



Patterns of species change in anthropogenically disturbed forests of Madagascar

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ABSTRACT

Five main conclusions arise from this review of the responses of species to anthropogenic disturbance in Madagascar: First, species' reactions to anthropogenic disturbance are generally negative, but remain poorly known. Our knowledge is patchy among and within higher taxonomic groups; we are still largely gathering case studies. Second, taxonomic groups vary considerably in which proximate factors are most important. Third, several groups show differing responses within different ecoregions. Whether these differences are consistent across groups requires further testing. Fourth, related species often have divergent reactions to disturbance, even within lower taxonomic groupings (families or genera). Thus, we cannot rely on phylogenetic relatedness or even ecological similarity to infer similarity in responses. Finally, disturbance typically reduces species diversity (especially of native and/or endemic species), but also causes species turnover, typically with forest specialists replaced by grassland generalists, and endemics replaced by non-endemics (including invasives). Given these knowledge gaps, we stress the urgency of applied studies that assess species' ecology, behaviour and health across disturbance gradients, including purely anthropogenic landscapes. Remaining natural vegetation and protected areas will be unable to preserve Madagascar's biodiversity under the impact of climatic change; we must understand responses of plants and animals to disturbance in order to create buffer zones and corridors combining secondary, degraded and natural habitats.

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1. Introduction

Madagascar is the world's fourth-largest island: 1600 km long, 580 km wide, and covering 587,000 km². It is topographically complex, with a central high plateau that drops gradually to coastal lowlands in the west, south and north, but is separated from eastern lowlands by a steep escarpment. Its highest point, the Tsaratanana massif, reaches 2876 m. This topographic variation, combined with wind and ocean currents, has caused great variation in climate (Cornet, 1974; Donque, 1972; Fig. 1). Eastern regions experience high rainfall, with no true dry season, and annual mean

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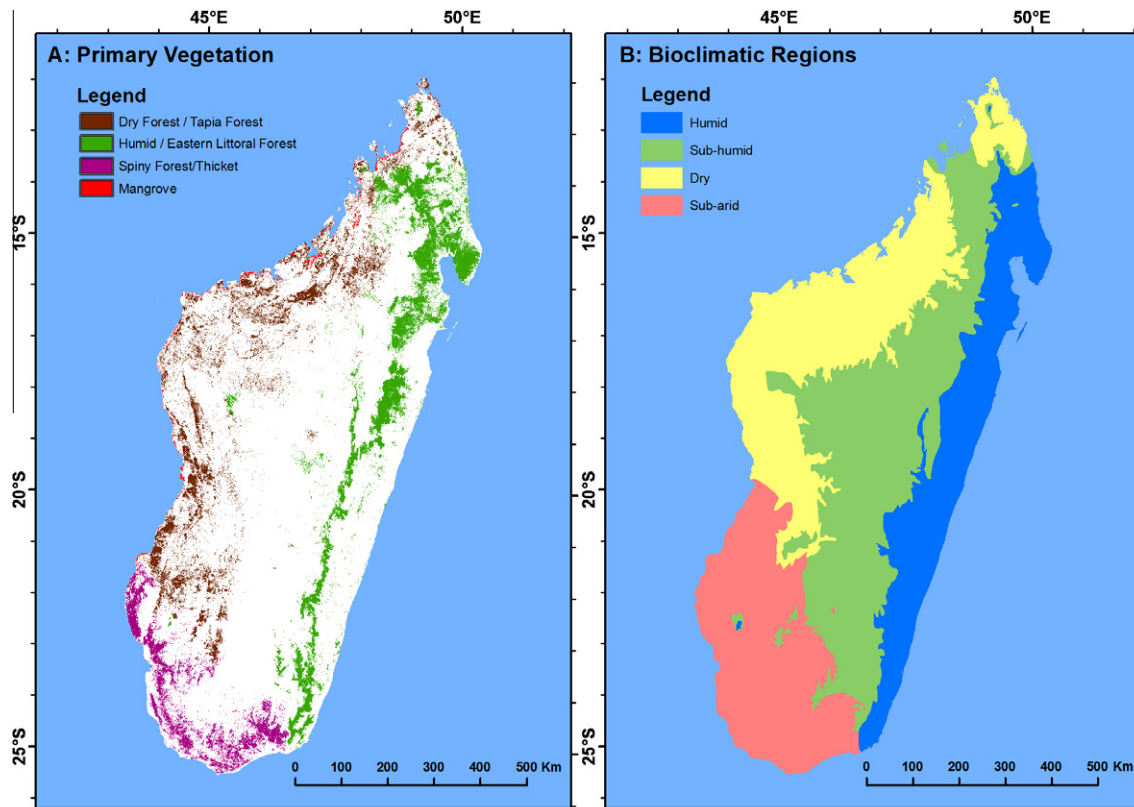


Fig. 1. Map of Madagascar showing: (A) remaining primary vegetation (following Moat and Smith (2007)); (B) simplified bioclimatic regions (following Cornet (1974)).

temperatures of 20–25 °C. Western regions experience moderate rainfall, with up to 8 dry months per year, and annual mean temperatures of 24–28 °C. The south and southwest are semi-arid to arid, with low rainfall, a long dry season, and highly-variable temperatures averaging 23–24 °C. The central plateau has low temperatures, with annual means of 14–22 °C (with frost and occasional snowfalls), variable rainfall, and a moderate dry season. This considerable environmental variation has led to stark differences in vegetation: closed-canopy evergreen rainforest in the east, deciduous forest in the west, and spiny thicket with gallery forests in the south.

Madagascar's unique and highly endemic biota evolved in isolation until the arrival of humans, thought to have occurred approximately 2300 years ago. This arrival was followed by a rapid loss of native large mammals (Burney et al., 2004), for which humans were likely largely responsible. Original forest cover is hard to estimate, and thus there are debates about how much of Madagascar was originally forested (Lowry et al., 1997). The already greatly-reduced cover in 1953, 160,000 km² (27% of the island), was further reduced to 99,000 km² (17%) in 2000 (Harper et al., 2007; Moat and Smith, 2007; Fig. 1). Despite increased environmental awareness in recent decades, deforestation continued, with 0.9% of remaining forest lost annually from 1990 to 2000. Even more disturbing is the lack of “remote” habitat: in 2000, more than 45% of forest existed in patches of <500 km², and over 80% of forest area was <1 km from an edge (Harper et al., 2007). Thus, understanding the prospects for wildlife in disturbed habitat is central to conservation efforts.

Madagascar has a human population of 20.5 million, growing at 2.7% annually (UNPF, 2008); the 61% of this population living outside urban areas causes various types of disturbance in natural ecosystems. Hunting is common in some regions (Goodman, 2006), clearance for agriculture remains a major driver of forest loss

(Agarwal et al., 2005), and extraction of timber, fuelwood and other forest products is widespread. Anthropogenic landscapes take on a variety of forms. Disturbed natural forests may look similar to undisturbed forest, but have altered structure and composition (Brown and Gurevitch, 2004). Secondary forest grows on abandoned agricultural land, but constitutes a small proportion of land area, and tree plantations are somewhat common. By far the dominant anthropogenic landscape is grassland, especially on the central plateau.

Here, we summarize how native Malagasy species respond to anthropogenically-disturbed habitats and explore how this knowledge can guide conservation efforts. It is important to remember that “disturbed habitat” has evolved differently in different regions – due to abiotic differences, but also differences in human pressure and land use, invasive and anthropogenic species, and biotic contrasts between natural and anthropogenic habitat. For example, eastern species might face sharper contrasts between closed rainforest and open rice fields, whereas southern species might face gentler contrasts between open spiny thicket and grazing lands used by livestock.

2. Plants

Madagascar has a rich flora (~13–14,000 higher plant species) that is mostly endemic (~95% for trees and large shrubs; Schatz, 2001), yet threatened by shifting cultivation, wildfires, invasive species, selective exploitation, and climate change. All vegetation in Madagascar has likely been impacted to some extent by human activities (Lowry et al., 1997), both subtle (e.g., invasive species, selective exploitation, climate change) and more obvious (e.g., forest clearance, burning), though recent studies indicate that some fragments of the littoral forests at sea level are not anthropogenic,

but due to fluctuations of the groundwater table (Virah-Sawmy et al., 2009). In general, with increasing human impact, primary formations (forest, woodland, thicket and shrubland) are transformed through various secondary woody formations to secondary grassland (Lowry et al., 1997). Vegetation may also be transformed into crop fields, tree plantations and other types of cultivation. Although secondary thickets, secondary grassland and plantations have been little studied by botanists (Sorg, 2006), it is possible to draw some conclusions concerning their importance for conservation.

Secondary thickets (“savoka”) develop when forest is cleared, the land cultivated and then abandoned. Initially, areas are colonized by native and alien heliophilous herbs and shrubs, which are gradually replaced by longer-living woody plants (Table 1), through seed dispersal, soil seed banks and regenerating stumps (Deleporte and Randrianasolo, 1996; Genini, 1996; Lowry et al., 1997; Randriamalala et al., 2007). The nature of secondary vegetation depends on the intensity and duration of cultivation, time since abandonment and the surrounding vegetation; when land is cultivated lightly and briefly, has been abandoned for a long period, and is near primary vegetation, secondary thicket can become secondary forest with many native species (Randriamalala et al., 2007). However, this situation is rare; secondary thickets usually experience further cultivation, causing impoverished soil and a vegetation poor in native species (although *Dicranopteris linearis* and *Ravenala madagascariensis* may be abundant) and dominated by aliens (especially *Grevillea banksii*, *Lantana camara*, *Litsea glutinosa*, *Melaleuca quinquinervia*, *Psidium cattleianum*, and *Rubus moluccanus*; Binggeli, 2003; Lowry et al., 1997); most remaining native elements are widespread species adapted to clearings and edges (Lowry et al., 1997; Randriamalala et al., 2007). With repeated cultivation periods separated by short fallows, secondary thickets become anthropogenic shrublands, bushlands and grasslands, with impoverished, alien-dominated floras (Koechlin et al., 1974). Madagascar’s species-rich littoral forests are acutely vulnerable; even one cultivation cycle can create a species-poor bushland dominated by *Psidium cattleianum*, *Psidium guajava*, *Pteridium aquilinum*, and *Erica* and *Helichrysum* species (Koechlin et al., 1974), though some littoral heath might be naturally occurring (Virah-Sawmy et al., 2009). Koechlin et al. (1974) regarded Malagasy forests as being more vulnerable to degradation than African counterparts because they are poor in pioneer species, and native

species have weak competitive abilities compared to aliens, a reflection of Madagascar’s insular nature.

The origin of the grasslands now covering most of central and western Madagascar is disputed. Some (Bond et al., 2008; Burney, 1993; MacPhee et al., 1985) argue that this formation is largely natural (see also Virah-Sawmy et al., 2009) whereas others (Humbert, 1927; Koechlin et al., 1974; Lowry et al., 1997; Perrier de la Bâthie, 1936) consider that grasslands, with few exceptions (mountain summits and rock outcrops, marshes, and within sclerophyllous woodland), are anthropogenic, derived from forest, bushland and shrubland through anthropogenic wildfires. This is an important issue, as recent research is highlighting the biodiversity value of “primary” grassland, and the threats it faces (Bond and Parr, this volume).

Whatever their origin, grasslands can differ considerably: montane grasslands and herbaceous vegetation within sclerophyllous woodland have rich floras including many local endemics, whereas the vast grasslands of central and west Madagascar have low diversity (usually <20 species, often as few as 6), include many aliens and few local endemics, and are regarded as botanical wastelands (Binggeli, 2003; Koechlin et al., 1974; Lowry et al., 1997). Secondary grasslands derived from eastern escarpment forests are somewhat richer, with 20–25 species in 100 m² (Rakotoarimanana et al., 2007). Secondary grasslands in southern Madagascar are formed when primary thicket is felled and burnt, followed by brief cultivation and abandonment. In the absence of grazing, these areas undergo succession from bushland, to shrubland, to thicket (including native and alien species); more commonly, grazing produces secondary grassland dominated by a few species or even bare soils. Charcoal production and selective timber exploitation can create degraded vegetation with abundant Didiereaceae (Koechlin et al., 1974).

Significant areas are occupied by plantations (primarily *Pinus patula*, *Eucalyptus robusta* and *Eucalyptus camaldulensis*). Randriambanona and Carrière (2007) found 125 native species (91 genera, 46 families), dominated by pioneers and ruderals, in an old disturbed eastern escarpment pine plantation; they considered that this vegetation could develop into secondary forest dominated by native species.

In conclusion, despite variation among regions, Madagascar’s vegetation generally becomes structurally simpler and botanically impoverished with increasing human impact. Local endemics decline, and are replaced by invasives. Secondary formations are thus of lesser conservation importance than less-disturbed vegetation, but not without importance; some plant species (e.g., *Schizolaena tampoketsana* on the Tampoketsa of Ankazobe) are only known from degraded habitats. Finally, with removal of anthropogenic pressures and elimination of aliens, some secondary vegetation has the potential to regenerate or to be restored to more botanically important vegetation.

Table 1

Common colonizing plants of secondary thicket (“savoka”).

	Western dry deciduous forest	Eastern rainforest
Colonizing plants	<i>Acacia</i> spp. <i>Croton</i> spp. <i>Grewia</i> spp. <i>Terminalia</i> spp.	<i>Aframomum angustifolium</i> <i>Ageratum conyzoides</i> <i>Clidemia hirta</i> <i>Dodonaea viscosa</i> <i>Conyza bonariensis</i> <i>Helichrysum cordifolium</i> <i>Lantana camara</i> <i>Psidium altissima</i> <i>Psidium cattleianum</i> <i>Pteridium aquilinum</i> <i>Solanum auriculatum</i>
Longer-lived woody plants that replace initial colonizers	<i>Croton</i> spp. <i>Dombeya</i> spp. <i>Indigofera</i> spp.	<i>Anthocleista madagascariensis</i> <i>Croton</i> spp. <i>Dombeya</i> spp. <i>Harungana madagascariensis</i> <i>Macaranga</i> spp. <i>Nuxia</i> spp. <i>Ravenala madagascariensis</i>

3. Insects

3.1. Terrestrial insects: ants as a case study

3.1.1. Forest fragments and disturbed forest

Arthropods are hyperdiverse, with many local microendemics, and sensitive to habitat disturbance (Stewart et al., 2007; Underwood and Fisher, 2006); many partition the world on a much finer scale than vertebrates. Many ants and other arthropods in Madagascar show restricted ranges and small population sizes; thus, small habitat patches likely hold unique species; deforestation has likely already driven many extinct. In a study including invertebrates such as ants, flies and butterflies, Allnutt et al. (2008) predicted that deforestation from 1950 to 2000 drove 9.1% of

Madagascar's species extinct. Kremen et al. (2008) showed that 15% of 326 ant species and 11.3% of 302 butterfly species only occur outside protected areas.

Moderate disturbance can increase insect diversity, especially when it causes greater habitat heterogeneity; with smaller fragments or heavier disturbance, species loss becomes increasingly likely, and ant communities become vulnerable to invasion (Holway et al., 2002; Suarez et al., 2005). Islands (Christmas Island: O'Dowd et al., 2003; Mauritius: Fisher, 2005) have experienced ecological 'meltdowns' triggered by invasive ants, disrupting nutrient cycling, seed dispersal and prey bases for higher trophic levels. Invasive species identified in Madagascar include the white-footed ant (*Technomyrmex albipes*) in eastern lowland rainforests, and *Pheidole megacephala* and *Solenopsis geminata* in the west. At Tampolo, the presence of *T. albipes* in disturbed, fragmented forest is associated with reduced native ant populations (Fisher et al., 1998).

3.1.2. Non-natural habitats

In a survey across Madagascar, over 60 native ant species were found along roads, urban areas, gardens, and coconut, vanilla, cacao, and coffee plantations (Fisher, unpublished, www.antweb.org). Grasslands harbour lower diversity, but some montane wet grasslands include native and endemic species, suggesting that grasslands were a natural component of Madagascar (Fisher and Robertson, 2002). Studies elsewhere have shown that shaded plantations preserve high invertebrate diversity in leaf litter and arboreal habitats (Delabie et al., 2007; Philpott and Armbrecht, 2006).

3.2. Aquatic insects

Madagascar's streams have highly diverse and endemic insect communities spanning six major orders (Elouard and Gibon, 2003). Local diversity can be high (140 morphospecies were recorded during 3 years from a single stream in Ranomafana; Rabeson, 2001), and some species are forest-dependent (Ross, 1956).

Little is known about responses to disturbance; most studies have focused on country-wide collecting (Benstead et al., 2000). Benstead et al. (2003) found that species richness was lower and community structure different in agricultural streams relative to primary forest in Ranomafana. Further anecdotal evidence suggests sensitivity to disturbance: for example, the mayfly *Eatonica josettae* seems to have disappeared at Mandraka, which now has deepened streams, ricefields, deforestation, and pollution, but two congeners still inhabit nearby primary forest at Anjozorobe (Elouard et al., 1998). In some groups, rainforest-endemic species do not seem to survive deforestation, being replaced by species from the already-deforested high plateau or drier western forest (Gibon and Elouard, 1996); this suggests that rainforest species are most vulnerable.

There is a high degree of micro-endemism (especially among Trichoptera, Plecoptera and Megaloptera; Elouard and Gibon, 2003), with many taxa restricted to rainforest streams (e.g., 75% of philopotamid Trichoptera; Gibon, 2000). It is therefore likely that deforestation has already caused extinctions (Courtney, 2003; Elouard and Gibon, 2003; Gibon et al., 1996); conversely, even small habitat patches may still hold endemic species.

Several factors may drive changes in diversity and abundance. First, food resources can be altered; forest streams are rich in collector-gatherers and collector-filterers of Trichoptera, Ephemeroptera, Plecoptera, and Diptera; depauperate agricultural streams are dominated by generalist collector-gatherers mostly within Ephemeroptera (Benstead et al., 2003). Second, sediment loads can change microhabitats. Third, many rivers have been invaded by exotic fish (Benstead et al., 2000), some of which prey

on macroinvertebrates. Finally, microclimate may be altered (e.g. increased water temperature, from light exposure due to deforestation, or climate change).

4. Fishes

From 1994 to today the number of native freshwater fish species recognized for Madagascar rose from 42 to over 160, of which 108 are endemic (Sparks, unpub. data; Sparks and Stiassny, 2008; Stiassny and Raminosoa, 1994); these numbers continue to grow. Thus, for its size, Madagascar is as diverse as other continental freshwater ichthyofaunas (Riseng, 1997; Sparks and Stiassny, 2008). Madagascar's fishes are being extirpated at an alarming rate, with some extinct at the time of description (e.g., Sparks, 2004); 23 additional endemic species are Critically Endangered or Endangered.

The persistence of native fishes within a drainage basin depends upon the extent to which human activity has affected its catchment area. In much of Madagascar, persistent stream flow depends on gradual release of water stored in forested watersheds during brief rainy seasons. Following deforestation, formerly perennial streams disappear during the dry season, extirpating local ichthyofaunas.

The massive erosional siltation characteristic of most western rivers is another consequence of deforestation. Native fishes thrive in silt-free, well-oxygenated water flowing over rocky bottoms; suspended silt imposes physiological stress, its deposition suffocates the benthic invertebrates they consume and destroys spawning sites (Benstead et al., 2000). Native and endemic species are poorly represented in highly turbid rivers, which are dominated by the more physiologically plastic exotics (Sparks and Stiassny, 2008).

Nevertheless, native species can persist without primary forest. The watershed of the Nosivolo River in eastern Madagascar is largely deforested, yet this river supports Madagascar's most species-rich endemic fish assemblage (15 species, 8 families; P. Loiselle, unpubl. data). Local conditions favour rapid growth of secondary thicket ("savoka") in deforested areas, curtailing erosion and preserving limnological integrity. It also appears that savoka, even when dominated by exotic plants, can generate an infall of terrestrial invertebrates sufficient for the trophic requirements of many native fishes. This may explain the persistence of aplocheilid killifishes and bedotiids, which rely upon allochthonous food sources, in streams whose watersheds are converted to savoka.

Interactions with exotic species (especially African tilapiines, Neotropical poeciliids, and the Asian snakehead) also negatively influence native fish communities. There is little doubt that predation by the mosquito fish, *Gambusia holbrooki*, caused the virtual extirpation of *Pachypanchax sakaramyi* from streams in northern Madagascar. Predation by the spotted snakehead, *Channa maculatus*, has comparably impacted *Bedotia* species throughout much of their range. Predation upon juveniles by black bass, *Micropterus salmoides*, and the spotted snakehead has contributed to the disappearance of *Paratilapia bleekeri* and *Ptychochromoides itasy* from the Central Highlands, though competition likely also played a role. Human predation upon adults (i.e., unsustainable fishing practices) also contributes to the decline of endemic cichlids.

However, one cannot assume a causal relationship between presence of naturalized exotics and scarcity of native species. There is no evidence that introduced tilapias caused the decline of native etropline (*Paretroplus*) cichlids in northwestern Madagascar; these genera have divergent diets and spawning site preferences. Tilapias presumably have replaced *Paretroplus* because they are better able to tolerate degraded habitats and withstand intense fishing

pressure, rather than preying upon or out-competing them (Sparks and Loiselle, pers. obs.).

Our primary objective must be to preserve the integrity of remaining habitats – preserving watersheds with perennial hydrological regimes and preventing erosion and siltation (e.g., by maintaining riparian buffer zones). There is no possibility of eradicating naturalized species; we can only limit their impact. Some offshore islands are still free of mosquito fish and spotted snakeheads; some mainland regions are also snakehead-free. Every effort needs to be made to prevent further spread of exotics. Finally, whereas every effort must be made to promote *in situ* conservation, it is impossible to avoid the conclusion that captive breeding offers the only hope for many native species. To date, half a dozen endangered Malagasy fishes are the beneficiaries of captive breeding programs in Europe and North America.

5. Amphibians and reptiles

Malagasy frogs constitute one of the world's richest groups of amphibians with about 240 described and 130–240 further candidate species. All native species and 88% of genera are endemic to Madagascar and neighbouring islands. Non-marine reptiles also show high diversity (363 species) and endemism (92%) (Glaw and Vences, 2007; Vieites et al., 2009). Although several surveys have been conducted, there are few studies of disturbance effects on amphibians and reptiles.

5.1. Forest fragments

Habitat destruction and fragmentation are the most important factors influencing extinction (Andreone et al., 2005a). Species diversity of rainforest herpetofaunas generally responds negatively to fragmentation (decreasing diversity with decreasing fragment size; Ramanamanjato, 2000; Vallan, 2000), forming nested subsets in fragments. Reptiles in western dry forest show no reduction in species richness but significant changes in community structure; common species in original forest (e.g., *Brookesia*) were completely lacking in fragments (Penner, 2005). In northeastern Madagascar habitat heterogeneity associated with elevational variation is more important than fragmentation in predicting herpetological species richness (Rakotondravony, 2007). The few studies on proximate causes of diversity loss in fragments indicate that edge effects are important, possibly via effects on microclimate; all edge responses were found (edge-avoiders, interior-avoiders, omnipresent species) and edge sensitivity is correlated with extinction vulnerability (Lehtinen et al., 2003).

5.2. Disturbed natural forests

Herpetological diversity decreases in highly disturbed areas, e.g. where intense clearing and burning have produced degraded secondary forest, forest mosaic, or plantations (Glos et al., 2008b; Jenkins et al., 2003; Scott et al., 2006; Vallan, 2002; Vallan et al., 2004). However, when disturbances were low-level, and/or sufficiently long ago, no clear effect on diversity was found in rainforest amphibian (Vallan et al., 2004) and dry forest reptile communities (Penner, 2005; Glos, unpublished). But again, species typical of pristine rainforest were replaced by species adapted to secondary habitats (Vallan et al., 2004).

5.3. Sensitivity to disturbance

Within the reptiles, studies of disturbance sensitivity are inconsistent. Tortoises are generally susceptible to disturbance (e.g., *Pyxis planicauda*, Bloxam et al., 1996; Young et al., 2008), however,

this threat is outweighed by overexploitation and collecting (Leuteritz et al., 2005). Many chameleon species are true forest-dwellers and habitat disturbance has negative effects on diversity and abundance (e.g., *Brookesia*; Brady and Griffiths, 1999; Jenkins et al., 2003), though this is not true for all chameleons (e.g., *Furcifer pardalis*; Andreone et al., 2005b). In dry forest, species higher in the food chain (e.g. snakes) decrease in presence and abundance in disturbed habitats (Glos et al., unpublished).

In amphibians, species that reproduce independently from running or standing waters are most vulnerable (i.e., microhylid frogs, some mantellid frogs; Vallan, 2000, 2002). Furthermore, species with narrow spatial and temporal niches are sensitive to microhabitat changes associated with disturbance (e.g., *Aglyptodactylus laticeps*, Glos et al., 2008a, 2008c).

5.4. Conservation priorities

It might seem paradoxical to appeal for intensive conservation where catastrophic declines have not yet been detected. There are no recorded extinctions of Malagasy frogs; indeed, new species are discovered at an exceptional rate. Chytridiomycosis, responsible for population and species extinctions worldwide, is absent from Madagascar. However, given the rate of habitat loss and degradation, extinctions seem inevitable. Amphibian conservation efforts have the possibility of being pro-active, rather than reactive (Andreone et al., 2008). Efforts should focus on areas of high herpetological species richness, or areas of otherwise high conservation interest such as riverbeds and adjacent gallery forests (Jenkins et al., 2003; Paquette et al., 2007), montane areas (Raxworthy et al., 2008; Vences et al., 2002) and dry forest (Glos, 2003; Glos et al., 2008b).

6. Birds

Of Madagascar's 298 bird species, 75 are visitors, erratic, migrant or allochthonous (introduced) (Goodman and Hawkins, 2008). The 223 native species include 21 endemics which went extinct during recent millennia, and 105 extant endemics. Endemism is high (52.0% for living native species, with 4 endemic families); the only oceanic island comparable to Madagascar in this respect is New Zealand (40% endemism, 8 endemic families; McDowall, 2008).

Studies of habitat disturbance, selective logging, and fragmentation have shown that the number of endemic species declines in disturbed habitat, especially within higher endemic taxa (Andrianarimisa, 1992; Andrianarimisa et al., 2000a,b; Goodman and Raherilalao, 2003; Hawkins and Wilmé, 1996; Langrand and Wilmé, 1997; Raherilalao, 2001; Raherilalao and Goodman, 2005; Raherilalao et al., 2001). The apparent proximate factors causing reduction in forest species include edge effects (Watson et al., 2004), distance of a fragment to a main forest block (e.g., Langrand and Wilmé, 1997; Raherilalao et al., 2001), and especially the presence of a river; riverine forests in some ecoregions harbour the highest diversity and density of species (Hawkins and Wilmé, 1996). Few further generalizations are possible, due to the relative paucity of disturbance research and the cryptic nature of some species.

Surprisingly, there are very few introduced species relative to nearby islands (Long, 1981). This may be due to Madagascar's higher native species diversity, allowing less opportunity for exotics to invade. Madagascar's forest birds are not known to be threatened by introduced species, probably because most species do not invade forest interiors; however, waterbirds may have suffered more (Pidgeon, 1996).

It is striking that over a quarter of known species within endemic families and sub-families have recently gone extinct. It is difficult to speculate about the causes, but it is worth noting that species in these groups are sensitive to habitat disturbance (Wilmé, 1996), being rare or absent in fragmented forests like Ambohitantely, Montagne d'Ambre or the Ranomafana–Andringitra forest corridor.

Birds are similar to other groups in that diversity usually decreases following forest fragmentation and disturbance, but differ in the importance of running water. The recent inclusion of wetlands, marshes, lakes, rivers and riverine forests in Madagascar's protected area network could help bird conservation and preserve future dispersion corridors (Raheirilalao and Wilmé, 2008; Jenkins et al., 2003).

7. Mammals

7.1. Lemurs

Of the groups considered here, the 99 lemur taxa (Madagascar's endemic primates; Mittermeier et al., 2008) have perhaps received the most research attention, yet relatively few studies have investigated responses to anthropogenic disturbance.

7.1.1. Forest fragments

Several studies have documented deterministic species extirpations (causing “nested” distributions) in fragments (Ganzhorn et al., 2003). At Tsinjoarivo (Irwin and Raharison, 2009), species loss increases with decreasing fragment size (which correlates with disturbance); species' susceptibility increases with body mass and degree of frugivory. At Ranomafana (Dehgan, 2003), species richness is reduced in fragments, but area does not predict richness, and the most important characteristic promoting resilience is “behavioural plasticity”. In general, the size of populations which can persist in isolated fragments for 20–40 years seems to be ~35 adults; fragments of ~1000 ha are needed to maintain all species (Ganzhorn et al., 2000a).

7.1.2. Disturbed natural forests

At the community level, intermediate disturbance might favour some species (via increased food abundance), but eventually all species decline and disappear with higher disturbance (due to food shortage or hunting; Ganzhorn et al., 1997). Species have variable responses to disturbed forests (including edges), showing higher, lower, or equal densities relative to undisturbed forest (Lehman, 2007; Lehman et al., 2006a,b; Petter et al., 1977).

Propithecus diadema in disturbed fragments have lower mass, smaller home ranges, reduced consumption of canopy tree fruit, increased mistletoe consumption, and reduced scentmarking, aggression and play (Irwin, 2006, 2008a,b). *Propithecus edwardsi* in selectively-logged rainforest exhibit reduced frugivory, reduced mass and less social interaction (Arrigo-Nelson, 2006). *P. edwardsi* have reduced mass in disturbed fragments, while *Eulemur* spp. have similar mass but greatly increased home range (Dehgan, 2003; Schwitzer et al., 2007).

Some species show little response: *Hapalemur griseus* in selectively-logged rainforest or forest remnants in agricultural landscapes show dietary differences and smaller ranges, but no sign of reduced health (Grassi, 2001; Martinez, 2008). Although few species have been studied, the fact that some relatively folivorous species (*H. griseus*) fare better than more frugivorous species (*Propithecus*, *Eulemur*, *Varecia*) is consistent with data showing that frugivores are more easily extirpated (Irwin and Raharison, 2009). However, anecdotal evidence also suggests great variation among “folivores”, especially bamboo specialists (e.g., *Hapalemur aureus*

is absent in fragments, *Prolemur simus* survives for decades; Wright et al., 2008).

Notwithstanding hunting, most studies suggest that food resources are the primary driver of density (Balko and Underwood, 2005) and behavioural changes (Irwin, 2007); as seen in studies of natural disturbance. *Varecia variegata* at Manombo (Ratsimbazafy, 2002; Ratsimbazafy et al., 2002) showed altered behaviour after a cyclone killed >50% of preferred fruit trees – feeding more on shrubs and invasive plants, reducing travel, increasing resting, losing mass, and halting reproduction for 4 years (Ratsimbazafy, unpublished). Other factors are less-studied but are potentially important (e.g., disruption of locomotion; higher parasite loads in degraded habitats: Raharivololona et al., 2007; Wright et al., 2009).

7.1.3. Non-natural habitats

Most species cannot survive in anthropogenic habitat, but tree plantations can provide buffer zones around forests, providing food in some seasons, typically for smaller, more omnivorous lemurs (*Microcebus*, Mirza; Ganzhorn, 1987; Ganzhorn et al., 1999). However, even the disturbance-tolerant *Microcebus murinus* does not maintain populations in secondary habitats linked to primary forests (Ganzhorn and Schmid, 1998), though it may exist in pure garden environments, such as in Fort Dauphin. Only *Daubentonia madagascariensis* and *Eulemur macaco* survive in anthropogenic landscapes for extended periods (Colquhoun, 1993; Simmen et al., 2007; Sterling, 2003).

In general, disturbed habitat is only valuable for some species; species richness declines with disturbance, though density of some species increases. Species that persist often exhibit altered physiology, ecology and behaviour, jeopardizing their long-term prospects. Future research should increase our sampling of landscapes and species, and investigate proximate mechanisms affecting extirpations (e.g. resource density, microclimate, predation, disease).

7.2. Non-primate mammals

This group is composed of carnivorans (Eupleridae, 8 species), tenrecs (Tenrecidae, 32 species) and rodents (Nesomyidae, 27 species; Goodman et al., 2008, unpublished; Olson et al., 2009); all of these taxa are endemic and most are restricted to natural forests. Shrews (Soricidae) are excluded, as both species occurring on Madagascar are probably introduced. Forty-three species of bats are recognized (Goodman et al., 2008, unpublished); few species are strictly forest-dwelling and thus they are not discussed here.

7.2.1. Forest fragments

Few studies have investigated the impacts of fragmentation on non-primate mammals. Tenrec species richness across fragments at Ambohitantely ranging from 0.64 to 1250 ha showed a nested distribution as a function of forest area. Several forest-dwelling tenrecs known from nearby Anjozorobe Forest, with similar vegetation and forested areas exceeding 5600 ha, were absent, indicating that fragments of 1250 ha already show impacts of fragmentation (Goodman and Rakotondravony, 2000; Olson et al., 2004).

In eastern littoral forests, Ganzhorn et al. (2000b) found that small mammal species richness doesn't decline with fragment size. However, interpretation is complicated: the largest remaining fragment is <500 ha, species' densities are low, and the small mammal fauna is depauperate. In western deciduous forests, Ganzhorn et al. (1996, 2003), and Ganzhorn (2003) showed that most small mammals are not forest-restricted; exceptions were the 1 kg rodent *Hypogeomys antimena*, unknown in forests smaller than

Table 2
Differential impacts of proximate drivers of species declines and losses across taxonomic groups in human-modified forests in Madagascar.

Taxonomic group	Habitat loss causes extinction of range-restricted species by destroying entire range habitat?	Habitat fragmentation: negative effects of decreasing fragment size/increasing isolation on local species richness?	Forest disturbance/edge effects: negative impacts on species richness?	Changes in hydrology (proximity to water for terrestrial taxa, water quality for aquatic taxa) negatively impact species?	Exotic/introduced species contributing to native species decline/loss?	Hunting/collecting contributing to species decline/loss?	Time lag (“extinction debt”) due to long generation times?	Region where taxa are most threatened by forest modification
Plants	?	?	++	?	++	++	+++	?
Terrestrial invertebrates	+++	+	+	?	(+)	–	–	?
Aquatic insects	+++	? ^a	+++ (via microclimate in water)	+++	?	–	–	Rainforest
Fishes	++	? ^a	+++ (via microclimate in water)	+++	+++	+	–	?
Reptiles and amphibians	?	++	++ (although some species increase)	+++ (documented for amphibians, not well known for reptiles)	–	++	–	Rainforest, dry forest
Birds	?	++	++	+++	+ (mostly threatening waterbirds)	+	–	?
Primates	–	+++	++ (although some species increase)	?	–	++	+++	?
Other mammals	–	++	?	?	+ (<i>Rattus</i>)	++	+	?

+ = detectable impacts.

++ = important impacts.

+++ = a primary driver of species loss.

(+) = impact present but magnitude not yet appreciated.

– = little or no impact.

? = unknown.

n/a = not applicable.

^a For aquatic taxa, we use “fragmentation” to refer to modification of watersheds in ways that subdivide once-mixing populations (e.g. lowland deforestation can isolate multiple populations of forest-dependent taxa upstream).

Table 3
Summary of studies assessing vertebrate species richness in undisturbed and nearby, disturbed forests in Madagascar.^a

Taxonomic group	Species richness in:							Site (ecoregion)	References	
	Undisturbed forest	Disturbed forest	Fragmented, disturbed forest	Burned forest	Secondary vegetation	Plantation	Grass-land			Rice field
Reptiles and amphibians	51		6–47						Mandena and Sainte Luce (East, Littoral)	Ramanamanjato (2000)
Amphibians	26		9–18				6		Ambohitantely (Central, subhumid forest)	Vallan (2000)
Reptiles	21 and 30	22	17						Kirindy CFPF (West, dry forest)	Penner (2005)
Amphibians	66				35	31		8	Andasibe (East, humid forest)	Vallan (2002)
Amphibians	39	40							An'Ala (East, humid forest)	Vallan et al. (2004)
Chameleons	6	5							Anjozorobe (East, humid forest)	Jenkins et al. (2003)
Lizards	13						7		Behara (Southwest, semi-arid forest)	Scott et al. (2006)
Amphibians	10 and 13	5–9							Menabe (West, dry forest)	Glos et al. (2008a–c)
Birds	54		5–23						Ranomafana (East, humid forest)	Raherilalao (2001)
Birds	62	44					29		Sainte Luce (East, littoral humid forest)	Watson et al. (2004)
Birds	23		5–16						Ambohitantely (Central)	Langrand and Wilmé (1997)
Birds	14.7	14.6							Kirindy CFPF (West, dry forest)	Hawkins and Wilmé (1996)
Birds	31			38			21		Ankarafantsika (West, dry forest)	Pons and Wendenburg (2005)
Lemurs	12		3–9						Ranomafana (East, humid forest)	Ganzhorn et al. (2003)
Lemurs	10		0–8						Tsinjoarivo (East/Central, humid forest)	Irwin (2008a,b)
Lemurs	8		0–7						Menabe (West, dry forest)	Ganzhorn et al. (2003)
Lemurs	6		2–6						Mandena (East, littoral humid forest)	Ganzhorn et al. (2000b)
Small mammals	5						3		Behara (Southwest, semi-arid forest)	Scott et al. (2006)
Tenrecs	9		2–7						Ambohitantely (Central, subhumid forest)	Goodman and Rakotondravony (2000)

^a Comparisons across groups and regions should be made with caution, because studies vary greatly in: (1) operational definitions of disturbance, (2) degrees of disturbance of habitats sampled, (3) methods used to measure species richness.

10,000 ha, and *Macrotarsomys bastardi*, not known from forests smaller than 600 ha.

7.2.1. Disturbed natural forests

The vast majority of animals considered here are classified as strict natural forest inhabitants, yet there are conflicting interpretations of the level of disturbance species can tolerate. Amongst carnivorans, certain taxa with large home ranges, such as *Cryptoprocta ferox*, occur in disturbed forests and move across anthropogenic formations (Hawkins, 1998; Irwin et al., 2009). The specialized shrew–tenrec *Microgale gracilis* has been considered restricted to undisturbed montane forest, but was found at the ecotone between native tree and pine plantations (Goodman et al., 1996). Disturbed forests at Tsinjoarivo hold at least 24 tenrec and nesomyid species (Goodman et al., 2000), one of the highest totals in Madagascar. In humid forests at Ranomafana, native rodent species show no marked differences between different degrees of disturbance (Lehtonen et al., 2001). Finally, the rodent *Eliurus webbi* seems to be restricted to natural forest fragments larger than 28 ha in southeastern littoral forests (Ramanamanjato and Ganzhorn, 2001), yet in littoral forest farther north, it was captured in a zone with mixed exotic and native trees (Rakotondravony et al., 1998). Invasive *Rattus* may negatively impact native rodents, but evidence for this is mixed (Ganzhorn, 2003).

7.2.2. Non-natural habitats

Very few non-volant, non-primate mammals live in these formations. Most species of Tenrecinae are abundant in anthropogenic grassland; several can even be found in cities (Goodman et al., 2008). Certain species of Oryzoricinae, such as *Microgale cowani* or *M. brevicaudata*, occur in secondary forests or open grasslands. Amongst carnivorans, *Galidia elegans* occurs in secondary habitats, at forest edges, and in exotic tree plantations near native forest (Goodman, 2003, unpublished).

In conclusion, the previous axiom that most species are restricted to intact forest seems to be not an exclusive rule. However, most species need natural forest, although many are tolerant of a certain level of anthropogenic degradation. Natural disasters, such as cyclones or fires, are a natural aspect of the environment; perhaps the adaptations of certain taxa are partially associated with such events. Finally, there is strong evidence of community nestedness in fragments; thus, protecting fragments large enough to preserve complete communities (and recognizing that minimum viable fragment size differs amongst mammalian groups) will be critical for long-term conservation goals (Ganzhorn et al., 2003).

8. Conclusions

We draw five main conclusions from this review. First, species' responses to anthropogenic disturbance are poorly known. Our knowledge remains patchy among and within higher taxonomic groups; we consider it too early to draw meaningful comparisons across taxonomic groups or ecoregions. Second, the proximate drivers of species change vary considerably across taxonomic groups (Table 2). Third, several groups show differing responses across ecoregions; whether these differences are consistent across groups awaits further testing. Fourth, related species often have divergent reactions, even within lower taxonomic groupings (families or genera). Thus, we cannot rely on phylogenetic relatedness or broad ecological similarity to infer similar responses. Finally, disturbance typically reduces species diversity (especially of native and/or endemic species) (Table 3), but also causes species turnover, typically with forest specialists replaced by grassland generalists, and endemics replaced by non-endemics (including invasives). Overall diversity increased in one study, in burned forest (Pons

and Wendenburg, 2005), but this reflects species turnover, with forest specialists replaced by grassland generalists, and endemics replaced by non-endemics.

Future research is essential for seeking whatever generalizations are possible, especially: which natural habitat types are most prone to disturbance and/or most slow to recover, which human-modified landscapes (e.g. plantations, secondary forest, disturbed primary forest, grassland) have the most conservation potential, and which proximate mechanisms of extirpation are most important. We especially need studies that more finely differentiate between types and levels of disturbance. We stress the urgency of applied studies which assess species' ecology, behaviour and health across disturbance gradients, including purely anthropogenic landscapes. Applied studies that help us preserve wild populations will buy time to pursue more "pure" research in the future; the reverse is not necessarily true.

Finally, we must remember that remaining natural vegetation and protected areas (~6 million ha in 2008) will be unable to preserve their biodiversity under the impact of shifting ecozones due to climatic change (Hannah et al., 2008; Kremen et al., 2008). Therefore it is important to understand responses of native plants and animals to disturbance in order to create buffer zones and corridors combining secondary and natural habitats.

In general, conservation actions must address the overwhelming threats of habitat loss and high-level disturbance, by assuring the stability of protected areas and by defining new protected areas. These should be based on high overall diversity and otherwise high conservation interest (Kremen et al., 2008; Wilmé et al., 2006), and should consider abiotic factors that research determines are important to individual groups (e.g., considering the importance of hydrology for birds). The results presented here underscore important differences among groups. For microendemic taxa (plants, insects), small habitat patches and secondary habitats may be valuable components of conservation strategies. Long-lived species (primates) require more habitat, but also illustrate the problem of short-term inventories. Many populations in disturbed habitats may represent non-viable populations; disturbed habitat populations may be remnants, or (when adjacent to undisturbed habitats) sustained only by immigration (source-sink dynamics). If true, this alters their conservation value. Effective conservation in Madagascar will require a broader approach considering these and other key differences between taxonomic groups and ecoregions (Gardner, 2009; Gardner et al., 2009).

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