Conserving Madagascar's Freshwater Biodiversity

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The island nation of Madagascar, an international conservation priority, is now also recognized as a global hotspot for freshwater biodiversity. Three emerging characteristics of Madagascar's threatened freshwater biota deserve increased attention from the scientific and conservation communities. First, species richness is not low, as was once assumed for both the freshwater fishes and the invertebrates. Second, many species are restricted to a specific region or even to single river basins. Often these species are also limited to streams or rivers draining primary forest habitat. Finally, many of the island's freshwater fishes are basal taxa, having diverged earlier than any other extant members of their clade. As such, these taxa assume disproportional phylogenetic importance. In the face of ongoing environmental threats, links among microendemism, forest stream specialization, and basal phylogenetic position highlight the importance and vulnerability of these species and provide a powerful incentive for immediate conservation action.

Keywords: conservation, freshwater biodiversity, hotspots, Madagascar, rivers and streams

Madagascar lies 400 kilometers off the African continent's southeastern coast and is the world's fourth largest island. For many reasons, however, Madagascar is often considered by biogeographers as more of a "microcontinent." Its complex topography includes numerous massifs and a steep escarpment running north to south along most of the east coast. The island's large size and varied topography combine with dramatic differences in the annual amount and seasonality of precipitation on different parts of the island, resulting in a substantial diversity of rivers, streams, and other freshwater habitats. This variability alone would make the island of interest to aquatic biologists. However, Madagascar is also noteworthy because it broke away from Africa about 160 million years ago and has been isolated from all other landmasses (most recently, India) for approximately 88 million years (Rabinowitz et al. 1983). As a result of this long isolation, Madagascar is characterized by high levels of endemism for many groups of organisms. The freshwater biota is no exception (figures 1, 2), and the island is now recognized as a global hotspot for freshwater biodiversity (Groombridge and Jenkins 1998).

Madagascar is also highly unusual in that humans colonized it only about 2000 years ago. Nevertheless, in that relatively short period of time, the human footprint has fallen heavily on the island's freshwater habitats and species. Native vegetation has all but disappeared from much of Madagascar's central highlands. Meanwhile, the eastern rain forest belt has been reduced to about 30% of its original extent (Green and Sussman 1990). These changes in vegetation cover have accelerated natural erosion processes, resulting in the dumping of millions of tons of sediment into the island's rivers. At the same time, overfishing and the introduction of numerous exotic species have affected many of the native fish species, leading to cascading effects through freshwater communities. The combination of deforestation, overfishing, and exotic species introduction has affected most of the island's freshwater habitats, making the freshwater fishes Madagascar's most threatened vertebrate taxa (figure 3).

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Figure 1. Madagascar's eastern rivers and streams are home to six species of crayfish in the endemic genus **Astacoides** *(Parastacidae). This* **Astacoides granulimanus** *is from a stream in Ranomafana National Park. Photograph: Jonathan P. Benstead.*

Figure 2. The web-footed tenrec, **Limnogale mergulus** *(Afrotheria: Tenrecidae). This endemic small (80-gram) mammal is the only semiaquatic member of the remarkable Malagasy tenrec radiation. It is known from only a handful of streams and rivers in eastern Madagascar. Photograph: Kevin H. Barnes.*

In this article, we review some of the striking properties of Madagascar's freshwater biodiversity. We concentrate on three topics recently revealed by scientists to be of direct relevance to freshwater conservation. These are the recent and dramatic increases in the number of species known from Madagascar's rivers, the single-basin endemism or microendemism seen in many groups (often combined with restriction to native forest biomes), and the prevalence of phylogenetically basal species (i.e., those forming the earliest diverging group in their clade) in the island's freshwater biota. We use examples from the fishes and two dominant orders of aquatic insects (the Ephemeroptera, or mayflies, and the Trichoptera, or caddisflies) because these are the best understood taxa. We then summarize the challenges associated with the current and future maintenance of the island's freshwater biodiversity and make suggestions for research and conservation activity.

Recent advances in knowledge

Scientific study of Madagascar's aquatic insects is still in its infancy. For example, research on Malagasy mayflies (Ephemeroptera) began in earnest only recently. In 1990 the Biodiversity and Biotypology of Malagasy Freshwaters (BBMF) program, jointly run by the Office de la Recherche Scientifique et Technique Outre-Mer in France and the Centre National de Recherches sur l'Environnement in Madagascar, began to survey the island's freshwater macroinvertebrates, including its mayflies. Stream sampling, rearing of larvae, and light trapping were performed at 1000 sampling sites in over 650 locations, encompassing most of the biologically important regions of Madagascar.

The increase in scientists' knowledge of this insect order has been spectacular (figure 4a). From the 15 valid mayfly species known in the early 1990s, the list in early 2002 had increased to 100 species and 41 genera, of which more than 60 new species and 8 new genera have been described from material collected by the BBMF program. We estimate that the true number is at least 200 species (Elouard and Gibon 2001). All the species except one, and about half of the genera, are endemic to the island (Sartori et al. 2000). Genera such as *Proboscidoplocia* (figure 5) and *Prosopistoma* (figure 6), which were previously considered to be monotypic, are now known from several distinct species. The most striking increase has been in species of Baetidae. From four species known from Madagascar in 1995, the number now recorded from the island exceeds 50 (i.e., roughly half of the described Malagasy mayfly species and genera; Gattolliat 2002). Other families, such as Caenidae and Tricorythidae, which were not even known from the island 10 years ago, have been shown to be highly diverse. Study of the Leptophle-

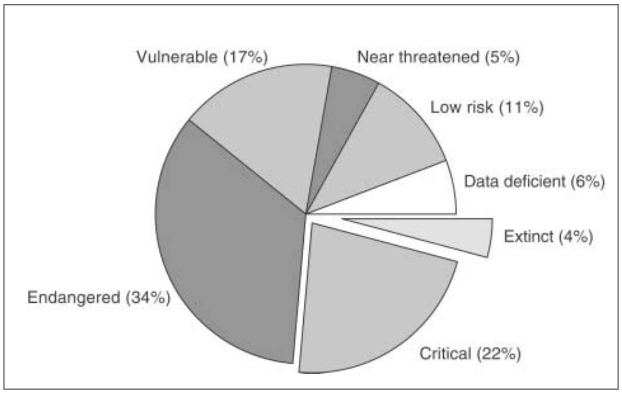

Figure 3. Conservation status of the Malagasy freshwater fish fauna. Level of threat is based on the opinion of a 2001 international panel of researchers, using criteria established by the International Union for Conservation of Nature and Natural Resources.

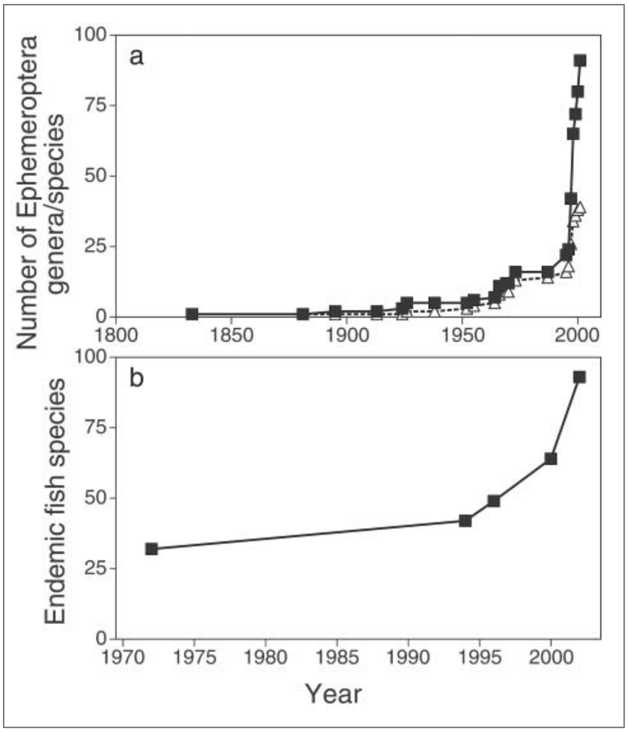

Figure 4. Recent increases in the number of (a) mayfly taxa (solid squares are species; open triangles are genera) and (b) endemic fish species known from Madagascar.

biidae, probably the most important and diverse mayfly family in Madagascar, has barely begun. A rough approximation of its diversity suggests that this family includes about 15 genera and almost 100 species that are new to science (see Bass [2003] for advances in knowledge of Caribbean freshwater biodiversity).

Until recently, the Trichoptera (caddisflies) were also poorly known. Only 52 described species of caddisflies had been catalogued in Madagascar up to 1994. Research by the BBMF program has since revealed Madagascar's rich Trichoptera fauna. The national inventory has brought the minimum number of species to more than 500 (not including the Hydroptilidae, or microcaddisflies), with a level of endemism between 98% and 100% (Elouard and Gibon 2001). Including undescribed taxa, more than 30% of all Afrotropical Trichoptera are now known to be endemic to Madagascar.

Recent increases in known species richness are not restricted to aquatic insects. Over the past decade, a remarkable increase in the number of native and endemic freshwater fishes of Madagascar has also been documented (figures 4b, 7; Sparks and Stiassny 2003). These findings contrast with the traditional notion, which has persisted for decades, of a depauperate Malagasy fish fauna (Kiener 1963, Kiener and Richard-Vindard 1972). In fact, the species richness of Madagascar's fishes is now known to be similar to that of other landmasses of continental origin, according to worldwide comparisons based on area and number of native fish species (Sparks and Stiassny 2003).

We now recognize 143 native freshwater fishes, belonging to 21 families and 54 genera, of which more than 65% are endemic to Madagascar (Sparks and Stiassny 2003). This represents a striking increase of 60% to 90% over the total number of endemic species recorded in the two most recent faunal inventory studies (de Rham 1996, Benstead et al. 2000) before the summary work of Sparks and Stiassny (2003). Whereas endemism is high at the species level, it is notably low at higher taxonomic levels; only two endemic families (9.5%) and 13 endemic genera (24.5%) are recorded from Madagascar. Recent surveys have also

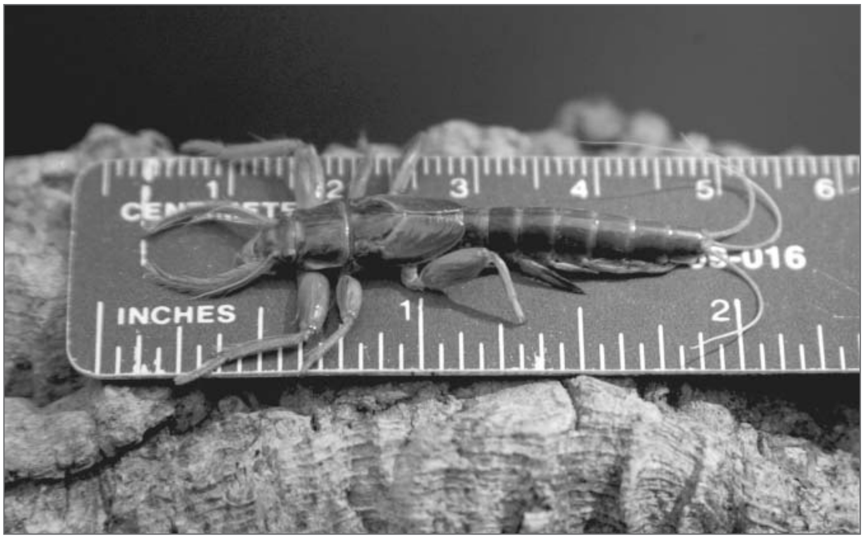

Figure 5. Madagascar's mayfly fauna includes some of the largest species in the world. This is a **Proboscidoplocia** *(Polymitarcyidae) nymph collected from Ranomafana National Park, eastern Madagascar. Photograph: Bud Freeman.*

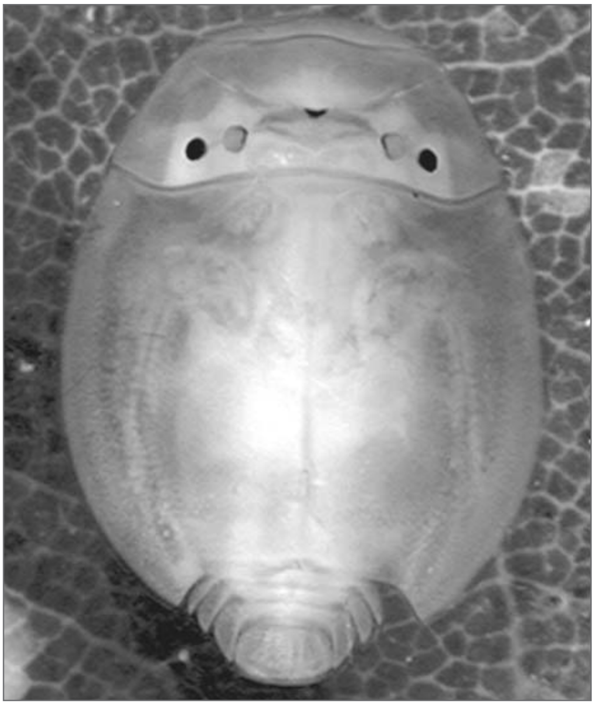

Figure 6. The mayfly family Prosopistomatidae was discovered in 1833 in Madagascar, but at the time, its atypical nymphs were thought to belong in the Crustacea. This **Prosopistoma** *nymph was collected in a forest stream in Ranomafana National Park, eastern Madagascar. The nymph is 6 millimeters in length. Micrograph: Jonathan P. Benstead.*

uncovered a second major region of Malagasy freshwater fish diversity. In addition to the upper and lower eastern basins, the freshwater systems of northwestern Madagascar are now recognized as hotspots of Malagasy fish diversity, with 71 native species recorded from this region.

Microendemism and the importance of the forest biome

Two clear patterns have emerged from recent studies of Madagascar's caddisflies (Trichoptera). The first is the restriction of certain groups to eastern rain forest stream habitats. Streams draining the primary humid forest are the exclusive habitat of several families, subfamilies, and genera of caddisflies. Moreover, many of the genera that colonize both the eastern rain forest and other environments have species that are restricted to forest streams (Gibon and Andriambelo 1999). The second pattern to emerge is a relationship between specialization to forest stream habitats and microendemism. Most of the species found outside the eastern rain forest are distributed throughout the island or have a wide latitudinal range. In contrast, forest species show a strong and general tendency toward microendemism. This trend is the driving force behind the exceptional species richness of the Malagasy caddisflies. A remarkable example is provided by the genus *Paulianodes.* Each point in its distribution represents a forest where one, or exceptionally two, species have been collected. But none of the 14 recently discovered species is found in two distinct forest zones. Even though the distributions of most species are not so restricted, this type of distribution pattern is the rule for most forest caddisfly species.

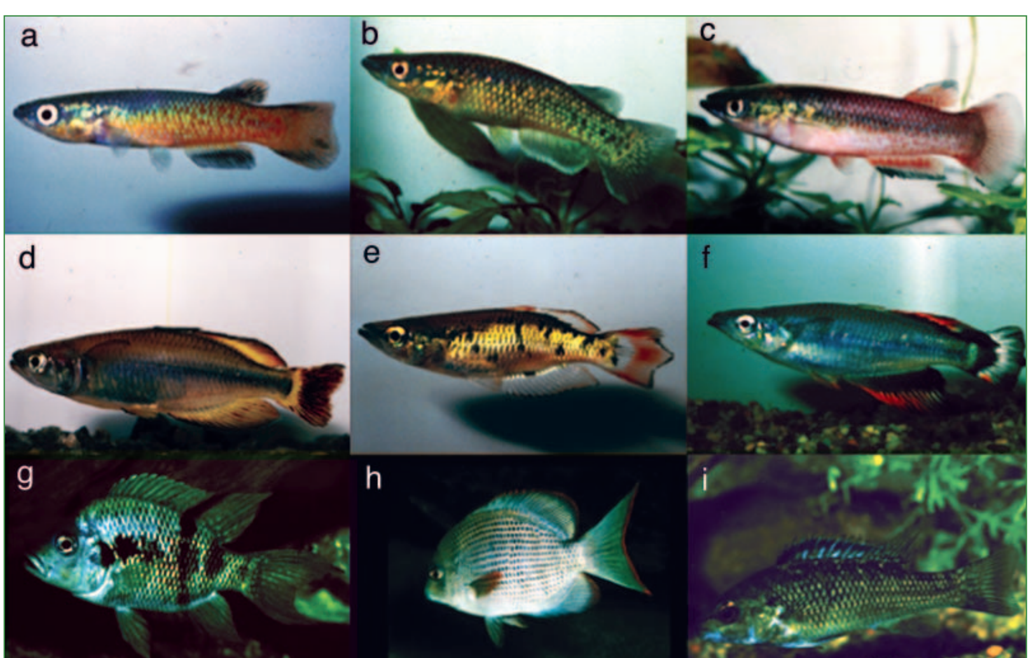

Figure 7. Some examples of Madagascar's endemic fishes: (a) **Pachypanchax sakaramyi,** *(b)* **Pachypanchax** *sp. nov., (c)* **Pachypanchax** *sp. nov., (d)* **Rheocles vatosoa,** *(e)* **Bedotia marojejy,** *(f)* **Bedotia** *sp. nov., (g)* **Ptychochromis oligacanthus,** *(h)* **Paretroplus menarambo,** *and (i)* **Oxylapia polli.**

The streams of Madagascar's eastern domain also contain the highest species diversity of mayflies. For most species in the largest families, such as the Leptophlebiidae and Baetidae, it is difficult to separate factors related to presence of primary forest from those related to hydrology. For smaller families such as the Polymitarcyidae and Palingeniidae, however, the situation seems much clearer. Each genus has one or two widespread, savanna-dwelling species, while the other species are limited to primary forest areas (Elouard and Gibon 2001). The mayfly genus *Manohyphella* (Teloganodidae; see figure 8) is probably one of the least common in Madagascar. It appears to be extremely sensitive to environmental changes caused by deforestation (McCafferty and Benstead 2002). The larvae live exclusively in strong current in cold, well-oxygenated montane streams. *Manohyphella*'s distribution and ecological requirements are probably similar to those of Madagascar's stoneflies (Plecoptera).

The mayfly families Caenidae and Tricorythidae are also composed of both widespread and narrowly distributed genera. In both cases, the species with limited distributions *(Madecocercus* and *Madecassorythus)* are considered more primitive and are restricted to forest areas, while the widespread and more recent genera *(Caenis* and *Tricorythus)* have a wider distribution in savannas and other degraded areas. This relationship between primitive species and forest specialization is also seen in the caddisflies.

Microendemism in mayflies is observed mainly at the species level. Among the roughly 100 mayfly species described from Madagascar to date, one-fifth appear to be restricted to a river, basin, or small group of basins; these areas of microendemism are all in the eastern rain forest region. The remainder have wide distributions, which generally include the eastern domain and part of the central highlands (Elouard and Gibon 2001). The streams and rivers of the drier western slope harbor very low mayfly species diversity, and the few species present are widespread.

On the basis of limited collecting efforts, early fish researchers assumed extensive distributions for many of the island's freshwater fishes (Sauvage 1891, Pellegrin 1933, Kiener and Maugé 1966, Kiener and Richard-Vindard 1972). Fieldwork undertaken since 1988, however, has revealed a very different pattern of fish distribution (Stiassny 1990, de Rham 1996, Sparks and Reinthal 2001, Sparks 2002, Sparks and Stiassny 2003). Distributional data for the four major groups of Malagasy freshwater fishes indicate that the rivers of the eastern and western slopes of the island support very different species assemblages (table 1). The same data reveal that single-basin endemism characterizes a significant number of Madagascar's endemic cichlids and the overwhelming majority of the endemic bedotiids (rainbowfishes) (figure 9). Finally, distributional data indicate that the number of endemic freshwater fish species present at any given locality is likely to be very low (figure 10).

Most of the fish taxa wholly or largely restricted to the eastern slope, such as *Bedotia, Rheocles, Pantanodon,*

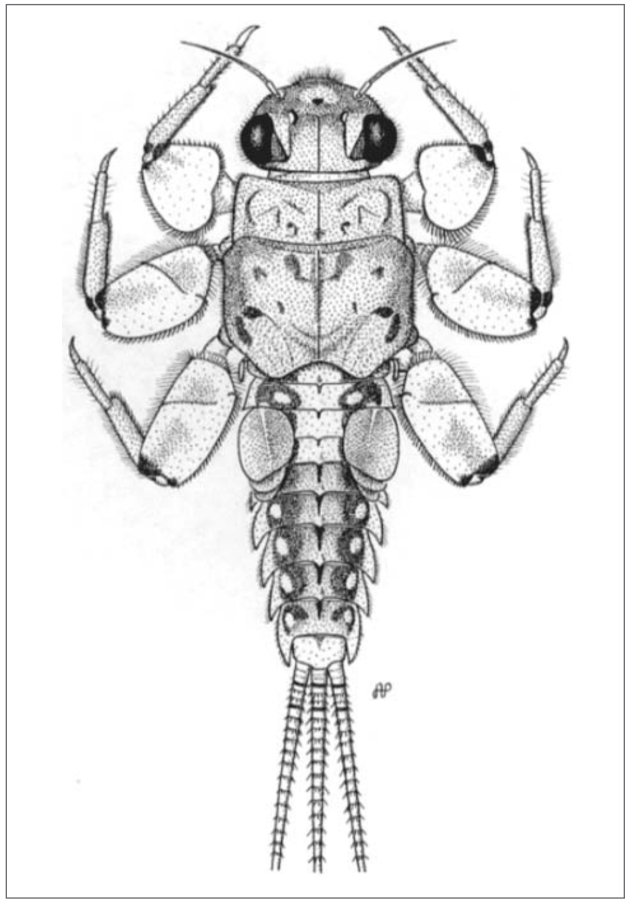

Figure 8. The mayfly* Manohyphella animosa *(Teloganodidae) was recently described from material collected in Ranomafana National Park, eastern Madagascar. This species is abundant only in undisturbed rain forest streams of the region. Reproduced from McCafferty and Benstead (2002).

Table 1. Distribution of endemic Malagasy freshwater fishes on eastern and western slopes.

Family	Number of species found on both slopes	Number of species restricted to one slope	
		Eastern slope	Western slope
Clupeidae	0	1	2
Ariidae	1	0	3
Anchariidae	0	2	1
Aplocheilidae	0	2	5
Aplocheilichthyidae	0	2	0
Atherinidae	0	1	1
Bedotiidae	1	23	1
Mugilidae	1	0	0
Teraponidae	0	1	0
Ambassidae	0	1	0
Cichlidae	1	11	22
Eleotridae	3	2	2
Gobiidae	4	1	2
Trichinotidae	0	1	0

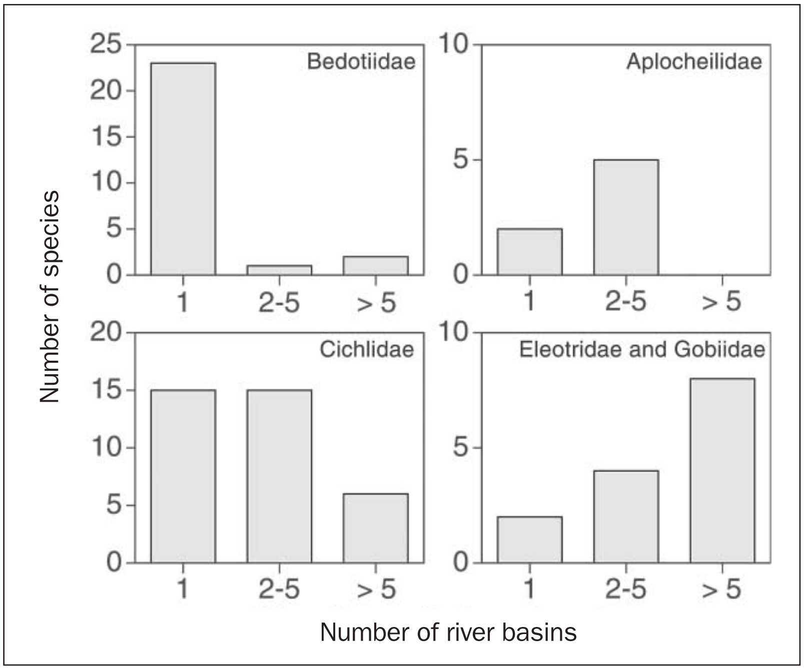

Figure 9. Distribution patterns of four major groups of Malagasy freshwater fishes with respect to the number of drainage basins within native range.

and *Ambassis fontoynonti,* can be legitimately characterized as forest stream fishes. However, those restricted to the island's western slope—notably some ariid catfishes; some representatives of the cichlid genera *Paretroplus, Ptychochromis,* and *Ptychochromoides;* and the majority of the island's endemic eleotrids and gobies—are instead characteristic inhabitants of the main channel of large rivers, lakes, or coastal lagoons.

The importance of phylogenetically basal species

A phylogenetic perspective (i.e., one that considers how species are related to each other) has become increasingly important in the consideration of Madagascar's freshwater biodiversity and conservation status. As discussed above, recent estimates have elevated the number of freshwater fish species recorded from Madagascar to a figure that is completely in line with area-based expectations. However, at higher taxonomic levels, the fish fauna remains puzzling. Missing in both the fossil and the contemporary record are representatives of many major groups of freshwater fish that, based on their presence on other Gondwanan fragments, might reasonably be expected also to occur on Madagascar (Stiassny and Raminosoa 1994). These include the knifefishes (Notopteridae), bagrid catfishes (Bagridae), air-breathing catfishes (Clariidae), snakeheads (Channidae), and climbing perches (Anabantidae), among others.

To account for such a striking series of absences, one is forced to conclude either that these groups were never present on the island or that there has been a series of major extinctions (for which there is no current evidence). The lack of fossil evidence of these modern groups and the predominance of archaic groups among the island's late Cretaceous fossil fauna have led some paleontologists to hypothesize that the island's extant fishes are descended from post-breakup (Mesozoic), intercontinental colonizers and not from freshwater taxa isolated on Madagascar by the fragmentation of Gondwana (Lundberg 1993, Krause et al. 1997, Gottfried and Krause 1998, Gottfried et al. 1998, Murray 2001). This view is apparently corroborated by data derived from "molecular clock" estimates of fish divergence (Vences et al. 2001, but see Kumazawa et al. 2000 for a conflicting finding) and by a range of other Indian Ocean terrestrial groups (Raxworthy et al. 2002). However, an oceanic dispersal model for Madagascar's fishes begs the question as to why a significant number of the taxa that *are* present on the island, and for which contemporary hypotheses of relationship have been argued, share transoceanic sister-group relationships broadly congruent with prevailing hypotheses of the sequence, if not the timing, of Gondwanan fragmentation (Rabinowitz et al. 1983, Storey et al. 1995, Hay et al. 1999). Despite conflicts with paleontological findings, with estimated dates of continental fragmentation and with calibrated molecular divergence levels, the phylogenetic relationships of many of Madagascar's freshwater fish clades continue to present intriguing support for vicariance (i.e., isolation caused by the fragmentation of Gondwana) as a viable explanation for their present distribution (Sparks and Stiassny 2003).

Phylogenetic analysis serves to highlight another intriguing aspect of the Malagasy fish fauna. Conforming to Millot's (1972) view that an "abundance of archaic groups" characterizes the island's fauna, the freshwater fish clades include a notable number of these "basal taxa" (Stiassny 1992; see figure 11c, d, e for examples). Basal taxa are particularly important because of the unique comparative information they contain, which in a sense is complementary to that of the entire membership of their frequently far more species-rich sister groups. The phylogenetic relevance of basal taxa is reflected at two levels. Character-state changes in these taxa can influence hypotheses of relationship among the remaining members of their lineage, regardless of states observed in more distantly related outgroups and in more recently evolved taxa. This influence often results in major changes in understanding of the phylogenetic relationships within the basal groups' sister taxa (Stiassny and de Pinna 1994, Schaefer 1998). In certain instances, basal taxa provide the *only* possible evidence for understanding the evolution of certain character-state transitions within related groups; as such, they represent an invaluable resource for evolutionary studies (Stiassny and de Pinna 1994).

In an observation that has direct relevance to arguments of conservation prioritization, Stiassny and de Pinna (1994) found that among many groups of freshwater fishes, basal taxa not only are often species poor (when compared to their

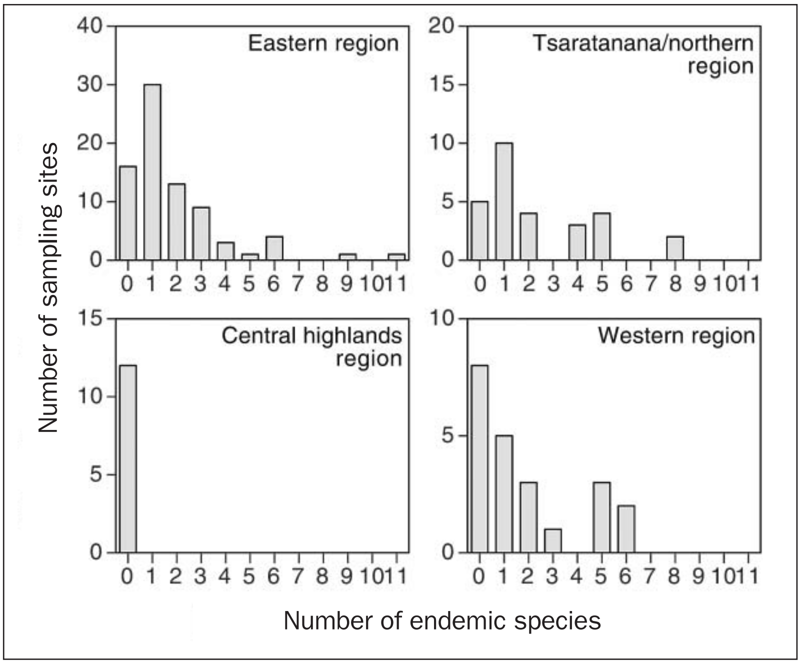

Figure 10. Representation of endemic freshwater fish species in samples collected in different regions of Madagascar.

regularly and causing greatly accelerated erosion of the underlying lateritic clay. The eastern belt of humid rain forest (0 to 1800 meters above sea level) that runs north–south along the island's steep escarpment has fared only slightly better. In the same period of time, it has been reduced to about 30% of its original extent (Green and Sussman 1990). Clearance of the eastern rain forest between 1993 and 1999 continued at a rate of 102,000 hectares, or 1.6%, per year (Dufils 2003). At this rate, all but the steepest slopes will be deforested by 2025 (Green and Sussman 1990).

Deforestation has many effects on stream and river ecosystems, including increased sediment delivery, higher insolation and water temperatures, enhanced nutrient loads, and changes in the relative availability of basal food resources. Of all these changes, increased sedimentation caused by accelerated erosion has had the most devastating effect on Madagascar's rivers, especially those draining the highly erodible lateritic soils of the central highlands. The consequences of heavy silt loads—which include a direct physiological burden on fish and other organisms that use gills to breathe, disruption of food webs due to sedimentation of benthic communities, and loss of spawning sites (Waters 1995)—can extend many kilometers downstream of the area immediately affected by forest loss (Benstead et al. 2000). This degradation of aquatic habitats adversely affects even those organisms that are not forest stream specialists.

Even where deforestation does not cause greatly increased sediment delivery, the removal of riparian vegetation can have dramatic effects on river and stream communities. For example, in the streams that drain Ranomafana National Park's deforested peripheral zone, insect assemblages are dominated by a few cosmopolitan mayfly taxa (Ephemeroptera). In contrast, stream communities draining the primary forest within the park are characterized by species-rich, diverse communities composed primarily of the orders Trichoptera, Ephemeroptera, Plecoptera, and Diptera (Benstead et al. 2003). This difference appears to be largely due to the inability of many forest stream insects to track the shifts in food resources (i.e., terrestrial detritus versus in situ algal production) caused by deforestation and the consequent loss of canopy cover.

Finally, annual patterns of precipitation in northern and western Madagascar impose a seasonal hydrological regime upon those regions' rivers. In the north and west, the extent to which a catchment is forested determines its water storage capacity and, consequently, whether the river draining it flows all year around or disappears during the dry season. Loss of forest cover has caused a shift from persistent to intermittent flow in the streams draining the northern and eastern slopes of the Massif d'Ambre in the extreme north of the island. Larger rivers are not immune to these hydrologic changes. Topographic maps printed in the late 1960s and early 1970s

sister groups) but also frequently have highly restricted geographical distributions (see figure 9). These factors in combination render such groups highly vulnerable to environmental degradation in a single region. The marked geographical localization (stenotypy) of many of Madagascar's endemic fishes and the presence of numerous phylogenetically basal taxa combine to strengthen arguments for broad regional conservation of this unique fauna. Related arguments for the incorporation of some measure of phylogenetic uniqueness or diversity *(sensu* Faith 1994) have recently been applied in a global hotspot context for mammalian diversity (Sechrest et al. 2002). From this perspective, Madagascar is once again revealed as an important reservoir of phylogenetic history.

Threats to Madagascar's freshwater biodiversity

The three principal threats to the freshwater biodiversity of Madagascar are deforestation, overfishing, and exotic species introductions. Although we review these factors separately below, it is important to bear in mind that they typically occur in combination. It is the synergistic relationships among these anthropogenic disturbances that have had such a detrimental effect, particularly on the native fishes.

Deforestation. Two thousand years ago, rain forest covered the eastern escarpment of Madagascar. At that time, the central highlands were a mosaic of montane rain forest, deciduous woodland, ericoid heath, and grassland. Since human colonization, the highlands have been almost completely transformed. They are now blanketed with a low-diversity assemblage of fire-resistant, mostly exotic grasses. This "pseudo-steppe" covers more than 40% of the island, burning

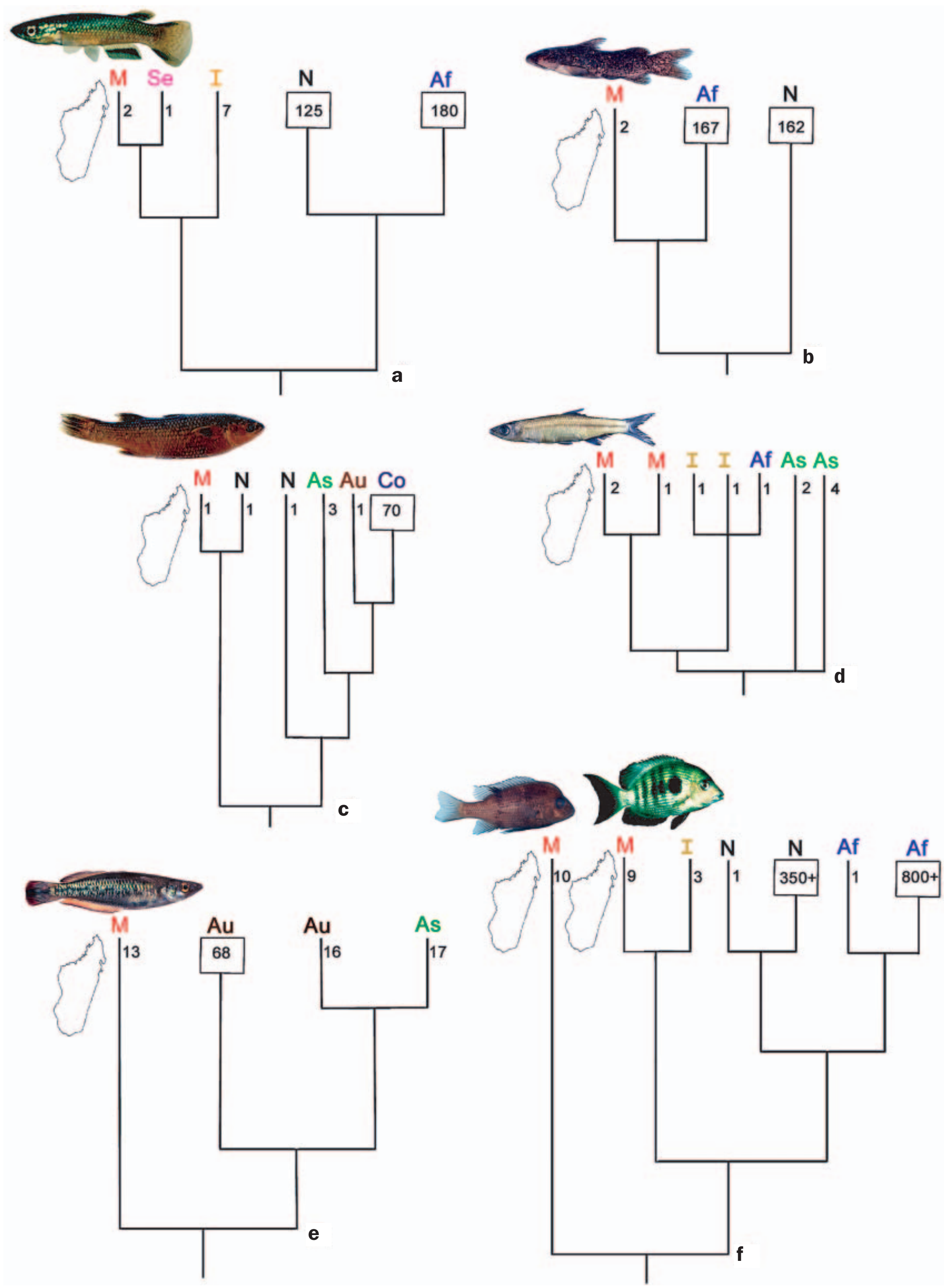

Figure 11. Phylogenetic relationships of some Malagasy fish clades, highlighting repeated Gondwanan affinities and the concentration of basal taxa on the island: (a) aplocheiloids, (b) doradoids, (c) mugilids, (d) ehiravin clupeids, (e) melanotaenioids, and (f) cichlids. Numbers on branches indicate species composition of clades; boxed numbers indicate radiations of more than 50 species. Color-coded letters at terminals indicate Gondwanan fragments (Af, Africa; As, Southeast Asia; Au, Australasia; Co, cosmopolitan; I, Indian subcontinent; M, Madagascar; N, Neotropics; Se, Granitic Seychelles).

depict the northeast-flowing rivers that rise in the Tsaratanana Massif as permanent bodies of water. Their upper and middle courses are now completely dry by the middle of October and remain so until the onset of the rainy season 8 to 10 weeks later, a change that, according to local residents, dates to the mid-1980s.

Overfishing. The impacts of fishing on Madagascar's freshwater fish fauna have largely been ignored until recently. This may reflect the fact that, with few exceptions, most of the island's endemic fishes have become too rare to support dedicated fisheries. However, this was not always the case. Native Malagasy species were once the basis of important fisheries (Grandidier 1886, Petit 1930, Kiener 1959, 1963). However, by the late 1950s, the decline of the endemic cichlid-based fisheries of Madagascar's western slope was sufficient to warrant official notice and the implementation of corrective measures, notably the introduction of several tilapia species for purposes of stock enhancement (Kiener 1963). Environmental degradation certainly contributed to the decline of some fish species in Madagascar, but the history of unregulated gill net and seine fisheries in East Africa, taken with what is known of the biology of Madagascar's native cichlids (Kiener 1963, Catala 1979, Loiselle 1996), strongly suggests that overfishing played a key role in this process. In the case of the *Ptychochromoides* species of the Onilahy and Maningory Rivers and Lake Itasy, overfishing has been specifically identified as a leading cause of their decline (Kiener 1959).

Exotic species. As anyone who has collected fish in Madagascar can attest, it is extremely difficult to locate a body of water, no matter how isolated, where the catch is not dominated by exotic species. It is even more difficult to find a freshwater system that is entirely free of exotic species (now restricted to a few remote regions of the island, including portions of the Masoala Peninsula; Sparks and Stiassny 2003). A walk through any local fish market confirms these observations. In addition to widespread degradation of aquatic habitats and overfishing, competition from and predation by introduced species is considered a major factor contributing to the currently disastrous state of the Malagasy freshwater fish fauna (Benstead et al. 2000). At least 24 species have been deliberately introduced into Madagascar's freshwaters, dating back to the mid-19th century (Kiener 1963, Moreau 1979, Reinthal and Stiassny 1991; see Brasher 2003 and Font 2003 for discussion of exotic species impacts on the Hawaiian Islands).

Tilapiine cichlids, introduced for aquaculture purposes decades ago, are the most ubiquitous of the exotics in terms of biomass and distribution; they also dominate the list of introductions in terms of number of species (see Reinthal and Stiassny 1991 for a list of introductions). Surprisingly (and unfortunately), the freshwaters of Madagascar are also home to introduced salmonids, centrarchids (basses and sunfish), cyprinids (goldfish and carp), poeciliids (mosquitofish, guppies, swordtails, and platies), belontiids (gouramies), anabantids (climbing perches), osphronemids (giant gouramis), and osteoglossids (bonytongues) (Kiener 1963, Reinthal and Stiassny 1991). Throughout most of the central highlands and much of western Madagascar, native fish communities have been entirely replaced by exotics (figure 10).

Far worse for the future of Madagascar's native freshwater fishes than any of these species, however, was the introduction of the Asian snakehead *(Channa maculata)* in 1978 (Raminosoa 1987). This voracious predator has since dispersed throughout Madagascar. (A closely related species, *Channa argus,* recently made US headlines because of its accidental introduction in Maryland.) The spread of this taxon has been extremely rapid because of its tolerance of poor water quality, extreme fecundity, and efficient biparental custodial care of its eggs and fry. A suprabranchial organ used for breathing air allows the Asian snakehead to survive and disperse through water with very low oxygen content (Ishimatsu and Itazawa 1981). This predator is present in most of Madagascar's large lakes and is responsible for the rapid decline in abundance of a number of native species. Another unfortunate introduction was that of the mosquitofish *Gambusia holbrooki.* This predator of the fry of native fishes has been implicated in the decline of several taxa around the island.

What will the future hold?

Although the future might look bleak for Madagascar's freshwater biodiversity, recent advances offer some hope. These include new national institutions working toward environmental conservation, such as the Office National pour l'Environnement and the Association Nationale pour le Gestion des Aires Protégées, as well as the recent, impressive expansion of the island's protected areas system. However, to preserve native freshwater communities and better understand a poorly known fauna, researchers must focus on accomplishing three main objectives.

First, it is imperative to continue survey efforts directed at remote regions of the island that have not been thoroughly inventoried for freshwater biota. Priority areas for survey include the headwaters of the Tsaratanana Massif, the forested regions of the southeastern highlands, the remote forested areas of the eastern and western highlands, and the Masaola peninsula (see Benstead et al. 2000 and Sparks and Stiassny 2003 for more comprehensive lists of biologically important areas in need of survey). Numerous taxa new to science have been discovered in recent years, emphasizing the importance of continued biotic inventories.

Second, systematic and ecological studies of poorly known taxonomic groups must be undertaken. It is impossible to accurately evaluate the conservation status of any particular group if little is known about its composition, relationships, or basic biology. Recent systematic studies focusing on native freshwater fish assemblages have greatly expanded biologists' knowledge base regarding the origin, relationships, diversity, and species boundaries of the island's major freshwater fish clades, including cichlids and bedotiids. Similar work must be conducted on other freshwater taxa, such as the crayfishes, mollusks, and aquatic plants.

Finally, and certainly of greatest importance, research must be directed at conserving freshwater resources in Madagascar. The inclusion of freshwater systems or entire watersheds within park and reserve boundaries, successfully implemented in the recent creation of the Masoala National Park (Kremen et al. 1999), must be a top conservation priority. Unfortunately, the importance of healthy aquatic systems for maintaining the integrity of entire ecosystems has rarely been discussed or fully appreciated in the past. The importance of science-driven ecosystem management in rectifying this situation cannot be overstressed. Given the dire state of Madagascar's freshwater systems, the spread of exotic predators, and the continued, widespread deforestation, it may be too late to save more than remnants of the island's freshwater fish fauna (e.g., the Masoala Peninsula, Nosy Be, and portions of the Tsaratanana region). Nevertheless, regions that still harbor intact, native freshwater communities can be identified and protected. These areas must be at the forefront of conservation efforts.

Persistence within original habitat is the optimal conservation strategy for any endangered species. Unfortunately, captive breeding now represents the only guaranteed means of saving a large proportion of Madagascar's endemic fishes from extinction (Loiselle 2003). Captive breeding efforts already undertaken by public aquariums, zoos, and individuals in North America and Europe have resulted in the establishment of managed populations of 33 Malagasy fish species. Five of these species are considered critically endangered; 19 are endangered; and one, *Paretroplus menarambo*, has not been seen in its last known habitat for 5 years and is presumed to be extinct in nature. While these efforts constitute a strong beginning, a formally recognized species survival program, identical to that already implemented by the American Association of Zoos and Aquariums for the haplochromine cichlids of Lake Victoria, should be implemented for the endemic freshwater fishes of Madagascar.

Conclusions

We have summarized the outstanding features of the freshwater biodiversity of Madagascar, emphasizing three emerging characteristics that warrant more attention from scientists and conservation managers working in the region. First, species richness is not low, as was once assumed for both the freshwater fishes and the invertebrates. Even on the basis of these taxa, Madagascar clearly deserves its status as a global hotspot for freshwater biodiversity. Future research may reveal similar patterns in other, more poorly known taxonomic groups. Second, many freshwater species are microendemic, restricted to a few river basins or even to a single river basin. Often these taxa are also limited to those streams and rivers that drain the island's remaining primary forest habitat. Finally, many of the island's freshwater fishes are basal representatives of their clades. Consequently, they are unique repositories of phylogenetic information. In the face of the ongoing threats we have reviewed here, links among microendemism, forest stream specialization, and basal phylogenetic position highlight the importance and vulnerability of Madagascar's freshwater communities and the need for immediate conservation action on their behalf.

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