

A method for quantifying biodiversity loss and its application to a 50-year record of deforestation across Madagascar

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Abstract

Madagascar is a top global conservation priority for high rates of deforestation and endemism. Deforestation has been extensive, but impacts of forest loss on biodiversity have not been well quantified, especially for nonvertebrates. We use generalized dissimilarity modeling (GDM) as a basis for estimating forest biodiversity remaining at different points in time. We predict that 9.1% of species in Madagascar have been committed to extinction from deforestation between 1950 and 2000. This quantity is higher than losses expected from random deforestation of the same total area, indicating that deforestation has been biased towards environmentally and biologically distinct areas. In contrast to traditional area-based methods, these techniques allow one to estimate biodiversity loss based on the location of deforestation and thus can inform land-use policies that aim to minimize biodiversity impacts of deforestation or development.

Introduction

As deforestation accelerates in many areas, there is a greater need than ever to assess the impacts of habitat loss on biodiversity. Reasonably accurate species range maps are now available for many vertebrate groups (e.g., Ridgely *et al.* 2007), and these data are increasingly used in conservation assessments (e.g., Brooks *et al.* 2004). Distributional data for plants, insects and other nonvertebrates, however, consist of relatively few inventories from scattered sites, despite the fact that these groups may represent more than 95% of all species on earth (May 1988). Assessing impacts of habitat loss on nonvertebrates using individual-species methods is, practically speaking, impossible: most have yet to be

described, distributions are available for only a fraction of those that are known, and conservation research and funding continues overwhelmingly to favor vertebrate species (Clark & May 2002). Therefore, there is an urgent need for methods to assess the conservation status of nonvertebrates in the absence of complete species-level distributional data for these groups.

The species–area relationship (SAR) (Arrhenius 1921) offers one way of inferring extinctions predicted to result from habitat loss. With a simple and well-supported power-law function, one of ecology's "few genuine laws" (Schoener 1976) describes the relationship between number of species (S), and area (A):

$$S = cA^z$$

[Correction added after publication 22 August 2008: author affiliations were initially added incorrectly, and have been updated since this Letter's original publication.]

where c and z are constants. This relationship is regularly used to predict the proportion of species in a region that will be retained over time if the habitat in that region is reduced to a specified proportion of the original area (Pimm & Askins 1995):

$$S_{\text{retained}}/S_{\text{original}} = (A_{\text{retained}}/A_{\text{original}})^z$$

A related approach uses the “endemics–area relationship” (EAR) (Kinzig & Harte 2000). EAR-based estimates potentially provide improved estimates of species losses from habitat clearing by considering the probability that species are endemic to (i.e., found nowhere else than in) the area that was cleared (Pimm & Askins 1995).

Both SAR- and EAR-based extinction estimates assume that habitat loss is distributed randomly relative to the distribution of species within a region and that the slope of the relationship, z , is constant across all scales and gradients (Seabloom *et al.* 2002). Often, however, both habitat loss and biodiversity are distributed unevenly in relation to environmental gradients. In fact, isolated tropical regions such as Madagascar are well known for being highly heterogeneous, as well as for having highly variable rates of spatial turnover in species composition within particular taxonomic groups (e.g., Fisher 1998; Kremen *et al.* 2008). Neither area method, therefore, considers how the location (as opposed to the total area) of habitat loss influences the magnitude of species extinction (Seabloom *et al.* 2002).

Understanding how the location of habitat loss affects the magnitude of species extinction would be particularly useful for hyper-diverse and highly threatened regions such as Madagascar, widely regarded as a top conservation priority for high biodiversity, high rates of deforestation, and a scarcity of remaining forest (Olson & Dinerstein 1998). Madagascar has four times as many palm species (Dransfield & Beentje 1995) and one-quarter as many vascular plant species as Africa in one-fiftieth the land area (Schatz *et al.* 1996). Similarly, the island has 3% of the world’s land snail species in 0.4% of the world’s land surface (Pearce, unpublished data). Over 83% of vascular plants (Schatz 2000) and as many as 86% of macroinvertebrates are endemic to the island (Goodman & Benstead 2005). Recent analyses using remote sensing reveal that only 10%–15% of original forest remains, with deforestation continuing at around 1% per year (Harper *et al.* 2007). Meanwhile, the human population has more than tripled since 1950, and continues to grow at nearly 3% per year (UNDP 2003). Several measures (e.g., GDP per capita, UNDP 2003) consistently place Madagascar’s economy at the bottom-tenth of all countries, potentially increasing pressure to use remaining natural forests.

We apply a recently developed method for assessing the collective state of biodiversity within any given region (Ferrier *et al.* 2004) to estimate the total proportion of species-level diversity lost (i.e., committed to extinction) as a result of deforestation in Madagascar between 1950 and 2000. This method extends the SAR-based approach to address the problem that species are not uniformly distributed through space, thereby allowing extinction to be estimated as a function of the spatial location of habitat loss. We do this by considering the spatial pattern exhibited by an emergent property (Gaston 2000) of species-level biodiversity: compositional turnover, or the difference in species composition between different locations (also referred to as beta diversity) (Whittaker 1972; Ferrier 2002; Ferrier *et al.* 2004).

Compositional turnover has been inadequately addressed in conservation assessment, despite the relationship between turnover and the better-known concept of endemism. Areas of high endemism are conservation priorities because they contain large numbers of species found nowhere else. The endemism of a given area, however, can also be expressed as a function of species turnover between this and all other areas. Working directly with turnover is advantageous because it provides information on species complementarity between areas. Complementarity is essential for conservation assessments where the objective is not simply to map discrete areas of endemism, but to assess how well alternative combinations of areas would represent (i.e., sample) biodiversity (Ferrier *et al.* 2004).

Because complete range data for most taxa are lacking, turnover is impossible to estimate directly. Instead, we model turnover by combining point-based biodiversity inventory data with continuous environmental data. Environmental data provide complete spatial coverage but are uncertain surrogates for biological patterns (Ferrier *et al.* 2007). On the other hand, biological inventory data are sparse in terms of spatial coverage but provide the real biological entities necessary to measure biodiversity. When linked statistically, the two data sources can be used to predict spatial pattern in biodiversity (Faith & Ferrier 2002; Ferrier *et al.* 2007).

In this article, we combine environmental and biological data in a turnover-based model to predict, and thereby map patterns of biological dissimilarity across the island of Madagascar. We use this model to estimate the proportion of species in our target biological groups that have been lost (i.e., committed to extinction: Simberloff 1986) due to deforestation between 1950 and 2000. By focusing on the ratio of biodiversity loss in forested areas from observed deforestation between 1950 and 2000, we minimize errors that may arise when considering single dates independently due to uncertainty surrounding

pre-human forest extent (Lowry *et al.* 1997). Finally, we test whether forest loss in Madagascar has been significantly biased towards environmentally and biologically distinct areas, resulting in greater species loss than if forest loss had been distributed randomly.

Methods

Data

We used three data sources only recently available across Madagascar: 1) multidecade forest cover data, 2) continuous 1 km² terrain and climate surfaces, and 3) biological survey datasets containing locations for large numbers of species across a wide range of taxa.

To measure deforestation over the study period, we compared a 1950s forest map to a 2000s forest coverage derived from satellite data. The 1950s map (Humbert & Darne 1965) is based on manual interpretation of 1:50,000 scale aerial photographs taken between 1949 and 1957, printed at a scale of 1:100,000, and hand-digitized in 2004 (Harper *et al.* 2007). We based our 2000s map on Harper *et al.*'s (2007) work, created by digitally processing Landsat TM (Thematic Mapper) and ETM+ (Enhanced Thematic Mapper) data from 1999 to 2001. We acquired and processed an additional 20 TM and ETM+ images to classify cloud-covered areas in the Harper *et al.* (2007) map, and then "filled" areas for which no cloud-free Landsat data were available with a MODIS (Moderate Resolution Imaging Spectroradiometer) product (Hansen *et al.* 2003) to produce a cloud-free 2000s forest cover dataset. We resampled the 1950s and 2000s data to 1 km² to match the resolution of the environmental data.

Environmental data consist of 19 monthly temperature and precipitation variables interpolated from data

collected at 177 weather stations between 1930 and 1970 (Hijmans *et al.* 2005). In addition, we used three elevation datasets: a standard 1 km² Digital Elevation Model and two indices of "ruggedness" wherein the value of each cell represents the standard deviation of elevation in a 5- and 10-km² radius.

For biodiversity data we used a wide variety of species-level plant and invertebrate collections (Table 1). We focused on nonvertebrates for two reasons. First, as noted, most species are not vertebrates: any comprehensive biodiversity assessment should consider nonvertebrates to the extent possible. Second, Madagascar's vertebrate distributions are generally better known than those of nonvertebrates, thus their status is well understood relative to other groups.

Modeling turnover in species composition

We modeled species turnover between pairs of sites as a function of their location in environmental and geographical space (first step in Figure 1). We define turnover as the mean proportion of species occurring in one location that are not expected to occur in the other location, measured using the Bray–Curtis index (Wilson & Shmida 1984; Faith *et al.* 1987). First, we divided the island into 1-km² square cells (approximately 590,000 cells total) to match the resolution of available environmental data. We then measured species dissimilarity between all pairs of collection localities for each species (Table 1). At this step, we also measured environmental differences at each pair of collection localities for all environmental variables.

Next, we used a nonlinear extension of permutational matrix regression called generalized dissimilarity modeling (GDM) (Ferrier 2002; Faith & Ferrier 2002; Ferrier *et al.* 2002; Ferrier *et al.* 2007) to model the dissimilarity

Table 1 Biological data used in the analysis

Dataset	Site count	Taxa included	Species count	Presence records	% spp. forest dependent	Source
Ants	191	All spp. in 10 genera	116	1112	98	B. Fisher
Butterflies	702	All described spp.	297	8803	70	C. Kremen, D. Lees
Ferns	136	78% of described spp.	474	3376	79	F. Rakotondrainibe
<i>Ficus</i>	165	All described spp.	24	205	– ^a	Missouri Botanical Garden
Land Snails	155	All described spp.	588	1616	84	T. Pearce
Legumes	2302	All described spp.	373	6449	– ^a	J-N. Labat, D. DuPuy
Palms	322	All described spp.	159	738	98	H. Beentje, J. Dransfield
Plants	1802	Subset ^b	165	2627	100	G. Schatz
Solanaceae	66	All described spp.	28	80	– ^a	Missouri Botanical Garden
Therevid flies	54	19 of 21 described spp.	19	110	84	G. Kampmeier, M. Irwin
Total	5895^c		2243		88	

^a Not currently enough information to assess.

^b Includes data for 165 species endemic to Madagascar.

^c Includes duplicate sites—often incidental—where more than one taxonomic group was surveyed at a single location.

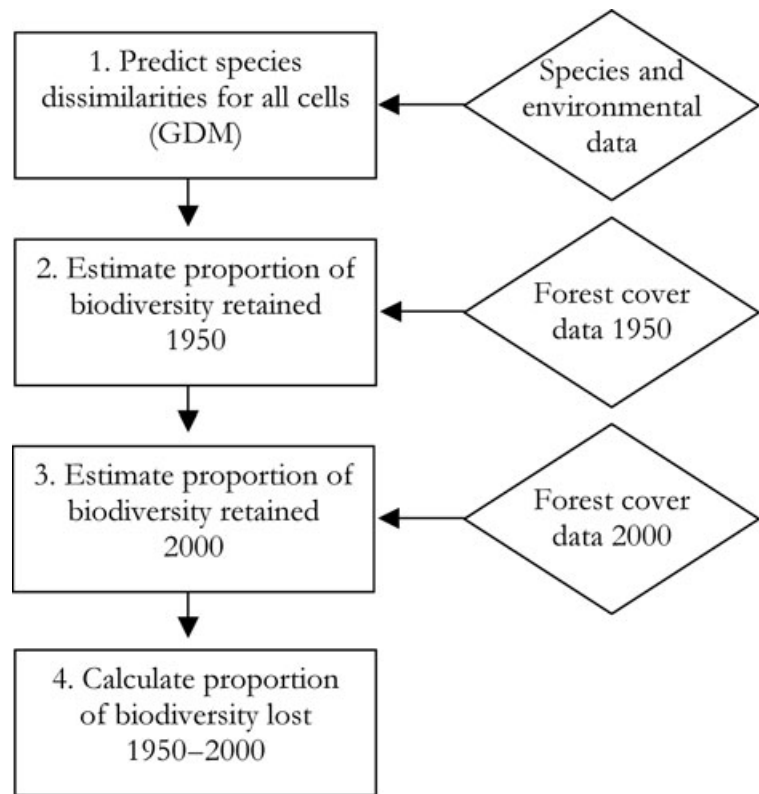


Figure 1 Schematic showing study methodology in four discrete steps.

(d_{ij}) in species composition between all pairs of cells i and j that contain collection localities. Dissimilarity is modeled as a function of the environmental values for the two cells concerned.

GDM produces a parameterized set of nonlinear regression equations, based on known pairs of cells, that relate biodiversity turnover between pairs of cells to differences in environmental and geographic variables. We averaged coefficients for taxon-specific equations to produce a composite model, which we then used to predict biological dissimilarity between any two grid-cells using environmental and geographic attributes alone. To compensate for the potential inflation of observed dissimilarities due to false absences in the biological datasets (i.e., a species may be present, but not recorded, at a location), we excluded the intercept term fitted in the GDM when making predictions from the model. This ensures that two sites with identical environmental values (and geographical locations) are predicted to have a dissimilarity of zero, and that the dissimilarity predicted between all other pairs of sites is scaled accordingly (Ferrier *et al.* 2007).

We derived a map depicting compositional turnover across the island by subjecting the predicted dissimilarities (from the composite model) to metric multidimensional scaling (principal coordinates analysis: Cox & Cox 2001),

and then colored each cell according to its position in relation to the first three axes of the resulting ordination space.

Estimating biodiversity loss

We used the predicted biological dissimilarities described above to derive indices of biodiversity retained in remaining forest areas in 1950, and again in the remaining forest in 2000, to estimate the total proportion of biodiversity lost over the study period. To do this, we followed an analytical approach first described by Ferrier *et al.* (2004). This approach, while rooted in the species–area relationship, differs from most SAR-based applications for measuring biodiversity loss in that it accounts for the effects of nonrandom habitat loss relative to observed spatial pattern in the distribution of biodiversity. By using information on the proportion of species we estimate to be shared between pairs of grid-cells, the approach explicitly takes complementarity into account. In this respect, it bears some resemblance to techniques such as “environmental diversity” analysis (ED, Faith & Walker 1996) and “maximization of complementary richness” (Arponen *et al.* 2008) that use biological dissimilarities, or environmental distances, to estimate the extent to which a selected set of sites represents (i.e., samples) the full

complement of species occurring within a region. In contrast to these other techniques, the approach we employ here invokes the species–area relationship to estimate not only the proportion of a region’s species represented initially in a particular configuration of extant habitat but also the proportion likely to be retained (i.e., to persist) in the longer term, accounting for lag or relaxation effects.

Our approach is nearly identical to that proposed by Ferrier *et al.* (2004); however, in the following description we break their original single formula into a series of steps to assist with explanation. For all n grid-cells across Madagascar we predicted the compositional dissimilarity between any pair of cells (d_{ij} above) and, for the year of interest (1950 or 2000), we knew the state (h_j) of habitat in each cell (1 = forested, 0 = cleared). To simplify subsequent calculations each dissimilarity (d_{ij}) was first converted to a similarity (s_{ij}):

$$s_{ij} = 1 - d_{ij}$$

For each cell i we then used a modification of the traditional SAR approach to estimate the proportion (p_i) of species historically occurring in this cell that are likely to be retained within remaining (uncleared) forest anywhere in their range:

$$p_i = \left[\frac{\sum_{j=1}^n s_{ij} h_j}{\sum_{j=1}^n s_{ij}} \right]^z$$

where z is the exponent of the species–area relationship. We used a z -value of 0.25, a value widely used for this type of assessment. The quantity within the square brackets, to which this exponent is applied, is an estimate of the proportion of forest habitat retained in relation to this particular grid-cell, equivalent to $A_{\text{retained}}/A_{\text{original}}$ in the standard SAR approach. Here, however, grid-cells were viewed as sitting within a continuum of turnover in biological composition, not within discrete community types. Therefore, we estimated the proportion of total forest retained for those species historically occurring in a given “focal” cell i as a weighted average of the state of all “related” cells within this continuum. The contribution that related cells made to the total estimated proportion of habitat retained for each focal cell was weighted according to predicted similarity between pairs of cells.

At this point, the overall proportion of species (p) retained across the island could potentially be estimated as a simple average of p_i values across all cells. However, this approach would not adequately consider the effects of compositional overlap between cells. To address these effects, p needs to be derived as a weighted average of the p_i values for individual cells:

$$p = \frac{\sum_{i=1}^n w_i p_i}{\sum_{i=1}^n w_i}$$

with weights (w_i) calculated as:

$$w_i = \frac{1}{\sum_{j=1}^n (s_{ij})}$$

These weights adjust for compositional overlap between cells, and play a vital role in ensuring that appropriate emphasis is given to more distinctive cells (i.e., cells that are similar to few other cells) relative to cells that are similar to many other cells.

To illustrate, imagine a set of 1,000 cells that are compositionally identical to one another (i.e., all cells within the set share the same species), and share no species with any other cells in the region. A second set of 10 cells is also compositionally identical within the set, with no species overlap beyond the set (including no overlap with cells in the first group). If no weighting is applied, the first group will have 100 times more influence, relative to the second group, in deriving an average p value for the region, simply because it has 100 times more cells. However, under the weighting scheme defined above, these two groups of cells would contribute equally to the weighted regional mean—which is appropriate given that both groups are internally homogeneous, and equally distinct from the remainder of the region.

We use the term “retained” here in the sense of long-term retention. As with any SAR-based approach, the predicted biodiversity loss may take time to be realized, due to lag or relaxation effects, and thus represents “commitment to extinction” (Simberloff 1986).

We estimated total biodiversity lost from deforestation between 1950 and 2000 by performing two runs of the analysis, one based on the state of cells (forested or cleared) in 1950 and the other in 2000.

Finally, we tested the effect of the spatial location of deforestation on biodiversity loss. To do this, we randomly distributed the same total area of deforestation from 1950 to 2000 within the actual forested region from 1950, and calculated biodiversity loss under this new pattern. We did this 500 times to produce a distribution of biodiversity loss under random spatial patterns of deforestation.

Results

Our analysis finds that forest in Madagascar covered 16.0 million ha in 1950 and 9.5 million ha in 2000, representing a 40.4% loss of forest during that period (Figures 2b

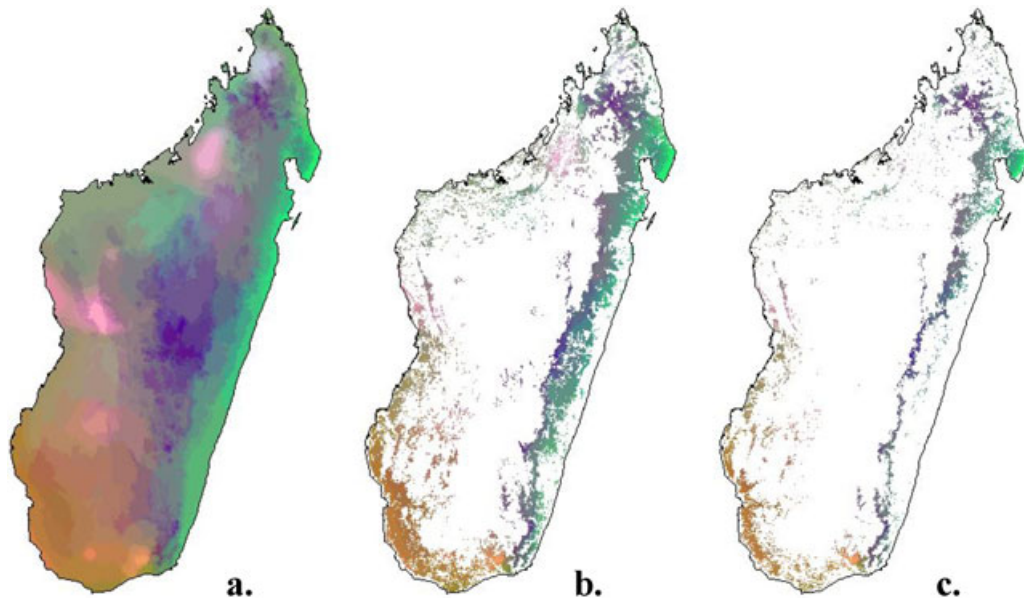


Figure 2 Predicted pattern of biological dissimilarity across Madagascar prior to habitat loss (a) and in remaining forest in 1950 (b) and 2000 (c). Cells are colored according to their positions along three axes of a metric multi-dimensional scaling space fitted to predictions from the composite

GDM model. Similar color tone indicates similar biological composition. We use GDM to estimate biodiversity retained in forest in 1950 and 2000 and subtract these figures to estimate total biodiversity lost over the study period.

and 2c). This latter estimate differs slightly from the most recent peer-reviewed island-wide analysis of Madagascar forest cover (Harper *et al.* 2007) due to the addition of cloud-free data and the resampling of the data to 1 km².

Our analysis predicts that 9.1% of species in Madagascar have been committed to extinction as a result of forest loss between 1950 and 2000. This number is in addition to the 32.9% of species we estimate to have been committed to extinction by habitat loss up to 1950 alone. The average of 500 random distributions of the same amount of deforestation yields an estimated biodiversity loss of 6.5% between 1950 and 2000, which is 28.6% lower than that estimated from the observed deforestation pattern. Only 16 of 500 randomizations produced a biodiversity loss greater than or equal to 9.1% ($p = 0.032$).

Discussion

The method applied here combines the complementary strengths of biological inventories and continuous environmental data (Ferrier *et al.* 2004) to predict biodiversity loss from deforestation. Using the model, we estimate that Madagascar lost 9.1% of its total biodiversity from deforestation between 1950 and 2000. Our total estimate of 42% biodiversity loss up to 2000 (third step Figure 1) is consistent with a recent report that found that 43% of

Madagascar's endemic forest dwelling *Helictopleurini* dung beetles are "effectively extinct" due to regional forest loss since 1953 (Hanski *et al.* 2007).

The estimated loss between 1950 and 2000 is higher than expected from simulations of random deforestation (6.5%), suggesting that actual deforestation patterns are biased towards environmentally and biologically distinct areas (Figures 2b and 2c). In other words, the distribution of deforestation is clumped within environmental and biological space. This means that the remaining (uncleared) forest is less effective in representing (sampling) the full diversity of the island, than if the same area of forest were distributed at random. This bias is not revealed with traditional, species–area methods for estimating biodiversity loss because they, like our randomizations, depend only on the amount of deforestation, without considering the spatial distribution of forest loss in relation to compositional pattern in the distribution of biodiversity.

There are several potential explanations for this result. Many studies document positive relationships between species richness, primary productivity, and human population density at regional to continental scales (e.g., Luck 2007). Madagascar might also follow this pattern, whereby humans selectively clear areas of high productivity that also contain high species richness and thus higher numbers of endemic species. Fjelds  (2007) suggests that areas of high topographical complexity

encourage species endemism by conferring climatic stability over short- and long-term time periods. Humans may also tend to select these areas for agriculture, as they would facilitate year-round cropping and buffer longer-term climatic fluctuations that challenge agriculture productivity in other regions (Fjeldså 2007).

Regardless of what is driving observed deforestation patterns, because forest clearing has been clustered in particular environments, remaining forest under-represents original diversity (both environmentally and biologically). Had deforestation been random, then additional sites would survive to represent additional species, and the magnitude of species loss would be lower than that found under the observed pattern. While further work is needed to clarify these and other mechanisms, the resulting deforestation bias is alarming and can inform conservation efforts immediately.

For example, the approach described in this article has potential to support an ongoing Madagascar conservation planning effort known as the “Durban Vision”—a plan currently underway to triple the protected area system (Norris 2006). Many large new parks have already been selected; much of the total area protected, however, will be subject to a wide range of uses (equivalent to IUCN categories I–VI). These techniques can help identify areas requiring strict protection to minimize species loss.

More generally, these methods can inform many types of policy and management decisions. GDM-based modeling has already been proposed (Faith & Ferrier 2005) as a way to approach the globally recognized 2010 biodiversity target (a reduction in the rate of biodiversity loss) under the Convention on Biological Diversity. Our work shows how this method can measure historic trends in biodiversity loss (Figures 2b and 2c), and can be used to propose remedies by mapping areas to minimize biodiversity loss of future development (Figure 2c). Conceivably, this technique has broad applicability to any land-use planning exercise where information is needed on biodiversity impact of past—or future—habitat loss.

Several other issues and caveats are worth noting. First, species vary widely in their degree of dependence on forest habitat, and some areas that are not fully forested still retain some of Madagascar’s pre-1950 biodiversity. Numerous endemic bird species, for example, can be found within even the most urbanized areas. Likewise, a number of species may be limited more by the presence of geologic formations rather than by native or intact forest. Examples include karst for several endemic land snails and cave roosting sites for bats (Goodman *et al.* 2005). Nevertheless, we estimate that at least 88% of analyzed species are not normally able to survive outside of relatively intact, mature forest (Table 1).

Second, this article has focused on changes in Madagascar forest cover since 1950, the earliest date for which island-wide forest cover data are available. However, 1950 serves as an arbitrary baseline from which to measure biodiversity change. Considerable deforestation and extinctions occurred prior to this date, including the loss of many species now known only from sub-fossils. We emphasize that the predicted biodiversity loss for 1950–2000 is additional to that lost before 1950: 9.1% represents a large fraction of an already greatly reduced biodiversity.

Finally, additional work is needed to clarify differences between several methods now available to measure biodiversity retention under alternative configurations of intact sites in time or space. Available approaches include Faith (1996), Arponen *et al.* (2008), and the methods presented here and in Ferrier *et al.* (2004). Although these approaches all provide a biodiversity loss/retention measure, they differ in specifics. For example, in contrast to the approach described here, under the ED method (Faith & Walker 1996), the amount of biodiversity estimated to be retained would depend more on how spread out intact sites are in environmental space, and less on the proportion of habitat retained in any part of this space. Further work is necessary to compare these alternatives in detail.

Though few places surpass Madagascar’s global biodiversity importance, many other regions are similarly characterized by high biodiversity, high threat, and a relative scarcity of information on the majority of threatened species. As such, it is generally most difficult to assess and plan for the conservation of biodiversity in the very places where it is most urgent and critical to do so. The model applied here helps to overcome this limitation by combining sparse biological data with environmental data to map relative biological dissimilarity and estimate biodiversity loss.

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References

- Arponen, A., Moilanen A., Ferrier S. (2008) A successful community-level strategy for conservation prioritization. *Journal of Applied Ecology* **45**, 1436–1445.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology* **9**, 95–99.
- Brooks, T.M., Bakarr M.I., Boucher T. *et al.* (2004) Coverage provided by the global protected-area system: is it enough? *BioScience* **54**, 1081–1091.
- Clark, J.A., May R.M. (2002) Taxonomic bias in conservation research. *Science*, **297**, 191–192.
- Cox, M.F., Cox M.A.A. (2001) *Multidimensional scaling*. Chapman and Hall/CRC, Boca Raton, FL.
- Dransfield, J., Beentje H. (1995) *The palms of Madagascar*. The Royal Botanic Gardens Kew and The International Palm Society, Norwich, UK, p. 475.
- Faith, D., Ferrier S. (2002) Linking beta diversity, environmental variation, and biodiversity assessment. *Science* **296** [Online]. Available from: <http://www.sciencemag.org/cgi/eletters/295/5555/636#504>. Accessed July 22, 2002.
- Faith, D.P., Ferrier S. (2005) Good news and bad news for the 2010 biodiversity target. Available from: <http://www.sciencemag.org/cgi/eletters/307/5707/212#1272>. Accessed September 5, 2008.
- Faith, D.P., Minchin P.R., Belbin L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.
- Faith, D.P., Walker P.A. (1996) Environmental diversity: on the best-possible use of surrogate data for assessing the relative biodiversity of sets of areas. *Biodiversity and Conservation*, **5**, 399–415.
- Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology*, **51**, 331–363.
- Ferrier, S., Drielsma M., Manion G., Watson G. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. *Biodiversity and Conservation* **11**, 2309–2338.
- Ferrier, S., Manion G., Elith J., Richardson K. (2007) Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions* **13**, 252–264.
- Ferrier, S., Powell G.V.N., Richardson K.S. *et al.* (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience* **54**, 1101–1109.
- Fisher, B. (1998) Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the western Masaola Peninsula, Madagascar. *Fieldiana: Zoology* **90**, 39–67.
- Fjeldså J. (2007) The relationship between biodiversity and population centres: the high Andes region as an example. *Biodiversity and Conservation* **16**, 2739–2751.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* **405**, 220–227.
- Goodman, S.M., Andriafidison D., Andrianaivoarivelo R. *et al.* (2005) The distribution and conservation of bats in the dry regions of Madagascar. *Animal Conservation* **8**, 153–165.
- Goodman, S.M., Benstead J.P. (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* **39**, 1–5.
- Hansen, M., DeFries R., Townshend J.R., Carroll M., Dimiceli C., Sohlberg R. (2003) 500m MODIS vegetation continuous fields. *The global land cover facility*, College Park, Maryland.
- Hanski, I., Koivulehto H., Cameron A., Rahagalala P. (2007) Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters* **3**, 344–347.
- Harper, G.J., Steininger M.K., Tucker C.J., Juhn D., Hawkins F. (2007) Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* **34**, 325–333.
- Hijmans, R.J., Cameron S.E., Parra J.L., Jones P.G., Jarvis A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.
- Humbert, H., Darne G.C. (1965) Carte internationale du tapis végétal et des conditions écologiques. 3 coupures au 1/1,000,000 de Madagascar. *Trav. Sect. Sci. Tech.* Institut Français de Pondicherry, Pondichery.
- Kinzig, A.P., Harte J. (2000) Implications of endemics–area relationships for estimates of species extinctions. *Ecology* **81**, 3305–3311.
- Kremen, C., Cameron A., Moilanen A. *et al.* (2008) Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* **320**, 222–226.
- Lowry, P.P., Schatz G.E., Phillipson P.B. (1997) The classification of natural anthropogenic vegetation in Madagascar. Pages 93–123 in S.M. Goodman, B.D. Patterson, editors. *Natural Change and Human Impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.
- Luck, G.W. (2007) The relationships between net primary productivity, human population density and species conservation. *Journal of Biogeography* **34**, 201–212.
- May, R.M. (1988) How many species are there on Earth? *Science* **241**, 1441–1449.
- Norris, S. (2006) Madagascar defiant. *BioScience* **56**, 960–965.
- Olson, D.M., Dinerstein E. (1998) The global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology* **12**, 502–515.
- Pimm, S.L., Askins R. (1995) Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 9343–9347.

- Ridgely, R.S., Allnutt T.F., Brooks T. *et al.* (2007) *Digital distribution maps of the birds of the Western Hemisphere, version 3.0*. NatureServe, Arlington, VA.
- Schatz, G.E. (2000) Endemism in the Malagasy tree flora. Pages 1–9 in W.R. Lourenço, S.M. Goodman, editors. *Diversité et Endémisme a Madagascar*. Mémoires de la Société de Biogéographie, Paris, France.
- Schatz, G.E., Lowry II P.P., Lescot M. *et al.* (1996) Conspectus of the vascular plants of Madagascar: a taxonomic and conservation electronic database. Pages 10–17 in J.G. van der Maesen, X.M. van der Burgt, J.M. van Medenbach de Rooy, editors. *The biodiversity of african plants*. Kluwer Academic, Wageningen, The Netherlands.
- Schoener, T.W. (1976) The species–area relation within archipelagos: models and evidence from island land birds. Pages: 187–197 in H.J. Frith, J. H. Calaby, editor. *Proceedings of the 16th International Ornithological Congress*. Australian Academy of Science, Canberra, Australia.
- SCHATZ (2000). *Diversité et endémisme a Madagascar*, EDITORS: WILSON. R. Lourenço And STEVEN M GOODMAN. Mémoires de la Société de Biogéographie, Paris.
- Seabloom, E.W., Dobson A.P., Stoms D.M. (2002) Extinction rates under nonrandom patterns of habitat loss. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 11229–11234.
- Simberloff, D. (1986) Are we on the verge of a mass extinction in tropical rain forests? Pages 165–180 in D.K. Elliott, editor. *Dynamics of extinction*. Wiley, New York.
- UNDP (2003) *Human development report: millennium development goals: a compact among nations to end human poverty*. United Nations Development Programme, New York.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* **21**, 213–251.
- Wilson, M.V., Shmida A. (1984) Measuring beta diversity with presence absence data. *Journal of Ecology* **72**, 1055–1064.

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