A review of the impacts of anthropogenic habitat change on terrestrial biodiversity in Madagascar: Implications for the design and management of new protected areas

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Abstract

Madagascar's recently established protected areas seek to contribute to both conservation and development objectives. They comprise mainly multiple-use protected areas in which a range of human activities are permitted, hence the impacts of forest use on biodiversity must be understood if such sites are to be designed and managed to minimize biodiversity loss. Here a review is conducted of the literature on the impacts of habitat change on Malagasy terrestrial biodiversity, and the associated range of responses of terrestrial taxa to habitat change are analyzed. Habitat change may lead to increases or decreases in species richness or abundance in the short term, but the use of measures of species richness alone may mask a turnover of taxa from specialists to generalists and from endemic to non-endemic. Dry forest species and communities may be less sensitive to habitat change than those of humid forests, and biodiversity impacts appear to follow a gradient of management intensity, with selective logging and edge effects having less impact on faunal communities than secondary forests and plantations. Priorities for future research are suggested and the implications of existing research for protected area management (including zoning, the choice of management objectives, target viability analyses and monitoring) are discussed. Although new protected areas provide complementary conservation services to the existing network of strict protected areas, the latter may be essential for the long-term maintenance of high priority endemic taxa.

Key words: biodiversity, degradation, SAPM, multiple-use protected areas, endemism

Résumé détaillé

Depuis 2003, Madagascar s'engage à mettre en place une nouvelle génération d'aires protégées, un processus émanant de la « Vision Durban ». Les aires protégées de la première génération sont gérées principalement dans le but de conserver la biodiversité, mais les nouvelles aires protégées ont plusieurs objectifs, dont conserver la biodiversité, conserver le patrimoine culturel, et favoriser l'utilisation durable des ressources naturelles pour la réduction de la pauvreté. La plupart des nouvelles aires protégées sont cogérées par des associations communautaires, et renferment des zones d'utilisation durable de plusieurs types ; ces forêts vont alors continuer à subir des impacts anthropiques. Ceci étant, la réussite de la conservation de la biodiversité dans ces habitats modifiés par l'action de l'homme nécessite l'évaluation scientifique des impacts de l'utilisation des ressources forestières sur la biodiversité terrestre, et l'utilisation des données qui en résultent pour mieux planifier et gérer les aires protégées.

Une revue de la littérature sur les impacts de la modification des habitats sur la biodiversité à Madagascar a été rédigée; 52 études sur l'impact de la coupe sélective, les feux, l'effet de la lisière et le pâturage, ainsi que la valeur des habitats anthropiques tels que les forêts secondaires et les plantations pour la biodiversité, ont été trouvés. L'impact de la modification des habitats varie selon le taxon étudié, le type de pression étudié et la région phytogéographique de l'étude, mais il est difficile d'en tirer des conclusions à cause des différences en termes de méthodologie entre les études. La richesse spécifique d'une forêt peut augmenter ou diminuer après un changement, mais l'utilisation des mesures de richesse peut cacher un changement dans la composition de la communauté ; en général, les espèces les plus spécialisées sont remplacées par les espèces généralistes, et les espèces endémiques sont remplacées par les espèces non endémiques suite à la dégradation de l'habitat. Les résultats indiquent que les types d'utilisation forestière les moins intensives, tels que la coupe sélective, ont moins d'impact sur la biodiversité que les grandes changements des habitats tels que la création des plantations.

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Tous les types d'impact ont des effets similaires sur la structure de la forêt ; il s'agit principalement de l'ouverture de la canopée et une augmentation de la densité du sous-bois. Il est possible que les espèces des forêts sèches soient moins sensibles à la dégradation que les espèces des forêts humides, mais les résultats des études existantes ne sont pas suffisantes pour pouvoir confirmer cette hypothèse. La plupart des études ont été réalisés à court terme et ne sont donc pas capable de démontrer si les espèces se trouvant dans les forêts dégradées sont capables de survivre à long terme dans ces habitats. Cette revue met en relief quelques lacunes dans les recherches antérieures ; l'impact du pâturage et de la collecte de bois mort est peu connu, l'impact de la dégradation sur les invertébrés n'est pas assez étudié, et très peu de recherche a été faite dans le domaine phytogéographique du Sud.

Les données issues des recherches sur l'impact de la dégradation sur la biodiversité peut informer la planification et la gestion des nouvelles aires protégées : Il est nécessaire que l'aménagement des sites soit planifié au niveau du paysage pour assurer la connectivité des blocs forestiers peu touchés par l'action humaine, et que les gestionnaires des aires protégées tiennent compte de la sensibilité à la dégradation des espèces phares. De plus, le suivi de l'efficacité de la gestion s'avère crucial pour assurer que la biodiversité ne subit pas des impacts négatifs à cause de l'utilisation de la forêt, mais le suivi doit concerner les espèces indicatrices qui sont sensibles à la dégradation. Des programmes de recherche sont essentiels pour identifier des synergies entre la conservation de la biodiversité et l'utilisation de la forêt à des fins de subsistance, et pour identifier le niveau d'utilisation qu'on pourra permettre sans avoir trop d'effets négatifs sur la biodiversité. En conclusion, la création des nouvelles aires protégées va diminuer le taux de défrichement national et contribuera fortement à la conservation de la biodiversité ; cependant, les Parcs Nationaux resteront essentiels pour la conservation des espèces sensibles à la dégradation, qui sont normalement les espèces phares pour la conservation.

Mots clés : biodiversité, dégradation, SAPM, aires protégées, endémisme

Introduction

Read almost any article on biodiversity or conservation in Madagascar and the introductory paragraphs will highlight the extraordinary rates of deforestation suffered throughout the island in recent decades. While deforestation is one of the principal causes of terrestrial biodiversity loss in Madagascar, there has been comparatively little focus on the parallel process of anthropogenic habitat change or degradation, i.e. changes to forest structure other than outright destruction. An understanding of the impacts of natural and anthropogenic habitat change on Madagascar's biodiversity is important given recent changes in the country's conservation politic, particularly with regards to the creation and management of new protected areas.

The first generation of protected areas in Madagascar are managed by the para-statal Madagascar National Parks (formerly ANGAP) in accordance with IUCN Categories I, II and IV, which represent the strictest protected area categories in terms of permitted uses (IUCN, 1994; Dudley & Phillips, 2006). These protected areas are managed principally for biodiversity conservation alongside research and recreation in some categories (Randrianandianina *et al*., 2003). The management and use of these protected areas are strictly regulated within national legislation - the Code de Gestion des Aires Protégées or COAP (Government of Madagascar, 2001), which forbids, among other activities, the destruction or collection of plants in all protected area categories (Article 41). Article 11 of the COAP states that the "valorisation of biodiversity will be achieved primarily through research and ecotourism" (author's translation from the original French) and, by implication, not through the extractive use of natural resources.

Following the launch of the Durban Vision (Ravalomanana, 2003), which entails the tripling of national protected area coverage from 1.7 to 6 million ha by 2012 (Mittermeier *et al*., 2005; Norris, 2006), a new generation of protected areas have been and are being established to form (alongside the Madagascar National Parks network), the Système d'Aires Protégées de Madagascar (Madagascar Protected Area System or SAPM). The three principal objectives of SAPM are to (author's translation from the original French):

1) Conserve the whole of Madagascar's unique biodiversity (ecosystems, species, genetic diversity),
2) Conserve Madagascar's cultural heritage,
3) Promote sustainable use for development and poverty alleviation (Groupe Vision Durban, 2006).

In accordance with SAPM's multiple objectives, all of the new Durban Vision protected areas that will be established by actors other than Madagascar National Parks are managed as IUCN categories III, V and VI and contain significant areas of sustainable use zones in various forms (up to 75% of their surface area, Pollini, 2007). Such protected areas, many of which are co-managed by local community associations (Raik, 2007), seek not only to conserve Madagascar's unique biodiversity but also to maintain and enhance the material well being of the communities surrounding them (see Gardner *et al*., 2008), or at least to avoid or mitigate any negative impacts (Government of Madagascar, 2006). The multiple objectives of both SAPM and individual protected areas are seen as vital to long-term protected area sustainability given the extent to which rural communities throughout Madagascar depend upon forest products and services for their survival; in the south-west, for example, 97% of households near Analavelona and 84% of households near Zombitse depend upon forest products for their subsistence and household income (Rabesahala Horning, 2003).

At first glance, the objectives of conserving biodiversity and promoting rural development could be considered as potentially conflicting: such development often depends on the extractive use of natural resources, which necessarily entails some habitat modification. If potential conflicts between management objectives are to be minimized and protected areas are to contribute to the goals of diverse stakeholders, it is vital that conservation practitioners, at least in part based on previous research, understand the impacts of anthropogenic habitat change on Malagasy biodiversity. The principal objective of this paper is to review the existing literature on the impacts of anthropogenic habitat change on biodiversity in Madagascar and to explore the implications of this information for conservation in general, and the design and management of new protected areas in particular. The review thereby aims to help bridge the research-implementation gap that is prevalent in conservation biology (Knight *et al.*, 2008).

Materials and Methods

Madagascar was first colonized by people approximately 2300 years before the present (BP): multiple lines of evidence suggest that their impact on natural environments was large, and includes the decline and eventual disappearance of the megafauna from around 1700 BP, followed by the extensive conversion of habitats (through fire) starting in the southwest and spreading to other coasts and the highlands (Burney *et al.*, 2004). Anthropogenic habitat change therefore has a long history on the island: it is defined herein as the modification of natural habitat structure arising from a suite of human activities including selective logging, fire, the creation of paths and the grazing of livestock. Also included within the scope of this review are other types of altered or artificial habitat such as secondary forests regenerating after clearance and plantation forests, but research into the impacts of outright forest clearance rather than degradation (e.g. Benstead *et al*. 2003; Scott *et al*., 2006), or research carried out within agricultural landscapes (e.g. Martin *et al.*, 2009) is not included. The impacts of habitat fragmentation have been reviewed elsewhere (e.g., Goodman & Raherilalao, 2003; Ganzhorn *et al*., 2003) and research focused on the effects of patch size and isolation (e.g., Andrianarimisa *et al*., 2000; Goodman & Rakotondravony, 2000; Raherilalao, 2001; Rakotondravony, 2007) will not be treated here. Edge effects, however, can be seen as functionally analogous to the types of habitat change listed above and so research that explicitly investigates these effects is reviewed herein.

No formal methodology was used to select publications and certain elements may have been missed. Because of the non-random sampling of the literature, it is not possible to analyze statistically trends in the existing research. The literature reviewed investigates a wide-range of anthropogenic impacts on different taxa within almost all vegetation domains in Madagascar. Because different methods are employed in each study, a formal meta-analysis is not possible. Much of the literature reviewed was published prior to recent revisions and nomenclatural changes of focal taxa; the original names from the cited publications are reproduced here, and updated names are provided in cases where the identity of the taxon has changed or is unambiguous. Trends in the research are analyzed by focal taxon, type of habitat modification and geographic distribution: in the latter analysis, the reviewed articles are grouped using Humbert's (1955) phytogeographic model because it is not always possible, from the information provided therein, to assign each paper to categories used in more detailed classification systems (e.g. Moat & Smith, 2007).

Analysis of impacts

For research papers in which the data were explicit, the impact of habitat change on species, species-groups or faunal communities was classified into three categories, as defined below:

Positive impact – the focal species/community demonstrates either an increase in abundance/density or species richness within modified habitats in comparison to control sites.

Negative impact – the focal species/community demonstrates either a decrease in abundance/density or species richness within modified habitats in comparison to control sites.

Neutral or mixed impact – A neutral impact is defined as no measurable change in either abundance/density or species richness between modified and control habitats. Research is classified as demonstrating a mixed impact when a) a study demonstrated an increase in abundance but a decrease in species richness, or vice versa, or b) when approximately equal numbers of species were found to benefit from habitat change as were found to be negatively impacted.

Results

Trends based on published research

I found, or found reference to, 52 papers investigating the impacts of anthropogenic habitat change on Madagascar's terrestrial biodiversity, see Figures 1-3 (note that the number of papers in these figures do not add up to 52 because some papers deal with multiple taxa, phytogeographic domains or types of impact). In terms of focal taxa, lemurs (18 papers), birds (13), terrestrial small mammals (9), reptiles (5) and amphibians (5) have received the most research effort. Comparatively little research has been carried out into the impact of habitat change on bats (2 papers), invertebrates (1) and vegetation (3), although a number of faunal studies also measure or otherwise note changes to vegetation structure.

In terms of the type of impact or habitat degradation studied, most of the papers reviewed here investigate the impacts of selective logging (17 papers), edge effects (15), secondary forests (13), general degradation (6) and fire (5). Two papers investigate the value of plantation forests for indigenous vertebrate fauna, while one paper investigates the impact of grazing.

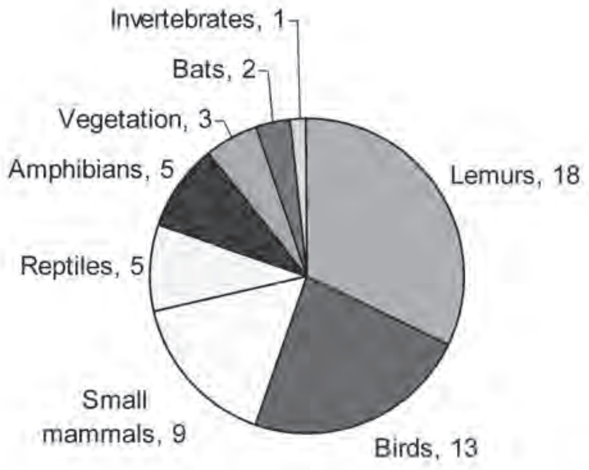

Figure 1. Number of reviewed papers by focal taxon.

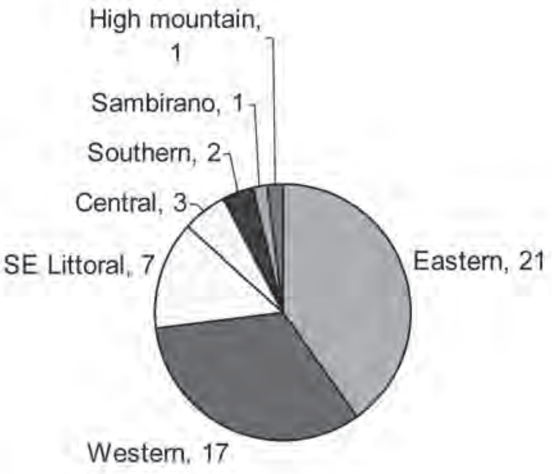

Figure 2. Number of reviewed papers by phytogeographic domain.

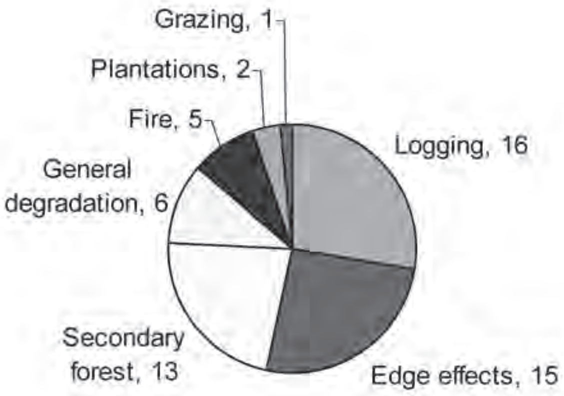

Figure 3. Number of reviewed papers by type of habitat change.

Grouping the research by Humbert's (1955) phytogeographic domains (but separating the southeast littoral forests as an entity because they have received so much attention in their own right), we see that the humid eastern domain (21 papers), the dry western domain (17) and the southeast littoral forests (7) have all received significant research effort. The central domain, with little remaining forest, has been the subject of three research papers, while the southern domain (2), the Sambirano (1) and the high mountain domain (1) are under-represented in terms of current research.

Review of the Literature

Birds

Community impacts

In Ankarafantsika, Pons & Wendenburg (2005) found that species richness and abundance, based on point count data, were higher in secondary regrowth after fire than in unburned natural forest, at least in the short-term. Secondary forests contain all the same species present in unburned forest, as well as an additional ten understory species. By creating an index of conservation value based on endemism, abundance and threatened status, these authors found that the conservation value of secondary forests was higher than that of unburned forests. Andrianarimisa (1992) also found an increase in species richness in secondary and selectively logged forests compared to non-degraded forests, noting that these habitats occur in a mosaic pattern on the landscape scale, thereby increasing habitat structural complexity and providing a greater number of niches for birds. Woog *et al*. (2006) found a higher species richness in forest edges than in the forest interior or agricultural matrix habitats within the Maromiza forest, due to the presence of species typical of open habitats at the forest edge. These authors, however, do not appear to have controlled for survey effort between habitat types.

Watson *et al*. (2004a) working in the southeast littoral forest, found significantly higher numbers of species within the forest interior compared to forest edge and secondary matrix habitats (primarily *Erica* scrub), although total bird abundance between forest interior and forest edge was similar. Of the 45 species recorded only in forest or forest edge, 68% were found to be edge-sensitive or intolerant. On the other hand, other research found no significant change in bird communities following habitat change. In the selectively logged dry forest of Kirindy/CFPF, Hawkins & Wilmé (1996) found no significant change in the number of species or number of individuals between selectively logged and unlogged forest areas, speculating that this may be due to the absence of rarer species from transects or the general absence of disturbance-sensitive guilds from the Kirindy/CFPF forest. Pons *et al*. (2003a) also found similar species diversity and abundance in both forest and matrix habitats immediately following a fire in the dry forest of Ankarafantsika.

Finally, Goodman *et al*. (1996) compared the bird communities of a mature plantation of indigenous *Weinmannia bojeriana* on the Ankaratra Massif with humid forests from the same altitudinal band in Anjanaharibe-Sud and Andohahela (parcel 1). They found the bird communities to be "more-or-less similar" between the three sites in terms of species richness, although the Andohahela community included a greater proportion of forest-dwelling species. The plantation community, however, appeared to be depauperate in endemic taxa (with only 12 endemic species observed), and particularly those endemic at higher taxonomic levels; no members of the Brachypteraciidae, Mesitornithidae, Couinae or Philepittinae were recorded, and only one endemic genus (*Newtonia*) was observed. The Ankaratra plantation was also depauperate in birds restricted to higher elevational zones, being populated mainly by altitudinal generalists.

Impact on foraging guilds

Several researchers have demonstrated that the sensitivity of birds to habitat degradation is related to a given species' foraging behavior, and that the relative abundance of foraging guilds therefore differs in habitats of varying quality or structure. In Ankarafantsika, Pons & Wendenburg (2005) found that both degraded and non-degraded forests are dominated by canopy and understory insectivores, followed by frugivores and aerial feeders. Further, after such zones were converted to savanna, granivores and aerial insectivores dominated the bird community. At the same site, Andrianarimisa (1992) found that granivores, frugivores, understory insectivores and aerial insectivores increase in abundance in degraded forests, while terrestrial insectivores decrease in abundance.

In the southeast littoral forest, Watson *et al*. (2004a) found all frugivore species to be edge-sensitive, as well as 88% of canopy insectivores, 46% of terrestrial insectivores and 25% of understory insectivores. Granivorous species and raptors, on the other hand, were found to be more abundant within the non-forest matrix or at the forest edge. Watson *et al*. (2004b) report similar results in an investigation of bird responses to habitat fragmentation, finding that canopy insectivores and large canopy frugivores are the most sensitive guilds to reduction in fragment size. Goodman *et al*. (1996) note the relative scarcity of insectivores and the relative over-representation of raptors within plantation forests at Ankaratra. Finally, Langrand & Wilmé (1997) note a decrease in understory and canopy insectivores and nectarivores from the smallest patches at Ambohitantely. These findings correspond closely to those of Gray *et al*. (2007) in a global review of foraging guild responses to habitat disturbance, indicating that the Malagasy avifauna does not respond differently to that of other tropical regions.

Endemic and non-endemic species

Wilmé (1996) states that "*the tolerance of the endemic forest avifauna to forest degradation is proportional to its degree of taxonomic endemism*", finding that of 32 endemic forest bird genera, 27 do not occur in secondary forests or anthropogenic grasslands (although some may occur in lightly degraded habitats). The literature reviewed here, much of it published after Wilmé's (1996) review, finds mixed support for this statement, although there is a clear geographical and taxonomic bias in the existing research.

Four studies directly investigated the response of individual endemic species or guilds to habitat modification, although a number of studies of bird communities also note the response of individual species or provide some insight into differential effects on endemic and non-endemic species. All of the studies in the former category focus on a suite of medium-sized, dry forest, terrestrial insectivores that are endemic at higher taxonomic levels. Hawkins (1991, 1993, 1994, cited in Chouteau *et al*., 2004) found that *Mesitornis variegata* benefits from an increase in the density of the shrub layer following logging, which provides increased cover from predation and heat, and an increase in potential nest sites. Likewise, Seddon & Tobias (2007) found that *Uratelornis chimaera* nesting density is greater in lower stature or degraded habitats, and that pairs will preferentially nest alongside a path or clearing if available in their territory. This is in contrast to the sympatric *Monias benschi*, which avoid more degraded habitats (Seddon *et al*., 2003). In studies of *Coua* spp. in Kirindy/CFPF (Chouteau, 2004) and Ankarafantsika (Chouteau *et al.*, 2004), species responses were found to vary according to the taxon in question and type of habitat change. In Kirindy/CFPF, *C. coquereli* density increased but *C. gigas* density decreased significantly in selectively logged forest; the former species prefers denser understory vegetation, which probably increases prey availability and cover from predators (Chouteau, 2004). In Ankarafantsika, however, *C. coquereli* is less abundant in once-burned forest than in unburned areas, in contrast to *C. ruficeps*, which is more abundant in once-burned forest and occurs in twice-burned areas (Chouteau *et al*., 2004). Hawkins & Wilmé (1996) also found *C. coquereli* to be more abundant in logged areas in Kirindy/CFPF, where *Schetba rufa* was the only species with a significant negative response to logging.

Of the 12 species belonging to endemic or near-endemic families and sub-families in Pons & Wendenburg's (2005) study in Ankarafantsika, two were more common in unburned forests (*Coua ruficeps* (in contrast to Chouteau *et al*., 2004) and *Vanga curvirostris*), one was more common in regenerating forests (*Leptopterus chabert*) and the rest showed no significant change. Also in Ankarafantsika, Andrianarimisa (1993, cited in Pons *et al*., 2003a) found that non-endemic birds increase in relative abundance in degraded forests.

Notably less research has been carried out on birds in humid forests than in the dry forests. In a study of fragmentation in Ambohitantely, Langrand & Wilmé (1997) found five species to be significant edge avoiders (*Atelornis pittoides, Phyllastrephus* [=*Bernieria*] *madagascariensis, Newtonia amphichroa, Calicalicus madagascariensis* and *Foudia omissa*); of these all are endemic, two belong to endemic families, one belongs to a near-endemic family and a fourth belongs to an endemic genus. While Watson *et al*. (2004a) did not analyze their data by endemism, they do note that *F*. *omissa* is an edge-tolerant species in littoral forest fragments, in contrast to the situation at Ambohitantely where this species is an edge-avoider (Langrand, 1994; Langrand & Wilmé, 1997). These results therefore indicate that the same species may respond differently to edge effects in different habitats.

Reptiles and amphibians

Jenkins *et al*. (2003) measured chameleon density in low-disturbance (selectively logged) and high-disturbance (regenerating) forests in the Anjozorobe forest site of Andranomay, as well as in riparian areas (which do not provide a comparable control). Of the four *Calumma* and two *Brookesia* species present at the study site, only *B. minima* was absent from forests regenerating after fire, while three of the four *Calumma* species were significantly more abundant in low-disturbance than in high disturbance forest. Metcalf *et al*. (2005) measured the edge effect from forest paths on chameleon abundance in Ankarafantsika, and found both *Furcifer oustaleti* and *F. rhinoceratus* to occur at significantly greater densities with increasing proximity to paths. This result is similar to that of Jenkins *et al*. (1999), who found *C. brevicornis* and *B. nasus* to occur at higher densities along well-established forest paths than in randomly placed transects within the forest interior. The only non genus-specific reptile study was carried out in Kirindy/CFPF, where Bloxam *et al*. (1996) found selective logging to have no significant effects on either species composition or abundance. These authors speculate, however, that logging may diminish habitat suitability for older individuals of the tortoise *Pyxis planicauda*, due to age-related color variation; older individuals, who are darker, are more likely to be found under a dense canopy.

Amongst research into frog communities, Vallan *et al*. (2004) found that selective logging has no significant impact on amphibian abundance or species richness in the An'Ala forest, but noted a marked shift in community composition from specialist to generalist species; terrestrial species (Mantellinae) were scarcer and arboreal species (Boophinae and Cophylinae) were more abundant, in logged compared to unlogged forests. A similar result was found by Andreone (1994) in Ranomafana, where he studied frog communities in undisturbed forests and a range of different degraded habitats (such as roadsides and banana plantations). This author found a higher proportion of arboreal species and a lower proportion of terrestrial species in degraded forests compared to non-degraded areas, with no indication of a difference in species richness: of the 40 species he recorded, 27.5% were restricted to non-degraded forests, 22.5% were restricted to degraded areas and 50% occurred in both habitat types. In a study on fragmentation at Ambohitantely, Vallan (2000) also found differences in disturbance-sensitivity (in this case edge effects) related to life-history: species which do not live in water (most microhylids, *Mantidactylus malagasius*, *M. aglavei*) were absent in small fragments due to the greater relative influence of edge effects, while stream-dwelling species were not affected.

Vallan (2002) studied frog communities in relatively undisturbed forest, secondary forest, *Eucalyptus* plantations and rice-fields near Andasibe, and found significant differences in species richness between habitat types; secondary forests harbor only 54%, plantations 46% and rice-fields 12% of the total number of species recorded in relatively undisturbed forests. Habitat preferences were found to reflect taxonomy, with the Hyperoliidae and Raninae [= Ptychadenidae] occurring only in rice fields, and the Mantellinae, Microhylidae and the genus *Boophis* being more species rich in relatively undisturbed forests.

Lehtinen *et al*. (2003) researched the impacts of edge effects on reptile and amphibian communities in littoral forest fragments of the southeast, and found strong seasonal differences in edge-sensitivity. All frogs were found to be significant edge-avoiders during the dry season, but during the rainy season a mix of responses were recorded, with one species (*Mantidactylus boulengeri*) being an edge-avoider, one being an interior-avoider (*Heterixalus boettgeri*) and the others showing non-significant differences in distribution. Among reptiles, three species (*Mabuya* [=*Trachylepis*] *elegans*, *Phelsuma lineata* and *Geckolepis maculata*) were interior-avoiders and none were edge-avoiders during the wet season. These authors also found a significant correlation between the strength of edge-avoidance and extinction risk, although this was non-significant when only reptiles were considered.

Small mammals

A series of papers by Ganzhorn and co-workers have investigated the effects of selective logging, habitat fragmentation and the introduced *Rattus rattus* on endemic small mammals in the forests of Kirindy/CFPF and the littoral forests of the southeast. Based on knowledge of the species' ecological requirements, Ganzhorn *et al*. (1996) hypothesize that selective logging would favor *Mus musculus*, *Suncus madagascariensis* and *Geogale aurita*, but would reduce habitat quality of the spiny tenrecs (Tenrecinae) *Tenrec ecaudatus*, *Setifer setosus* and *Echinops telfairi*. Trapping results, however, show no significant effect of logging on either *S. setosus* or *T. ecaudatus*. Similarly, Ganzhorn *et al*. (1990) found that selective logging has no impact on the density of *T. ecaudatus* but does slightly impair habitat quality for *E. telfairi*. All of the spiny tenrec species mentioned above are known to be tolerant of habitat degradation and anthropogenic environments (Nicoll & Rathbun, 1990; Ganzhorn *et al*., 2003).

Ganzhorn and colleagues investigated the effects of fragmentation and different habitat types on endemic rodents in the forests of Kirindy/CFPF

(Ganzhorn, 2003) and the southeast littoral forests (Ramanamanjato & Ganzhorn, 2001). In Kirindy/CFPF, *Macrotarsomys bastardi* was not captured outside of relatively intact forests, but *Eliurus* spp. occurred in all forest types (including secondary forests dominated by the invasive *Ziziphus mauritiana*) that occurred within 50 m of the ecotone with relatively undisturbed forest (Ganzhorn, 2003). *Eliurus webbi* was not captured outside of the least disturbed littoral forest fragments (Ramanamanjato & Ganzhorn, 2001).

Amongst studies carried out within humid forest ecosystems, Lehtonen *et al*. (2001) investigated the density of rodents across a gradient of habitat degradation from intact forest to heavily logged forest and secondary scrub. They found that all five endemic rodent species occur in relatively undisturbed and secondary forest, but that *Mus musculus* is limited to secondary forest. The total number of endemic rodents was higher in relatively undisturbed than in secondary forest. *Nesomys rufus* was most abundant in selectively logged forest but was absent from secondary scrub, while *N. audeberti* was most abundant in heavily logged forest and was also absent from secondary scrub. All three *Eliurus* spp. occurred in heavily logged forest. While no species was most abundant in the relatively undisturbed forest areas, heavily modified habitats were inhospitable for all endemic species except *E. tanala*. Low-intensity selective logging was found to have little effect on the native rodent fauna, but high-intensity logging was associated with the loss of endemic species.

Stephenson (1993) compared small mammal abundance between three relatively undisturbed forest sites and one site in secondary forest in Analamazaotra. The greatest species richness was found in the least disturbed site, to which four species were restricted, but this site had the lowest total abundance of individuals. The lowest species richness was recorded from a site heavily impacted by tourism, and two species were only recorded from secondary forest. Stephenson (1995) also investigated small mammal abundance in relatively undisturbed forest and logged secondary forest at Andranivola, in the northeast. Here endemic species richness was found to be higher in relatively undisturbed forest, and two species (*Microgale talazaci* and *Eliurus webbi*) were found to be significantly more abundant in this habitat than in secondary forest. Three endemic species (*Oryzorictes hova*, *M. pulla* [=*parvula*] and *Nesomys rufus*) were not recorded in secondary forest, while *Hemicentetes semispinosus*, and the introduced *Rattus rattus* and *Suncus murinus* were not trapped in relatively undisturbed forest.

Rasolonandrasana & Goodman (2006) compared small mammal faunas in an area of recently burned forest with an adjacent control site in the upper elevational sclerophyllous forest of Andringitra. They found that *Eliurus minor* and *Nesomys rufus* did not recolonize burned areas after three years, but in this area, these species are at the limit of their altitudinal range and occur naturally at low densities. In contrast, *Microgale longicaudata* and *M. fotsifotsy* were more abundant in the burned area, while no significant differences were found between the abundance of *M. cowani*, *M. dobsoni* and *Monticolomys koopmani* in burned and unburned areas. When introduced rodents were excluded, the burned area had a lower total rodent density than the control site. Finally, Goodman *et al*. (1996) investigated small mammal presence and density in a plantation forest of native trees at Ankaratra and compared the observed fauna to that of other sites. They found no significant differences in the species richness and abundance of Lipotyphla [=Afrosoricida] between the plantation and natural forests in Anjanaharibe-Sud, although relative density of endemic rodents was significantly lower within plantations than in natural forests in other areas.

Effects of introduced species

Compared to other taxa, research into the tolerance of endemic small mammals to habitat degradation is confounded by the presence of introduced invasive species (e.g. *Rattus rattus* and *Mus musculus*) which, although they are capable of penetrating relatively undisturbed forest, occur at highest density in degraded and anthropogenic habitats. The interactions between endemic and introduced small mammals have been discussed elsewhere (e.g. Goodman, 1995) and are beyond the scope of this paper. In brief, the diets of introduced and endemic species do overlap to varying extent (Goodman & Sterling, 1996), but there appears to be no firm evidence of a reduction in endemic small mammal density or species richness as a result of competition with introduced species. Ramanamanjato & Ganzhorn (2001) failed to find evidence of competitive exclusion within littoral forest fragments, but suggest that *Rattus* may out compete native species within degraded or marginal habitats that may otherwise have supported endemic species in the absence of introduced competitors.

Lemurs

In a series of papers investigating the influence of edge effects on lemur communities in the Vohibola III Classified Forest in central eastern Madagascar, Lehman and colleagues found a high degree of interspecific variation in edge-tolerance. Lehman (2007) found *Eulemur fulvus rufus* [= *E. rufus*] to occur at lower densities at the forest edge than in the forest interior, while *Lepilemur mustelinus* showed no significant spatial variation in density. The author suggests that this pattern can be explained by the distribution of food resources; edge effects have a greater impact on the distribution of fruit resources than on leaf resources, with the result that folivorous species demonstrate greater edge tolerance than frugivores. Lehman *et al*. (2006a) surveyed eight species along transects at varying distances from the forest edge, collecting sufficient data to analyze the distributions of four species. Of these, three species (*E*. *rubriventer*, *Avahi laniger* and *Microcebus rufus*) demonstrated positive edge effects, while one species demonstrated a neutral edge effect (*Hapalemur griseus*). For a further three species (*Propithecus diadema edwardsi* [= *P. edwardsi*], *L. microdon* and *E. f. rufus* [= *E. rufus*]), insufficient observations were made to provide statistically significant results, but descriptive statistics indicate that these species are more likely to show a neutral edge effect than a negative edge effect. The authors predicted that *E. rubriventer*, being a frugivorous species, would demonstrate a negative edge effect due to a strong observed negative edge effect on the distribution of their food plants. This hypothesis was not supported by the data, possibly because the study was conducted at a time of low fruit set when the species behaves more as a folivore/frugivore. In a parallel study in the same forest, Lehman *et al*. (2006b) found three species demonstrated neutral edge effects (*Avahi laniger*, *E*. *rubriventer* and *H*. *griseus*), two species demonstrated positive edge effects (*P. d. edwardsi*, and *M. rufus*), and one species demonstrated a negative edge effect (*Cheirogaleus major*). These observed distributions are explained largely by the distribution of food resources; the three species showing neutral edge effects are folivorous or frugivorous/folivorous during the survey period, while the two edge-preferring species have varied diets. The edge-avoidance of *C. major* is hypothesized to be the result of increased ambient temperatures at the forest edge which inhibit torpor, although further research (Lehman *et al*., 2006c) demonstrated that the observed distribution of this species was more closely correlated to variation in tree diameter than to ambient temperature; the authors therefore hypothesize that the edge-avoidance of this species is due to a lower abundance of fruit resources at forest edges, as fruit production is correlated with tree diameter.

Ganzhorn (1995) measured the effects of low-intensity selective logging on primary production, leaf chemistry and lemur populations in the forest of Kirindy/CFPF, and found that the increased light penetration in logged areas results in increased leaf quality (which compensates for reduced leaf biomass) and increased fruit production in tree species favored by frugivorous lemurs. For all lemur species present at the study site (*Eulemur fulvus*, *Propithecus verreauxi*, *Cheirogaleus medius*, *Lepilemur mustelinus*, *Microcebus* spp., *Mirza coquereli* and *Phaner furcifer*), observed densities were higher in logged than in unlogged forest, although these relationships were only significant for three species. These findings are related to the distribution of food resources, with logged areas having higher quality leaves, greater fruit production and a greater availability of plant exudates eaten by *P. furcifer* (as a result of logging damage). The author stresses that the results should be interpreted with caution and for some species may represent shifts in home ranges to take advantage of seasonal leaf flush/fruiting rather than genuine increases in population density. While low-level forest disturbance may be beneficial for lemurs, encounter rates of most of the lemurs of the dry deciduous forest decreased at higher intensity logging.

Merenlender *et al*. (1998) monitored the demographics of *Varecia variegata rubra* [= *V. rubra*] and *Eulemur fulvus albifrons* [= *E. albifrons*] in both undisturbed and selectively logged forest on the Masoala Peninsula; they found no significant differences in population density, group size or female fecundity between forest types in either species, but did observe a female-biased adult sex ratio of *E. f. albifrons* in selectively logged forest. This observation is explained by an increase in male dispersal in disturbed forests due to insufficient food resources, with the result that these areas may function as population sinks for this species. In contrast, studies of *Varecia* elsewhere have shown *V. v. variegata* to be susceptible to forest degradation. Balko & Underwood (2005) found the species to be absent from logged areas in Ranomafana for over a decade post-harvest, while White *et al*. (1995) also note that the species is sensitive to forest conditions.

Two studies have looked at the distribution and density of lemur faunas in forest patches across a landscape. Rasolofoson *et al*. (2007) surveyed lemur populations at 12 sites within the Makira forest and observed 14 species; they found the relative densities of 11 species to be negatively correlated with the density of cut stumps, although the surveyed forests are heavily hunted and otherwise disturbed, and it was not possible to disentangle the effects of selective logging from other factors. Lehman *et al*. (2006d) surveyed seven sites within the Fandriana-Marolambo Corridor and found lemur diversity to be significantly negatively correlated with altitude and agricultural intensity; the relationships between lemur diversity and both hunting pressure and logging intensity were also found to be negatively correlated, although these results were statistically insignificant.

Andrianasolo *et al*. (2006) investigated the correlation between nocturnal lemur density and structural vegetation parameters across a gradient of degradation in the southeast littoral forests. These authors found *Microcebus* spp. to be the least specialized in terms of microhabitat use, and *Cheirogaleus* spp. and *Avahi laniger* to show increased specialization. *Avahi laniger* was observed to select areas with a high density of large trees, and the authors suggest that this preference is due to the mode of locomotion of this species rather than due to the distribution of food resources. Forest structure has also been found to influence patterns of locomotion in *Propithecus diadema edwardsi* [= *P. edwardsi*], *Eulemur fulvus rufus* [= *E. rufus*] and *E. rubriventer* within the forests of Ranomafana (Dagosto & Yamashita, 1998). Ganzhorn & Schmid (1998) investigated the population dynamics of *Microcebus murinus* within relatively undisturbed and secondary forests in the Menabe. They found that *M. murinus* occurs at lower density, has lower body mass and lower survivorship in secondary forests compared to relatively undisturbed forest, and that females are less likely to enter into daily torpor and hibernation in secondary forests. The authors suggest that both the higher ambient temperatures and the relative scarcity of large trees with tree holes in secondary forests inhibit energy-saving torpor, which, coupled with lower food abundance, reduces the ability of the species to survive the dry season. These findings are corroborated by Ganzhorn (2003), who found that although *M. murinus* occurs in all relatively undisturbed and secondary forest formations in the Menabe, capture rates decreased in secondary forests of increasing size, indicating that these habitats are suboptimal for this species. In the southeast littoral forests, however, Ramanamanjato & Ganzhorn (2001) failed to capture *M. murinus* in secondary formations over three years of trapping, even though the species is known to utilize plantations elsewhere in the region. Within relatively undisturbed forests, capture rates for *M. murinus* were higher in areas with greater canopy cover.

Rendigs *et al*. (2003) investigated the habitat utilization of two sympatric *Microcebus* species (*M. murinus* and *M. ravelobensis*) in two forest areas in Ankarafantsika. They found both species to occur in a non-degraded area of forest with a high density of large trees, but only *M. ravelobensis* to occur in the more degraded area. The degraded area contains fewer large trees with tree holes, which are thought to be a critical resource for *M. murinus* but not for *M. ravelobensis*. Both species may occur sympatrically in structurally heterogeneous forests.

Arrigo-Nelson & Wright (2004) investigated the distributions of *Hapalemur* spp. in relation to the distribution of bamboo species and human disturbance. They found that small-culm bamboo occurred at greatest density at forest edges and within light gaps, with the result that *H. griseus* and *H. aureus* are likely to use forest edges. This edge-tolerance may have adverse effects on these species, exposing them to greater hunting pressure.

Ralison *et al*. (2006) investigated the presence of *Eulemur collaris* in littoral forest fragments near Tolagnaro in relation to patch size and habitat characteristics. They found *E. collaris* to be present in only four out of 10 patches, with a minimum patch size of 220 ha. These patches were characterized by greater canopy height, canopy cover, tree diameter and *Pandanus* density than patches in which the species was absent (i.e. they occur in the least degraded patches). This study, however, was unable to disentangle the effects of habitat degradation, patch size and edge effects. *Eulemur m. macaco*, in contrast, is known to survive in both degraded forests and well-established secondary forests on Nosy Be and the adjacent mainland, and in areas where it feeds on cultivated fruit trees is able to reach greater population densities than in relatively undisturbed forest (Bayart & Simmen, 2005). Cultivated fruit trees have also been observed to attract other species when adjacent to natural forest, e.g. *E. coronatus* and *Daubentonia madagascariensis* feeding in mango trees (*Mangifera indica*, Anacardiaceae) on the Montagne des Français (pers. obs.).

Ganzhorn (1987) investigated the use of plantation forests by lemurs at Analamazaotra (primarily *Eucalyptus*) and Ampijoroa (mixed-species plantations). At Analamazaotra, three species were regularly observed to use and forage within mature *Eucalyptus* plantations with dense undergrowth – *Microcebus rufus*, *Cheirogaleus major* and *Eulemur f. fulvus* [= *E. fulvus*]. Three small folivorous species (*Avahi laniger*, *Hapalemur griseus* and *Lepilemur mustelinus*) were observed to occasionally forage within these plantations, while *Indri indri* made only occasional use of plantations to cross between areas of natural forest. No lemur species were recorded within young *Eucalyptus* plantations lacking substantial understory vegetation. At Ampijoroa, three species were either resident or regularly observed within mixed-species plantations contiguous with natural forest; *Propithecus verreauxi*, *L. mustelinus* and *E. fulvus*. This mixed-species plantation was used to a much greater extent by lemurs than mature *Eucalyptus* plantations in the east. No lemur was recorded within a mature plantation of the indigenous *Weinmannia bojeriana* in Ankaratra by Goodman *et al*. (1996).

The research reviewed above reveals a high degree of interspecific variation in degradation tolerance among lemurs. Amongst the species shown to respond positively to either edge effects or forest degradation, all are thought to benefit from an increase in the availability of food resources in such areas. Such resources include artificial food sources (Bayart & Simmen, 2005), food plants growing preferentially in light gaps (Arrigo-Nelson & Wright, 2004), and forest food plants producing food of increased quality due to reduced competition for light (Ganzhorn, 1995; Lehman *et al*., 2006a, 2006b). Conversely, some lemur species respond negatively to equivalent habitat change because such change reduces the availability of their food resources. This applies particularly to frugivorous species, as the distribution and density of fruiting trees is commonly reduced by forest degradation (Balko & Underwood, 2005; Lehman *et al*., 2006c; Lehman, 2007). The availability of food resources is not, however, the only factor influencing the habitat use of lemurs: Microclimatic conditions, in particular stability, is an important factor determining the viability within degraded habitats of cheirogaleid species that enter torpor (Ganzhorn & Schmid, 1998; Rendigs *et al*., 2003; Lehman *et al*., 2006b), while habitat vertical structure can also be limiting for taxa with specialized patterns of locomotion (Ganzhorn, 1987; Dagosto & Yamashita, 1998; Andrianasolo *et al*., 2006).

Bats

Compared to non-volant mammal species, relatively little research has been carried out into Malagasy chiropterans (Goodman *et al*., 2003), in particular with regards to habitat utilization. Kofoky *et al*. (2007) used trapping and acoustic sampling to investigate bat species composition, abundance and activity in three habitats (forest interior, clearings and forest edge) within and around Tsingy de Bemaraha National Park. Results differed according to the method employed; while four species (*Triaenops rufus* [=*T. menamena*], *T. furculus*, *Miniopterus manavi* and *Myotis goudoti*) were strongly associated with the forest interior based on trapping data, acoustic sampling revealed *T. rufus* and *Miniopterus manavi* at the forest edge. Overall, bat activity differed significantly between habitats, being lowest within the forest interior and highest at the interface of forest and agricultural land. Because trapping within the forest interior was conducted along trails adjacent to cave roosts, the authors hypothesize that species trapped in the forest were likely using these trails as thoroughfares leading to the forest edge where most foraging takes place. These findings suggest that while forests are important in providing shelter around cave roosts, forest edge constitutes a more important foraging habitat for microchiropterans.

A parallel study in the humid forests of Mantadia and Analamazaotra (Randrianandrianina *et al.*, 2006) found similar results, with the highest taxonomic richness of any site being recorded within relatively intact humid forest, but the greatest activity levels occurring within *Eucalyptus* plantations and agricultural land. Four species were captured only within intact forest and two species only within agricultural land, although capture rates were low, while *Rousettus madagascariensis* was recorded only within plantations. Based on acoustic sampling, *Myotis goudoti* was the only species to be strongly associated with relatively intact forest. As Kofoky *et al*. (2007) demonstrated within dry forests, a matrix of non-forest land surrounding protected forests contributes greatly to chiropteran diversity within eastern Madagascar.

The results of the above studies are corroborated by Goodman *et al*. (2005) who, based on surveys throughout the dry regions of Madagascar, suggest that no more than five out of 27 recorded species are dependent on large expanses of intact forest. In addition to the species in the above studies, other species known to use anthropogenic habitats and non-indigenous food plants include *Eidolon dupreanum*

(Ratrimomanarivo, 2007) and *Pteropus rufus* (Hutcheon, 2003). One striking example of a species potentially benefiting from forest degradation is the sucker-footed bat *Myzopoda aurita* of the endemic family Myzopodidae. This species appears to be closely associated with *Ravenala madagascariensis*, in which it roosts, and has benefited from an increase in *Ravenala* within secondary and degraded habitats (Eger & Mitchell, 2003).

Invertebrates

Olson & Andriamiadana (1996) compared the leaf litter invertebrate faunas of unlogged, selectively logged and edge habitats (along logging trails) in the dry forests of Kirindy/CFPF. Edge habitats were found to support a lower number of individuals and total biomass, but species richness and community composition did not differ significantly between forest edge and unlogged forest blocks. Selectively logged sites also demonstrated similar species richness and composition to unlogged sites.

Vegetation

Cadotte *et al*. (2002) surveyed the vegetation of three littoral forest fragments in Sainte Luce and one fragment in Lokaro to the north of Tolagnaro. The Lokaro fragment is closer to the sea, more isolated and more heavily impacted by local communities than the Sainte Luce fragments, and contained significantly fewer species and families than the latter forest blocks. The Lokaro fragment also demonstrated significantly lower tree density and Shannon-Wiener diversity, and was largely dominated by one tree species, *Tambourissa purpurea* (Monomiaceae). This study, however, did not directly measure degree of anthropogenic disturbance between plots, and so is unable to disentangle the effects of edaphic factors, isolation and degradation on the observed patterns.

Sussman & Rakotozafy (1994) investigated forest structure and composition in three areas at Beza Mahafaly: gallery forest on humid soils, spiny thicket on dry soils (both of which were fenced and therefore not subject to grazing), and an unfenced patch of spiny thicket on dry soils. They found tree density to be lower in the grazed area than the equivalent, fenced spiny thicket area, but higher than in the gallery forest. The grazed forest also had a higher proportion of indigenous trees than the fenced areas, although indigenous tree species richness was lower. In seedling plots established in the same forest patches, no appreciable differences were found in the proportion of saplings and juveniles of middle and upper stratum trees, indicating that grazing was not having negative impacts on the regeneration of these species (although grazing intensity was not quantified). Grasses, however, were proportionally more common within the grazed area, and herbs less common, presumably because of preferential grazing of herbs by livestock. The authors note that the indigenous vine *Sarcostemma viminale* (Asclepediaceae) behaves as an invasive within this forest and was controlled by grazing prior to the establishment of the reserve: Controlled grazing is now under consideration as a management tool in order to control this species (M. Nicoll, pers. comm.).

Brown & Gurevitch (2004), working in Ranomafana, investigated differences in vegetation structure and composition between unlogged forest, forest selectively logged 50 years previously, and forest clear-cut and subsequently abandoned 150 years previously. They found that logging significantly decreases species diversity and increases percentage invasion by exotic plants, primarily *Psidium cattleianum* (Myrtaceae). The presence and abundance of native plants was significantly different between logged and unlogged areas, but no significant or biologically meaningful differences were found between stands logged 50 years previously and stands clear-cut 150 years previously. Logging facilitates strongly invasion by exotic plants, and plant invasion is a major predictor of reduced plant diversity. Once established, *P. cattleianum* forms dense monospecific stands and prevents the establishment of native species, with the result that selectively logged forests may never recover their original structure or composition once invaded. Invasive exotic plants are also known to prevent regeneration within degraded forests in other regions of Madagascar, e.g. *Ziziphus mauritiana* in the Menabe (Ganzhorn, 2003), *Opuntia* spp. in the south (Middleton, 1999), *Acacia* spp. in the Central Highlands and eastern escarpment (Kull *et al*., 2008) and several others (Carrière & Randriambanona, 2007), but I am not aware of any research that has investigated the dynamics of these species in degraded forest areas.

Table 1 provides a summary of vegetation responses to forest degradation from the reviewed publications in which vegetation structural variables were measured, estimated or mentioned. These studies measured a range of variables using different methodologies, and as a result, it is not possible to compare the vegetation response to different types of impact or to compare vegetation responses between

Table 1. Summary of vegetation responses to habitat degradation.

Source	Floristic domain	Type of impact	Vegetation response
Ganzhorn *et al*. (1990)	Western	Selective logging	Increase in trails, logging debris and density of herb-layer, decrease in canopy tree size, number of species, depth of litter layer and regeneration of woody species. Predicted to lead in long-term to decline in tree species diversity.
Chouteau (2004)	Western	Selective logging	Understory vegetation denser and canopy sparser in logged areas.
Hawkins (1991, 1993)	Western	Selective logging	Increase in understory vegetation in logged areas.
Hawkins & Wilmé (1996)	Western	Selective logging	Leaf litter depth and large tree density decrease, herb layer and shrub layer increase in logged areas.
Bloxam *et al*. (1996)	Western	Selective logging	Reduction in canopy cover.
Ganzhorn (1995)	Western	Selective logging	Increased light availability to remaining trees increases foliage quality and fruit production.
Ganzhorn & Schmid (1998)	Western	Selective logging	Tree densities significantly lower in secondary forest for all size classes. Tree species richness and diversity significantly higher in relatively undisturbed forest.
Vallan *et al*. (2004)	Eastern	Selective logging	Forest gaps colonized by heliophilous vegetation.
Lehtonen *et al*. (2001)	Eastern	Selective logging	Herbaceous cover increased and canopy cover decreased with increasing degradation.
Balko & Underwood (2005)	Eastern	Selective logging	Reduction in tree height and diameter, and increase in tree dispersion, in most degraded site compared to least degraded.
Rasolonandrasana & Goodman (2006)	High mountain	Fire	Only 1 of 7 forest tree species survived fire, and regeneration of other species was low. Thicket species survive better and dominate regenerating cohort.
Chouteau *et al*. (2004)	Western	Fire	Increase in understory vegetation and decrease in canopy cover following fire.
Pons & Wendenburg (2005)	Western	Fire	Increase in density of understory vegetation.
Jenkins *et al*. (2003)	Eastern	Fire	Bamboo and ground fern density significantly lower in regenerating forest.
Vallan (2002)	Eastern	Secondary forest	Undisturbed forest has greater vegetation structural complexity.
Stephenson (1995)	Eastern	Secondary forest	% light penetration, woody stem density and tree fern density higher in secondary forest; woody species number, herbaceous species number, herbaceous stem density,% herbaceous cover, fallen log dispersion,% exposed rock and liana stem density higher in relatively undisturbed forest.
Lehman (2007)	Eastern	Edge effects	Trees at forest edge had significantly lower height and diameter than in forest interior, and lower stem density.
Lehman *et al.* (2006a)	Eastern	Edge effects	Significant negative edge effects on the density and size of lemur food trees.
Lehman *et al.* (2006c)	Eastern	Edge effects	Tree height and diameter lower at forest edge.
Watson *et al*. (2004a)	SE littoral	Edge effects	Forest edge has significantly greater shrub cover, but reduced canopy cover and leaf litter cover.
Arrigo-Nelson & Wright (2004)	Eastern	Edge effects and general degradation	Small-culm bamboo is more abundant in forest edges and gaps.
Andrianasolo *et al*. (2006)	SE littoral	General degradation	Density of small (DBH < 10 cm) and especially large (DBH > 10cm) trees is reduced in more degraded patches.
Ralison *et al.* (2006)	SE littoral	General degradation	Average tree height and diameter decrease with increasing degradation.
Seddon & Tobias (2007)	Southern	General degradation	Reduction in canopy height and leaf litter depth in degraded areas.
Metcalf *et al*. (2005)	Western	Paths	Thin opening of canopy above paths.

vegetation domains. Nevertheless, it appears that vegetation responses tend to be rather uniform, with different types of degradation resulting in a reduction of mean canopy height and percentage cover, tree density, tree diameter, tree species richness and leaf litter cover, and an increase in the density of herb and shrub layers. In general, vegetation structural complexity is higher in non-degraded forests.

Conclusions from the research

Effects on overall biodiversity

The above review demonstrates a notable level of variation in the impacts of habitat change on Malagasy terrestrial biodiversity in terms of species richness or species abundance/density, both between and within different taxonomic groups. Of the publications for which the data were explicit, 10 papers found that habitat change had a positive impact on biodiversity, 14 demonstrated a neutral or mixed response, and 20 demonstrated a negative response. Differences in methodology, focal species, ecosystems, and types of anthropogenic impacts between these studies make it difficult to draw general conclusions regarding the impacts of habitat change on Malagasy biodiversity. In some cases species responses are highly idiosyncratic, including different responses to the same type of habitat degradation between members of the genus *Coua* (Chouteau, 2004; Chouteau *et al*., 2004), and the same species (*Foudia omissa*) in different regions (Langrand & Wilmé, 1997; Watson *et al*., 2004a). These findings suggest that, given the diversity of Madagascar's biota, ecosystems and social-ecological interactions, it is probably unrealistic to search for general rules to explain and predict the impacts of habitat change nationwide.

Impacts by biome

Although it is not possible to perform a formal meta-analysis of the reviewed papers for a number of reasons, these data appear to indicate that there may be differences in the degree of disturbance sensitivity of faunal taxa between humid and dry forest biomes. Table 2 summarizes the impact of habitat change on faunal species and communities into positive responses, negative responses and neutral or mixed responses. In total, 39% of studies carried out within humid forest ecosystems demonstrated a positive or neutral effect on biodiversity, while 81% of studies carried out in dry forest ecosystems showed a positive or neutral impact.

Table 2. Summary of biodiversity responses to habitat change in humid and dry forests.

Taxon	Humid ecosystems			Dry ecosystems		
	Positive impact	Neutral/mixed response	Negative impact	Positive impact	Neutral/mixed response	Negative impact
Birds	1	0	1	4	4	0
Amphibians	0	2	1	0	0	0
Reptiles	0	1	1	1	1	0
Herpetofauna	0	0	1	0	0	0
Small mammals	0	1	3	0	2	1
Lemurs	3	1	7	1	0	2
Total	**4**	**5**	**14**	**6**	**7**	**3**

While these findings appear to indicate that dry forest taxa are less-disturbance sensitive than humid forest taxa, the results must be interpreted with caution and a number of caveats must be stressed. Firstly, the humid forest sample is biased by lemur research (generally demonstrating negative impacts),while the dry forest sample is biased by research into birds (demonstrating positive and neutral impacts); because the order Primata is clearly more forest-dependent than the class Aves, this weighting is likely to have influenced the observed pattern. Secondly, it is important to note that the degree or intensity of the habitat degradation investigated has not been controlled for, and much of the research from dry forests has been carried out at Kirindy/CFPF under conditions of low-intensity logging. There may therefore exist a bias in impact-intensity between the research from dry and humid regions. Nevertheless the sample shows that a greater proportion of the research carried out within humid forests has demonstrated a negative impact on biodiversity, while the majority of research from dry forests found a positive or neutral overall impact, perhaps indicating that dry forest taxa are less disturbance-sensitive.

If a differential response to habitat change does exist between faunal species and communities of dry forests and humid forests, and is not simply an artifact of non-random sampling or research effort, this may reflect differential levels of naturally occurring heterogeneity between these biomes, and therefore differences in the degree of habitat specialization amongst their constituent species. The literature suggests two possible mechanisms for such differences. Firstly, Seddon & Tobias (2007) note that because of the "sparse, deciduous nature" of the Mikea forest, an increase in light within and around forest gaps and edges makes little difference to the understory. Dry forests may therefore be less susceptible to the impacts of habitat disturbance than humid forests because the naturally greater light penetration means that the opening-up of forest structure has less drastic impacts than in darker humid forests. A second hypothesis stems from the greater climatic variability of dry forests compared to humid forests in Madagascar, as manifested in greater inter-annual variation in rainfall (Dewar & Richard, 2007) and greater intra-annual variation in temperature (Donque, 1972). Therefore dry forest species may be adapted to greater variability in certain abiotic aspects, and are therefore less susceptible to micro-climatic changes occurring as a result of habitat degradation.

Effects on community composition

While the reviewed body of research fails to provide an equivocal answer to the question of whether anthropogenic habitat change has negative impacts on overall biodiversity, there is strong evidence that habitat degradation does lead to a community turnover from specialist to generalist species, or from endemic to non-endemic species. This has been observed in bird communities (Andrianarimisa, 1992; Goodman *et al*., 1996; Watson *et al*., 2004a; Woog *et al*., 2006), among amphibians (Andreone, 1994; Vallan, 2002; Vallan *et al*., 2004) and particularly within small mammal communities, among which the introduced *Rattus rattus* and *Mus musculus* increase in relative abundance in more degraded habitats (Stephenson, 1993, 1995; Goodman, 1995; Lehtonen *et al*., 2001; Rasolonandrasana & Goodman, 2006).

The relative increase in habitat generalists at the expense of specialists is a concern for conservationists as it leads to the homogenization of biodiversity: As degraded forest sites progressively lose their most specialized species, their faunas increasingly resemble each other and are dominated by the same few widespread species (McKinny & Lockwood, 1999). This is a particular concern in Madagascar where the majority of the endemic biota is composed of forest specialists (Goodman & Benstead, 2005), and the level of habitat specialization and taxonomic level of endemism are correlated, at least for some taxa, such as birds (e.g. Wilmé, 1996). Habitat degradation is therefore expected to impact most heavily on the island's endemic taxa, which for conservationists represent the most important and valuable component of the biota.

Source-sink dynamics and population viability

Much of the research I have reviewed suggests that modified or degraded habitats can support levels of species diversity, and population densities of certain species, that can match or even exceed that of undisturbed forests, at least in the short term. There is little research, however, investigating the long-term viability of biodiversity in degraded forest areas, and there is some evidence that, at least for certain taxa, such habitats may be sub-optimal and therefore act as population sinks in which populations are maintained only through immigration from adjacent source areas (see Pulliam, 1988). Jenkins *et al*. (2003), for example, found all four of the *Calumma* species at their study site were present in secondary regeneration following fire, but speculate that chameleon abundance in these areas is probably maintained by dispersal from contiguous low-disturbance forest or by recruitment from eggs laid before the fire, and that such secondary forests will probably not support viable chameleon populations in the long-term.

Many researchers have found *Microcebus* spp. to tolerate degraded habitats (e.g. Ganzhorn, 1995; Andrianasolo *et al*., 2006; Lehman *et al*., 2006a, 2006b), giving the impression that such areas offer suitable habitat for these species. Ganzhorn & Schmid (1998), however, found that while *M. murinus* does occur in secondary forests in the Menabe, it occurs at lower densities than in relatively undisturbed forest, has lower body mass, lower survivorship, and is less likely to enter into energy-saving torpor due to the higher ambient temperatures of secondary habitats. Although not explicitly stated by the authors, it is possible that the *Microcebus* population within the secondary forests studied functions as a sink population, being maintained only by dispersal from the relatively undisturbed forests that surround the secondary patch. Finally, while Pons & Wendenburg (2005) found an increase in species richness in regenerating forests compared to relatively undisturbed forests, they suggest that this may "*conceal potential demographic problems for certain species*" (i.e. *in situ* recruitment may not offset mortality).

Types of habitat change

While differences in research methods and focal taxa make empirical comparisons difficult, this review appears to demonstrate a gradient of increasing severity of impact on either species richness or species abundance with increasing intensity of forest modification. Of the types of habitat change I have reviewed selective logging appears to have the least impact on biodiversity, and many studies have found either no impact or a positive impact on species richness or abundances (Hawkins, 1993; Ganzhorn, 1995; Bloxam *et al*., 1996; Ganzhorn *et al*., 1996; Hawkins & Wilmé, 1996; Merenlender *et al*., 1998; Vallan *et al*., 2004). Jenkins *et al*. (2003) found that while selective logging does negatively impact chameleon densities, this impact is less severe than the effect of fire, a similar finding to that of Lehtonen *et al*. (2001) for rodent communities. Research into edge effects has provided contradictory results for bird communities (Watson *et al*. (2004a) recorded a decrease in species richness, while Woog *et al*. (2006) found the reverse), and mixed results for herpetofauna (Lehtinen *et al*., 2003) and lemurs (Lehman *et al*., 2006a, 2006b), among which some species are found to be edge-preferring and some are edge-avoiding.

Regenerating or secondary forests have been shown to be more species rich than relatively undisturbed forests for birds (Andrianarimisa, 1992; Pons & Wendenberg, 2005), but less species rich for amphibians (Vallan, 2002) and endemic small mammals (Stephenson, 1995). Rasolonandrasana & Goodman (2006) found no significant change in small mammal species richness in high mountain sclerophyllous forests regenerating after fire. Although little research has been carried out into the biodiversity value of plantations, Ganzhorn (1987) found plantations of both native and exotic trees to be suboptimal for all lemur species, and Vallan (2002) found *Eucalyptus* plantations to support only 46% of the number of frog species found in natural forests.

It therefore appears that of the types of human impact on forests that have been researched in Madagascar, selective logging has the least impact on biodiversity, followed by edge effects and secondary or regenerating forests, while plantations (which represent the greatest degree of human modification) are of lower value for the conservation of endemic taxa. A similar trend of increasing impacts on biodiversity along a gradient of increasing management intensity was noted by Gardner *et al*. (2007a) in a global review of the impacts of habitat change for herpetofauna.

Discussion

Future research priorities

Types of impact

The impacts of fire, selective logging, paths and edge effects on biodiversity have all been the subject of some research in Madagascar (see Figure 3), and in some cases these impacts have been investigated for a range of taxa and in very different natural ecosystems. Certain types of forest use or modification, however, have received little research attention. Perhaps the most important use of forests that remains under-researched is the grazing and browsing of livestock, which can be expected to have some impact on forest structure and composition as has been demonstrated on other continents (e.g. Evans *et al*., 2006; Enright & Miller, 2007; Mata-González *et al*., 2007). Livestock primarily graze and browse vegetation within reach of the ground, clearly impacting regeneration. If some species are unpalatable to livestock, these can be expected to increase in dominance within the regenerating cohort; this is thought to be the case within the PK32-Ranobe protected area, for example, where *Didierea madagascariensis* (Didiereaceae) appears to be more dominant in heavily grazed areas (P.-J. Rakotomalaza, pers. comm.). Domestic livestock may also act as seed predators; this is thought to be the case in the Tsimanampetsotsa National Park, where livestock predate the seeds of the southern endemic genera *Lemuropisum* (Fabaceae) and *Androya* (Buddlejaceae), with presumed negative impacts on the reproduction of these species (Madagascar National Parks, 2008).

There are a number of reasons why an understanding of the impacts of grazing is important for the management of new, multiple-use protected areas. Firstly, grazing is prevalent in most protected areas within the dry regions of Madagascar, and it provides a strong incentive for forest conservation by pastoralist communities because standing forests provide grazing reservoirs and serve to shelter cattle from thieves (Rabesahala Horning, 2003; Kaufmann & Tsirahamba, 2006, although see Réau, 2002). In addition, the rearing of cattle is culturally important to the people of the dry regions of the island. Hence, grazing cannot be restricted within co-managed protected areas without a) removing incentives for forest conservation, and b) risking conflict between protected area authorities and local communities and management structures, leading to the erosion of local support for the protected area (Gardner *et al*., 2008). Livestock grazing, therefore, is likely not only to impact forests but also to remain a significant conservation issue in many of the country's existing and new protected areas.

The second major use of forests that remains unstudied is the collection of firewood, which appears to be amongst the most common and important uses of forests by local communities throughout Madagascar. While collectors normally target deadwood and therefore may not impact forest structure, rotting wood provides an important habitat for a number of endemic vertebrate taxa (e.g., Glaw & Vences, 2007), as well as economically important bee species (Bodin *et al*., 2006). Large scale removal of deadwood from forests could also be expected to disrupt the essential processes of decomposition and nutrient cycling (Golley, 1977), but such impacts remain unstudied in the Malagasy context.

Biogeographical focus

Figure 2 shows that 87% of the reviewed publications are based on research carried out in the eastern and western domains, including the southeastern littoral forests. To a large extent this may reflect the existence of forest areas in which conditions or management regimes provide excellent natural experiments into particular phenomena (e.g. selective logging in Kirindy/CFPF, fragmentation in Ambohitantely and the southeast littoral forests). In contrast the high mountain domain, the Sambirano transitional zone and, in particular, the spiny thicket of the south are under-represented in terms of existing research. While the biodiversity of the high mountain domain is threatened primarily by climate change and not human activity (Raxworthy *et al*., 2008), the lack of research within the southern ecosystems is a concern given that a) they currently suffer the fastest rates of forest loss in the country (MEFT *et al*., 2009), b) they possess high rates of local endemism for some taxa (Phillipson, 1996; Stattersfield *et al*., 1998), and c) they are thought to be particularly susceptible to degradation as they have low regeneration capacity (Seddon *et al*., 2000; Rioux Paquette, 2008; Soarimalala & Raherilalao, 2008, although see Elmqvist *et al*., 2007). For these reasons, it is recommended that further research is carried out into the impacts of habitat degradation on the biodiversity of the south.

Taxonomic focus

While birds, reptiles, amphibians, small mammals, lemurs and to a lesser extent bats have all been relatively well studied as a whole, there remain certain taxonomic groups that have received little research attention in terms of the impacts of habitat degradation. Amongst the reptiles, for example, research has focused particularly on chameleons (reflecting the relative ease of surveying chameleons at night), with the result that little is known about the disturbance sensitivity of other lizards, snakes, or chelonians. That no such research appears to have been carried out into terrestrial chelonians is surprising given that all four of Madagascar's indigenous species are now classified as Critically Endangered (IUCN, 2008). Although habitat degradation is not among the main threats suffered by any of these species (which are threatened primarily by hunting for domestic consumption, particularly *Astrochelys radiata* (O'Brien *et al*., 2003; Leuteritz *et al*., 2005), and collection for the international pet trade (Pedrono & Smith 2003; Walker *et al*., 2004), a deeper understanding of the responses to habitat degradation of these species would allow conservation practitioners to better advance and implement conservation management plans for these species. *Astrochelys radiata*, at least, fares well in degraded habitats dominated by the invasive *Opuntia* spp. (Leuteritz *et al*., 2005) and *A. yniphora* occurs in secondary habitat within its core range (Pedrono & Smith, 2003).

Bird communities have been well studied in both the dry and humid forest ecosystems of Madagascar, but research focused on the responses of individual species to habitat degradation have been limited to the country's dry regions, and little is known about species-specific responses amongst the endemic terrestrial, understory and canopy insectivores of the humid forests. Such research would provide insight into the process of degradation within humid forest ecosystems as well as permitting comparison with equivalent research into western species.

Only one study was found investigating the impacts of habitat change on invertebrates, in this case leaf litter invertebrates of the Kirindy/CFPF deciduous dry forest (Olson & Andrimiadana, 1996). Further research into the disturbance-response of invertebrate communities in a range of ecosystems would provide insight into the mechanisms by which habitat degradation influences certain vertebrate species (e.g. Afrosoricida and insectivorous birds). Research into the differential impacts of degradation on invertebrate functional groups, such as pollinators and detritivores, would also provide valuable information to understand cascade effects and the process of ecosystem decay; defined as the sequential loss of species and erosion of ecosystem function triggered by habitat fragmentation or other disturbances (Laurance *et al*., 2002).

Long-term research

The research reviewed herein has focused almost entirely on the short-term response of select taxa to forest degradation. Little is known, therefore, about the long-term effects on ecological processes and ecosystem function resulting from the loss or reduction in density of certain species or taxonomic groups. In some cases, such impacts can be predicted; many lemur species, for example, are known to be important seed dispersers (Dew & Wright, 1998; Ganzhorn *et al*., 1999; Spehn & Ganzhorn, 2000; Birkinshaw, 2001; Bollen *et al*., 2004a, 2004b; Lahann, 2007), and their disappearance from forests (through hunting or habitat degradation) is therefore expected to lead to the further loss of plant species adapted to lemur dispersal (Ganzhorn *et al*., 1999). Other cascade effects, such as the loss of insect pollinators dependent on tree holes or deadwood for reproduction, or disequilibrium resulting from the loss of predators or competitors, are likely to occur within forests impacted by human agency, and further research is needed to identify and possibly mitigate their impacts if Madagascar’s new generation of multiple-use protected areas are to successfully conserve the country’s unique biodiversity.

Most of the faunal research carried out to date has involved ‘snapshot’ studies of species responses to habitat change, which may not be sufficient to accurately identify species population trends within degraded habitats, and may even give the misleading impression that such habitats are suitable for the species in question. A number of authors (e.g. Ganzhorn & Schmid, 1998; Merenlender *et al*., 1998; Jenkins *et al*., 2003; Pons & Wendenburg, 2005) have found that while a species may persist in a degraded habitat, the mere fact of its presence may mask demographic problems associated with suboptimal habitats, and that populations may be maintained only through source-sink dynamics and immigration from non-degraded areas. It is therefore essential that long-term research is carried out into the dynamics of disturbance-sensitive taxa (especially those of high conservation priority) under a range of forest management regimes, if we are to understand the factors influencing their long-term viability and manage protected areas accordingly.

Quantification of impact intensity

Our understanding of observed patterns in impacts of forest degradation is hampered by differences in scope and methodologies within the existing research, most of which fails to quantify the types of habitat change under investigation, instead classifying changes using terms such as ‘low-impact’ and ‘high-impact’. If we are to further our understanding of the impacts of habitat change, it is vital that future research explicitly quantifies the intensity of human forest use through the measurement of a standardized set of micro- and macro-habitat variables, such as that employed by Stephenson (1995).

Reconciling resource use and conservation

New multiple-use protected areas with the twin management objectives of conserving biodiversity and contributing to sustainable rural development must simultaneously attempt to maximize value for different stakeholder groups; for conservation stakeholders the primary value of protected areas is biodiversity conservation, but for local communities and management associations the value of primary concern is the sustainable provision of economically and socially important environmental goods and services. It is not possible, however, to plan protected area management to simultaneously maximize these disparate values without an understanding of how forest use impacts both types of value.

While the research contained within this review provides insight into the impacts of forest use on biodiversity value, we have little idea of how such use impacts the generation of economic and social value within managed forests. Research is required to investigate the distribution of economic and social values across gradients of land-use intensity, and to compare this with the distribution of conservation value across the same gradients; such research would allow the identification of synergies and trade-offs between conservation and forest use, and thereby permit the development of management regimes that maximize the benefits of protected areas for all stakeholders.

Implications for conservation and the design and management of new protected areas

The body of research reviewed above provides a great deal of information on the impacts of anthropogenic habitat change on Madagascar’s biodiversity. Given that the primary focus of conservation actions in Madagascar is the conservation of biodiversity within different categories of protected areas, it is important to explore the implications of the research findings for the creation and management of such zones. While the incorporation of such theoretical aspects into protected area planning can help ensure the long-term viability of these sites, there remain a number of practical realities (such as a lack of capacity) that hamper successful protected area management. It is beyond the scope of this paper, however, to explore these practical aspects.

Protected area design and zoning

Most of the newly established or proposed Durban Vision protected areas are composed of large areas of sustainable use zone of various types, with relatively small areas designated as strict conservation zones. The new protected area of Ankodida, for example, has a total surface area of 10,744 ha, of which only 2019 ha is designated as a priority conservation zone; the remaining 8725 ha is composed of zones of sustainable use, charcoal production, wood exploitation, etc. (WWF, 2008). The zoning of new protected areas, particularly those that are co-managed by local community associations, must account for a number of factors in addition to biodiversity-related priorities. Chief among these are the requirements of local communities in terms of access to natural resources or culturally important sites, which must be among the main management considerations if protected areas are to avoid having negative impacts on the ability of local communities to satisfy their material and spiritual needs in line with guidelines for the protected area system (Government of Madagascar, 2006; SAPM, 2007). Nevertheless, it remains essential that protected areas be designed and zoned in such a way as to maximize the long-term viability of their biodiversity.

For taxa that are sensitive to degradation, areas of degraded natural habitat may be unable to maintain viable populations even when they occur within areas of contiguous forest cover. The result is that undisturbed habitat patches may function as ecological islands within a matrix of unsuitable, degraded habitat, yet without adequate knowledge of the ecological requirements of target species, protected area managers may assume that the species occurs and is viable throughout the mosaic of degraded and non-degraded forest. Research from the fields of island biogeography and meta-population dynamics has long been used to inform protected area design so as to maximize species and ecosystem viability within human-impacted landscapes, and such insights must equally be applied to the creation of new, multiple-use protected areas in Madagascar. The research reviewed indicates that certain taxa can survive in suboptimal habitats as sink populations when such areas are connected to non-degraded forest patches, which serve as population sources. This suggests that high levels of biodiversity can theoretically be maintained even in human-dominated landscapes, if degraded areas are interspersed with non-degraded areas, and if these less-degraded patches are linked through suitable habitat corridors. While the zoning of protected areas is often constrained by other (e.g. social) priorities, it is essential that the spatial distribution of conservation, sustainable use, and restoration zones be designed so as to maximize the viability of disturbance-sensitive taxa within mosaics of habitat of varying quality.

Protected area management objectives

As we have seen, habitat modification can, in some circumstances and for some taxa, lead to equal or higher levels of biodiversity (in terms of species richness) than exists in equivalent unmodified habitats. The maintenance of species richness, however, can mask a shift in community composition from forest specialists to generalists. All species are not equal in terms of conservation importance, and in Madagascar most endemic species are restricted to forests and show a greater degree of habitat specialization than non-endemic taxa (Wilmé, 1996; Goodman & Benstead, 2005). Because species richness is a poor indicator of conservation value (Barlow *et al*., 2007; Gardner *et al*., 2007a), protected area managers must decide whether their objective is to conserve and maximize overall biodiversity, or whether they intend to provide effective protection for certain target taxa or ecosystems of conservation importance

Any changes to forest habitats within protected areas as a result of human use will influence a whole range of taxa; for some the impact will be positive, but for many the impact will be negative and it is the taxa of greatest conservation value that are most likely to suffer. Protected area managers must therefore highlight the species that are important to them (globally threatened species, local endemics or species under-represented within the protected area system), and devise management strategies explicitly targeted towards these species. Fortunately, most if not all protected areas in Madagascar use target-driven management planning systems, whereby the identification of primary conservation targets forms the basis for management planning. Such systems should therefore allow protected area managers to develop management regimes that maximize the long-term viability of the most important taxa, provided that sufficient information on the ecological requirements of these species is known, and that the required management is not constrained by social and development management objectives (see below).

Reconciling natural resource use and conservation

Much of the literature reviewed herein reflects a well-established pattern in ecology, namely that low or intermediate levels of forest disturbance can promote diversity (the "intermediate disturbance hypothesis", Connell, 1978). While this implies that Madagascar's new generation of multiple-use protected areas may be effective in protecting biodiversity if disturbance can be limited to "intermediate levels" (but see section entitled "Effects on community composition"), the important point is that protected area managers are currently not in a position to identify the appropriate levels of natural resource use that maximize biodiversity. For any given type of forest use, a low level of the activity may benefit certain species or overall biodiversity, but the same activity carried out at greater intensity may become detrimental to those same species or communities: the identification of such thresholds thus becomes critical if conservation and forest use are to be reconciled.

Protected area management worldwide is constrained by a lack of funding (James *et al*., 1999; Balmford & Whitten, 2003), and this is particularly so in developing countries (Balmford *et al*., 2003; Bruner *et al*., 2004). Given the scarcity of available funding and the high initial costs of implementing new protected areas, it could be expected that research budgets of new protected areas will not be sufficient to provide the data necessary for fully informed management decision-making. Without research to identify the rates of forest use that can be accepted without significant negative impacts on biodiversity, the precautionary principal (Principal 15 of the Convention on Biological Diversity, 1992) suggests that such use should be prohibited or strictly controlled. Adherence to this principal is not, however, an option for the managers of new protected areas in Madagascar because such sites are expected to contribute to national development goals and the safeguarding of local livelihoods as well as the conservation of biodiversity.

If it is not possible for protected area managers to identify sustainable levels of forest use during planning and regulate natural resource extraction accordingly, then the only remaining option is to carry out regular monitoring to evaluate the impacts of forest use and to alter management regimes on this basis (adaptive management). Whether true adaptive management will be possible within the context of new, co-managed protected areas in Madagascar remains to be seen, as the requirements of local communities may place constraints on available management options. If, for example, the extraction of fuel-wood within a sustainable use zone is found to be having negative impacts on biodiversity, will it be possible to reduce permitted extraction rates without diminishing the appropriation and support of the protected area by local communities? Whether adaptive management is possible or not, the relative lack of information with which to inform and plan natural resource use within protected areas means that increasing emphasis must be placed on monitoring the impacts of such activities.

Monitoring and evaluation

Ecological monitoring is vital for protected area managers to evaluate the effectiveness of their management and, if necessary, adapt and change; this is particularly important for protected areas in which the harvesting of natural resources by local communities is permitted (Kremen *et al*., 1998). Monitoring is, however, expensive, and places a great strain on protected area management budgets, hence the need for monitoring programs that can effectively detect population trends at minimal cost (Danielsen *et al*., 2005; Hockley *et al*., 2005). In Madagascar, increasing emphasis is being placed on participatory ecological monitoring, carried out by designated members of local communities who receive some training as para-ecologists (Andrianandrasana *et al*., 2005; Durrell Wildlife Conservation Trust, 2007). Although questions remain about their ability to produce reliable data, such systems have the advantage of not only being comparatively cheaper than monitoring carried out by conservation professionals, but also of actively involving local communities in protected area management, thereby increasing appropriation and understanding of these areas amongst local communities, and increasing communication and cooperation between different management stakeholders (Becker *et al*., 2005; Danielsen *et al*., 2005).

The research reviewed above, however, suggests that the choice of taxa for monitoring must not be based simply on considerations of feasibility, but must explicitly target those taxa that are sensitive to disturbance if real trends are to be detected and failures of management highlighted. Monitoring of disturbance-tolerant taxa can give the false impression that management of the protected area is successfully maintaining biodiversity, while underlying negative trends may not be detected because the most sensitive taxa are not being monitored. It is therefore essential that the selection of indicator taxa is not based solely on logistical considerations, and that indicators are chosen which accurately reflect the pressures on a protected area's ecosystems, and which are sensitive to the resulting changes.

The reviewed research also has implications for the selection of areas in which monitoring is carried out. Because of logistical difficulties associated with research in forests, monitoring is normally carried out along existing path systems; as we have seen, however (Jenkins *et al*., 1999; Metcalf *et al*., 2005), such paths represent modified habitats in their own right and so can not be used to conduct research into biodiversity within undisturbed habitats, or to monitor changes in taxa that may be sensitive to the types of disturbance typical of paths. Without knowledge of the direction and strength of any disturbance-sensitivity associated with paths, monitoring data collected along existing path systems may not accurately reflect population trends within the target taxa.

Evaluating viability and extinction risk

An understanding of the response of species to habitat degradation and disturbance is vital if the viability of remaining populations is to be accurately assessed. Extent of remaining habitat is often used as a proxy measure of population size, but this measure cannot provide accurate estimates without detailed knowledge of species' habitat requirements. A forest block of 10,000 ha, for example, may provide 10,000 ha of suitable habitat for a species that is tolerant of edge effects and moderate degradation, but substantially less for a species dependent on relatively intact forest, which may be restricted to a smaller core. Most new and existing protected areas in Madagascar use the target-based "5S" or Miradi management planning systems, whereby conservation strategies are developed based on an assessment of threats and of the viability of designated conservation targets (i.e. species or habitats). An analysis of target species viability therefore provides the basis for most site-based conservation management in the country, making it particularly important that such assessments accurately reflect long-term population viability. If protected areas are to successfully conserve populations of priority taxa, it is vital that knowledge of a species' vulnerability to habitat degradation be incorporated into viability assessments and subsequent management planning.

The vulnerability of species to habitat degradation is also important in evaluating global extinction risk, yet this is not amongst the criteria utilized in determining threat status by the IUCN (IUCN, 2008). Raxworthy & Nussbaum (2000) highlight the problems with IUCN Red List classifications for Malagasy herpetofauna, which reflect a historical bias towards conservation of chelonians and boid snakes. Madagascar's three boa species, for example, are all classified as globally Vulnerable (IUCN, 2008), yet all are tolerant of habitat degradation and survive even in agricultural land and in villages; because the loss of forests alone does not result in the extirpation of these species, they appear to be at much lower risk of extinction than species which are dependent on relatively undisturbed forest (Raxworthy & Nussbaum, 2000). An interesting illustration of this point is provided by two sympatric bird species restricted to the Mikea forest of southwest Madagascar, *Monias benschi* and *Uratelornis chimaera*. Both species are classified as globally Vulnerable (IUCN, 2008) based on rates of habitat loss and associated population decline. The global population of *M. benschi* is estimated at over 100, 000 individuals (Tobias & Seddon, 2002), while that of *U. chimaera* is estimated at around 20,000 (Seddon & Tobias, 2007). While *M. benschi* is considerably more abundant within relatively undisturbed habitat, the Mikea forest is increasingly degraded over much of its extent (Seddon *et al*., 2000), creating conditions more favorable to *U. chimaera*. Despite having a much smaller population size and similar extent of occurrence, Seddon & Tobias (2007) suggest that *U. chimaera* may be less vulnerable to extinction than *M. benschi* because it is more tolerant of degraded habitat.

Prioritization of conservation areas

Research carried out into the conservation value of strict and multiple-use protected areas in eastern Africa has shown that while species-richness did not decrease in less well-protected areas, these sites did harbor distinctly different communities of a range of faunal taxa (Gardner *et al*., 2007b). The conclusion from this research is that both strictly conserved protected areas (Categories I-IV) and lower-protection categories (V and VI) are required to ensure the conservation of the biota of a landscape. The findings of a number of other researchers working in continental areas also suggest that maintaining a mosaic of pristine and disturbed habitats across a landscape is necessary to ensure conservation of the maximum biodiversity (e.g. Pons *et al*., 2003b for European birds; Borghesio, 2008 for African birds; Todd & Andrews, 2008 for North American snakes), indicating that the lower protected area categories can provide complementary conservation services to strict protected areas.

The Malagasy fauna differs from continental faunas, however, because on continents a much higher proportion of the fauna are generalists not adapted to natural forest environments. While multiple-use conservation areas on continents support a high diversity of species not found within forests, such areas are less important for conservation in Madagascar, where the majority of species of conservation importance (i.e. endemics) are forest-dependent (Wilmé, 1996; Goodman & Benstead, 2005). This presents a dilemma for Madagascar, where, with limited funds, the government and conservationists are in the process of establishing a large number of new, multiple-use protected areas, while simultaneously attempting to ensure the conservation of the well-established network of strict protected areas.

If human use of new multiple-use protected areas is not planned and managed so as to minimize negative impacts on key biodiversity targets, then we are likely to see the gradual, successive loss of disturbance-sensitive species and a homogenization of the fauna across the new generation of conservation areas. Such a process increases the importance of the Madagascar National Parks network of strictly protected areas for conserving disturbance-sensitive taxa. It is therefore important that the Durban Vision does not draw conservation funds and attention away from the Madagascar National Parks network of strictly protected areas, which must continue to be seen, and managed, as the “crown jewels” of the national protected area system. The “*Fondation pour les Aires Protégées et la Biodiversité de Madagascar*” has been established as a sustainable financing mechanism for Madagascar’s protected areas (see Klug *et al*., 2003) and requires that such sites demonstrate their success in conserving biodiversity and their contribution to biodiversity representation within SAPM as key funding criteria (M. Nicoll, pers. comm.). Such mechanisms should help to ensure that conservation attention remains focused on the most important conservation areas and thereby help promote the conservation of all of Madagascar’s unique biodiversity in line with the objectives of the Madagascar Protected Area System.

Summary Conclusion

The Durban Vision, which entails the tripling of Madagascar’s protected area coverage, will help slow the loss of forests and is undoubtedly a great boost to the conservation of the country’s unique biodiversity. Much of the expanded protected area system, however, will be used to satisfy local subsistence needs, and the biodiversity therein will be under pressure from anthropogenic habitat change. Conservation practitioners, policy-makers and funders cannot therefore assume that the expansion of the protected area system alone will be sufficient to ensure the conservation of high-value, disturbance-sensitive taxa and careful thought must be put into the design and management of new multiple-use protected areas if they are to succeed in conserving Madagascar’s unique biodiversity while simultaneously contributing to national development objectives.

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