et al. 1991; Bynum et al. 1997), and autosomal and Y-chromosome DNA (Evans et al. 2001). All toads at each locality carry identical mtDNA sequences and identical toad sequences are also present in some adjacent localities, especially if there is not a macaque contact zone between the sites. Two exceptions to the congruent geographic distributions of monkey endemism and toad mtDNA occur in the Northeast where toad sequence N (Northeast) clusters with O (North Central) rather than P (Northeast), and in the Northwest where toad sequence J crosses a monkey contact zone from the West Central to the base of the Northwest area of monkey endemism (Fig. 1).

When toad sequences from each area of monkey endemism are constrained to be monophyletic, the lengths of the observed tree and the constrained tree are not significantly different for mtDNA sequences from the Northeast ($P = 0.078$) but are significantly different for sequences from the North-

west ($P < 0.001$), according to parametric bootstrap tests (Hillis et al. 1996). Thus, at five of six monkey contact zones we found no significant difference in the boundaries of endemism within the Celebes toad and species of Sulawesi macaque.

In contrast, we found that four of the eight monkey species/populations on Sulawesi and nearby islands have paraphyletic mtDNA lineages (Fig. 2; Evans et al. 1999). Monophyly is significantly rejected by parametric bootstrap tests in three of these macaque species/populations ($P < 0.01$), but not in the Northwest species *M. hecki* ($P = 0.065$).

Nested clade analysis of toad sequences indicates that toad mtDNA phylogeographic patterns are due to range fragmentation at the sites of macaque contact zones but isolation by distance within the West Central region (Fig. 3). However, NCA of an unrooted network of macaque mtDNA sequences from locations near the toad samples (Evans et al. 1999) does not reject the null hypothesis of no geographical association among sequences (data not shown).

DISCUSSION

Sulawesi Biogeography

Biologists have long recognized a high turnover of Asian fauna of the Sunda Region (Borneo, Sumatra, Java, Penin-

TABLE 1. Location and coordinates of genetic samples, all of which were collected in Indonesia. MZB refers to the Muzeum Zoologicum Bogoriense, TNHC is the Texas Natural History Collection, and AMNH is the American Museum of Natural History.

Species	Museum tag	Genbank accession no.	Location (province, nearest town)	Coordinates
<i>Bufo divergens</i>	AMNH A166504	AY180243	Kalimantan Timur, Kutai National Park	N 00°22.293', E 117°28.638'
	AMNH A166505	AY180213	Java Barat, Depok	S 06°22.720', E 106°49.882'
<i>B. melanostictus</i>	AMNH A166506	AY180226	Sulawesi Tenggara, Kendari City	S 03°80.000', E 122°50.000'
	AMNH A166507	AY180227	Sumatra Barat, Padang	S 00°57.000', E 100°21.000'
<i>B. celebensis</i>	AMNH A166508	AY180214	Sulawesi Utara, Klabet mountain	N 01°29.386', E 124°50.520'
	AMNH A166509	AY180217	Sulawesi Utara, Tangkoko National Park	N 01°34.205', E 125°09.416'
	AMNH A166510	AY180215	Sulawesi Utara, Tangkoko National Park	N 01°34.205', E 135°09.416'
	AMNH A166511	AY180216	Sulawesi Utara, Tangkoko National Park	N 01°34.205', E 135°09.416'
	AMNH A166512	AY180219	Sulawesi Utara, Tangkoko National Park	N 01°34.205', E 125°09.416'
	AMNH A166514	AY180220	Sulawesi Utara, Kotamobagu	N 00°43.752', E 124°17.005'
	AMNH A166515	AY180221	Sulawesi Utara, Bogani Nani Wartabone National Park	N 00°33.748', E 123°54.230'
	AMNH A166516	AY180222	Sulawesi Utara, Bogani Nani Wartabone National Park	N 00°34.004', E 123°53.272'
	AMNH A166517	AY180237	Sulawesi Utara, Marisa	N 00°33.096', E 121°58.129'
	AMNH A166518	AY180238	Sulawesi Utara, Paguyaman	N 00°37.743', E 122°41.562'
	AMNH A166519	AY180239	Sulawesi Utara, Tolabulu	N 00°30.801', E 123°14.571'
	AMNH A166520	AY180240	Sulawesi Utara, Mooat	N 00°45.090', E 124°26.954'
	AMNH A166521	AY180224	Sulawesi Tengah, Kolonodale	S 01°59.196', E 121°20.368'
	AMNH A166522	AY180231	Sulawesi Tengah, Luwuk	S 00°57.054', E 122°47.493'
	AMNH A166523	AY180235	Sulawesi Tengah, Parigi	S 00°47.304', E 120°07.620'
	AMNH A166524	AY180236	Sulawesi Tengah, Lemo	S 00°26.449', E 119°58.978'
UI 1144*	AY180244	Sulawesi Tengah, Lemo	S 00°26.449', E 119°58.978'	
TNHC 59135	AY180233	Sulawesi Tengah, Marawo	S 00°56.950', E 121°27.100'	
MZB AMPH 4008	AY180234	Sulawesi Tengah, Siuna	S 00°44.675', E 123°02.010'	
AMNH A166525	AY180223	Sulawesi Tengah, Lore Lindu National Park	S 01°27.016', E 119°59.394'	
AMNH A166526	AY180218	Sulawesi Selatan, Malino	S 05°15.561', E 119°55.594'	
AMNH A166527	AY180228	Sulawesi Selatan, Bantimurung	S 05°01.120', E 119°40.416'	
AMNH A166528	AY180229	Sulawesi Selatan, Gunung Karua	S 02°54.130', E 119°41.840'	
AMNH A166529	AY180230	Sulawesi Selatan, Enrekang	S 03°36.146', E 119°45.981'	
AMNH A166530	AY180242	Sulawesi Selatan, Barru	S 04°29.643', E 119°45.998'	
TNHC 59133	AY180232	Sulawesi Selatan, Mt. Lompobattang	S 05°40.000', E 119°00.000'	
AMNH A166531	AY180225	Sulawesi Tenggara, Kendari	S 03°54.434', E 122°30.281'	
AMNH A166532	AY180241	Sulawesi Tenggara, Lasusua	S 03°30.607', E 121°52.916'	
AMNH A166535	AY180245	Sulawesi Tenggara, Buton Island	S 05°27.014', E 122°38.516'	

* University of Indonesia field tag.

demism that correspond almost exactly in monkeys and toads: toad mtDNA, monkey morphology, and monkey autosomal and Y-chromosome DNA all show similar biogeographical patterns. Thus, the ranges of all species of macaque on Sulawesi (data insufficient for *M. brunnescens*) and both populations of *M. tonkeana* (Fig. 1; Evans et al. 2001) define seven distinct areas of genetic endemism.

Distributions of other endemic species are also parceled among different parts of Sulawesi, though their exact geographic ranges are not as well known as in macaques (Ciani et al. 1989; Watanabe and Matsumura 1991; Watanabe et al. 1991; Bynum et al. 1997; Evans et al. 2001) or Celebes toads (this study) because studies with high geographic resolution have not been attempted. Carpenter bees (*Xylocopa*), pond skaters (*Ptilonera*), whiteeye birds (*Zosterops*), cicadas (Cicadoidea), and tarsiers (*Tarsius*), for example, each have allopatric species or subspecies on Sulawesi (Duffels 1990; Iskandar and Tjan 1996; Holloway 1998; Whitten et al. 2002). Molecular differentiations of grasshoppers, genus *Chitaura*, are also closely allied with those of monkeys and toads (Butlin et al. 1998) although again, exact locations of contact zones have not yet been identified with high geographic resolution. Two genetic studies in progress with dense geographic sampling both suggest that fanged frogs (*Limnonectes*) and flying lizards (*Draco*) also have phylogeographic patterns and contact zones that are similar to Sulawesi toads and monkeys (Evans et al. 2002; McGuire 2002).

Divergence and phylogenetic relationships among areas of endemism vary among taxonomic groups and are influenced by initial location of colonization, routes of subsequent dispersal, demography, effective population size, and time. In general, diversification is faster in animals with shorter generation times, drift and founder effects are more significant in small populations, diversity is more homogeneous in animals that disperse over long distances, and neutral polymorphism is greater in large populations (Kimura 1968; Crow 1985). Greater divergence could also arise if one taxon was fragmented for a longer period than another. In this study, although macaques are longer-lived and more vagile than toads, these primates have a lower effective population size, are more subject to the vagaries of genetic drift and founder effects, and exhibit higher, or at least more obvious, morphological divergence among areas of endemism.

Geographic boundaries of the contact zones might be fluid in nature since the barriers that fragmented Sulawesi may no longer be present. If hybridization is not maintained by a stable ecological gradient, the breadth and position of these contact zones might shift in different ways for different taxa (Barton and Hewitt 1985). The lack of exact geographic concordance in monkeys and toads between the North Central and Northeast contact zones and between the Northwest and West Central contact zones, for example, could be due to movement of the contact zone in either one or both taxa. Indeed, comparisons of old and new macaque specimens suggests that the location of the hybrid zone between *M. tonkeana* and *M. hecki* was once north of its current position (nearer the contact zone between the Northwest and West Central areas of endemism in toads) but has recently shifted, possibly as a result of road construction (Bynum et al. 1997).

Colonization and dispersal of monkeys and toads on Su-

lawesi probably occurred at different times and in different ways. It is unclear whether Sulawesi was a continuous landmass in the past that was fragmented and then recently reunited (a vicariance hypothesis) or whether it was always an archipelago until recent uplift unified these islands (a dispersal hypothesis). In either case, colonization of macaques may have occurred in the Central West, Northwest, and/or Southwest Area of Endemism (Fig. 2; Fooden 1969; Albrecht 1978; Evans et al. 1999), whereas an early split in toad mtDNA sequences suggests that an ancestor of this taxon may have first arrived to the north peninsula of Sulawesi (Fig. 1). Interestingly, mtDNA sequences from the southern peninsulas are monophyletic both in toads and in monkeys. However, we expect relationships among areas of endemism in other terrestrial fauna to depend on the location of initial colonization, pattern of dispersal on Sulawesi, and ancestral population structure prior to fragmentation (under a vicariance hypothesis), even though relationships within each area are expected to frequently be monophyletic due to lineage sorting in fragmented populations. Animals that colonized Sulawesi very early (prior to macaques and toads), might also have a geographic structure influenced by the micro-islands that collided to form Sulawesi (Hall 2001), or other ancient ephemeral processes that might not have affected younger endemics of Sulawesi.

On Sulawesi, nested clade analysis of toad mtDNA sequences suggests that fragmentation played an important role in influencing the distribution of genetic variation in toads at or near the locations of monkey hybrid zones (Fig. 3). We do not know definitively what caused range fragmentation on Sulawesi, though some recent events may be implicated. Pleistocene and Holocene oceanic inundation into the contact zone between *M. maura* and *M. tonkeana* separated the Southwest peninsula from the rest of the island and inundation into the contact zone between *M. hecki* and *M. nigrescens* split the northern peninsula (Whitten et al. 2002). Oceanic inundation, large rivers, and different soil and/or vegetation types may have hindered migration across other contact zones. Climatic fluctuations can also fragment populations and impact phylogeographic patterns by altering paleoecological conditions (Hugall et al. 2002). Whatever the causes, range fragmentation of Sulawesi was sufficient to compartmentalize biodiversity of unrelated taxa with different life histories and demography. Within an area of endemism, there is evidence for isolation by distance in toads (Fig. 3) but geographic structure of other taxa may differ within an area of endemism due to differences in life history and demography.

Conservation of Sulawesi Biodiversity

Without protection, much of the remaining tropical biodiversity will be lost in the near future (Myers et al. 2000) and this situation is particularly dire in Indonesia (Jepson et al. 2001). Since protected areas can significantly mitigate logging, land clearing, hunting, burning, and grazing in tropical areas (Bruner et al. 2001), joint consideration of molecular phylogeography, morphology, and demography can generate practical information for conservation management by identifying areas of genetic endemism for protection (Moritz and Faith 1998). Endemism on Sulawesi is partitioned; be-

TABLE 2. Proportion of land with protection status for each area of endemism on Sulawesi, ranked by percentage of land protected.

Area of endemism	Total area protected (ha)	% of area of endemism protected
North Central	300000	21.21
West Central	547000	6.32
Southeast	325500	5.97
Northeast	23883	2.81
Southwest	14990	0.65
East Central	7911	0.45
Northwest	1963	0.06

cause of this, to best preserve biodiversity, areas with complementary, nonredundant diversity should be targeted for protection (Vane-Wright et al. 1991). Unfortunately, the current distribution of protected areas indicates that some large conservation areas such as Lore Lindu and Morowali National Parks may be restricted to a single area of genetic endemism (West Central) while other areas of genetic endemism such as East Central, Northwest, and Southwest Sulawesi are barely protected (Table 2; IUCN 1992; Whitten et al. 2002). However, substantial portions of each of these regions have been proposed for protection including Bakiriang in East Central Sulawesi; Mt. Lompobatang in Southwest Sulawesi; and the Palu Mountains, Mt. Sojol, Mt. Dako, the Toli-Toli Mountains, and the Marisa complex in Northwest Sulawesi (Whitten et al. 2002). Protection of these sites would complement biodiversity present in existing reserves.

Congruence of this pattern of fragmentation in toads with variation in morphology and autosomal DNA in monkeys suggests that vicariance on Sulawesi affected the evolution of a breadth of fauna comparable to, for example, the multi-taxon phylogeographic disjunction across the Apalachicola River in the southeastern United States (Avise et al. 1979; Bermingham and Avise 1986; Walker and Avise 1998; Burbrink et al. 2000). The number of independent vicariant events in this small geographic area is of comparable concentration to those of the Hawaiian, Philippine, or Caribbean Islands (Rosen 1975; Heaney 1986; Wagner and Funk 1995), although today the sources of vicariance on Sulawesi are not as obvious or perhaps no longer persistent. Thus, today Sulawesi is a single landmass, but from a biogeographical perspective it is a recently amalgamated archipelago. Efforts by Indonesian and international organizations, including international financial support, to protect and manage each area of endemism would make significant strides toward preserving much of the remaining biodiversity on Sulawesi.

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