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# Using nestedness and species-accumulation analyses to strengthen a conservation plan for littoral forest birds in south-eastern Madagascar

**James E.M. Watson[1,2]\*, Alexander W.T. Watson[3], Joern Fischer[4], J. Carter Ingram[5] and Robert J. Whittaker[2]**

[1]Centre for Applied Environmental Decision Analysis, The Ecology Centre, The University of Queensland, St Lucia, Queensland 4072, Australia.
[2]Biodiversity Research Group, Oxford University Centre for the Environment, Oxford, OX1 3QY, United Kingdom.
[3]Centre for Ecosystem Management, Edith Cowan University, 100 Joondalup Drive, Perth, WA, 6027, Australia.
[4]The Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia.
[5]Earth Institute, Columbia University, 1200 Amsterdam Avenue, 10th Floor Schermerhorn Extension, New York, NY 10027-5557, United States of America.

**The littoral forests of south-eastern Madagascar are among the most threatened ecosystems on the island. A conservation plan has been developed for the region due to a proposed mining venture. Here, we provide a novel methodology to assess if the planned conservation measures would effectively conserve the bird diversity inhabiting these forests. Bird community composition within 30 littoral forest fragments was quantified with each fragment characterized by measures of fragment area, isolation, and internal habitat complexity. A nestedness and cumulative species–area analysis was conducted to ascertain the contribution of forest fragments of different sizes in capturing the overall bird species richness. Datasets representing the overall and forest-dependent bird assemblages were found to be significantly nested. The pattern of nestedness appeared to be driven by fragment size. However, cumulative species–area analyses showed that the assemblages were imperfectly nested with ten species displaying idiosyncratic distribution patterns. When a modest conservation target was set (the occurrence of a bird species in three or more fragments), the proposed conservation plan would only protect approximately half the species found in the littoral forests. We show that protecting an additional four large patches would mean that the proportion of forest-birds captured in three or more patches would increase to 70%.**

**Key words:** Madagascar, conservation, littoral forest, mining, fragmentation, nestedness.

## INTRODUCTION

The island of Madagascar, a biodiversity hotspot and one of the poorest countries in the world, has experienced alarming deforestation (Smith, 1997; Mittermeier et al., 1998; Dufils, 2003). Every forested ecosystem on the island has been subject to deforestation (Jolly and Jolly, 1984; Kull, 2002; Kistler and Spack, 2003). However, deforestation has not been uniform, and some ecosystems are more fragmented than others (Du Puy and Moat, 1996; Ingram and Dawson, 2005), none more so than the littoral forests along the eastern coast (Dumetz, 1999; Ganzhorn et al., 2001; Bollen and Donati, 2006; Consiglio et al. 2006). Human activities (e.g. selective logging and slash-and-burn agriculture) and natural hazards (e.g. cyclones) have reduced this forest type so that no more than 48 000 ha remains (Du Puy and Moat, 1996; Ganzhorn et al., 2001).

Madagascar's littoral forest is distributed along a narrow band of sand and alluvium within approximately 10 km of the eastern coast (Lowry and Faber-Langendoen, 1991; Schatz, 2000). It is recognized as a floristically distinct ecosystem containing endemic invertebrate and plant species, and special combinations of vertebrate fau-

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\*Corresponding author. E-mail: james.jameswatson@gmail.com

na (Dumetz, 1999; Ganzhorn et al., 2000; Cadotte et al., 2002; Watson et al., 2005a). The littoral forest in the southeast of the island is of special interest because it contains approximately 4000 ha of Madagascar's most intact littoral forest fragments and therefore is considered a stronghold for littoral forest conservation (Figure 1; Dumetz, 1999). It also contains a unique bird assemblage in that it supports both spiny-forest and humid forest-dependent species (Watson et al., 2005a). Within this region, two different sub-types of littoral forests ('Petriky' and 'Mandena/Ste-Luce') have been identified based on vertebrate and plant communities (Dumetz, 1999; Ingram, 2004; Watson et al., 2005a; Figure 1).

The littoral forests found in the southeast continue to be slowly degraded as a result of charcoal-making by itinerant people (Ingram, 2004) and clearance for tavy (shifting cultivation) in Ste. Luce (JW, JCI field observations). Local people use the littoral forest trees for a variety of purposes, such as fuel-wood, construction materials, food and medicine (Ingram, 2004). Unlike forest clearance, these selective-use practices tend to alter the internal structure of the forest rather than forest extent (Ingram, 2004).

Although it is difficult to predict how the use from local communities might change in the future, a more specific threat to littoral forests is provided by a proposed mining venture. QIT-Fer et Titane (QMM), a subsidiary of Rio Tinto plc (Andrianarimisa et al., 2000), have stated they aim to clear up to 80% of the littoral forests of southeastern Madagascar for the production of Titanium Dioxide in the next 60 years. The company conducted an extensive exploration program along the east coast of Madagascar surrounding Fort Dauphin for heavy mineral sands in 1986, which led to the discovery of a potentially economically-viable ore body located underneath the littoral forest fragments. As part of the mining plan, QMM have identified five conservation zones that are to be preserved within the 4000 ha of littoral forest. These conservation zones include four large blocks in the Mandena/Sainte Luce sub-type (totalling 820 ha) and one block in the Petriky sub-type (60 ha) (Vincelette et al., 2003). The littoral forest outside of these conservation zones will be part of the long-term mining operation planned for the region. The conservation zones were selected in consultation with people living in the surrounding communities, Eaux et Forêts authorities, and experts collaborating with the QMM project. It was argued that '…their preservation, in concert with well designed restoration activities, should permit the maintenance of a significant portion of biodiversity in the mining zone beyond the end of the proposed mining activities' (Vincelette et al., 2003).

The aim of this paper is to assess whether the conservation zones effectively capture the bird diversity inhabiting littoral forest of the larger northern sub-type of Mandena and Ste-Luce. Birds were used because they were easier to survey than other taxa and they are also the best-studied taxon in the littoral forests of southeastern

Madagascar (Goodman and Patterson, 1997; Bollen, 2003; Bollen et al., 2004a, b; Watson et al., 2004, 2005a, b). The effective conservation of birds is a necessary but, by itself, not a sufficient condition for the conservation of biodiversity more generally.

Two sets of analyses were employed to assess whether the protection of four relatively large fragments would be sufficient to capture the littoral forest bird communities in Mandena and Ste-Luce littoral forests. First, several measures of community 'nestedness' were used to assess if the protection of a small number of large fragments is a suitable strategy for bird conservation in the region. Nestedness can arise, in theory, from several different mechanisms, including differential colonization of fragments, differing area requirements, habitat nestedness and differential extinction from isolates (Whittaker and Fernández-Palacios, 2007; Ulrich et al., 2009). However, the principal focus of nestedness analyses in fragmentation research is with the last of these mechanisms within a framework derived from island theory and focused on the process of species relaxation. Some studies have reported that this process can result in a nested assemblage, whereby the species present in smaller fragments are a subset of those in successively larger fragments (Patterson and Atmar, 2000; review in Whittaker and Fernández-Palacios, 2007), indicating predictable, differential vulnerability of species to extinction as a function of fragment size. If a series of habitat fragments are perfectly nested for a particular taxon and if species richness of that taxon monotonically increases with area, it follows that the single largest fragment will always have more species than will any combination of several smaller small reserves of equal area (Patterson, 1987). Nestedness has been analysed for a range of organisms, including amphibians (Baber et al., 2004), reptiles (Mac Nally and Brown, 2001), mammals (Lynam and Billick, 1999), butterflies (Fleishman and Murphy, 1999), fungi (Berglund and Jonsson, 2003), plants (Berglund and Jonsson 2003; Jacquemyn et al., 2007) and birds (Blake, 1991; Fernandez-Juricic, 2002; Hannson, 1998; Mac Nally et al., 2002; Lazaro et al., 2005;). Perfect nestedness is rare, but empirical work to date supports a significant tendency towards nestedness for many systems (Wright et al., 1998; Whittaker and Fernández-Palacios, 2007).

The second set of analyses followed Quinn and Harrison's (1988) methodology for using species accumulation curves to assess the contribution of patches of different sizes in capturing the overall species richness of the given landscape (Fischer and Lindenmayer, 2002a). This analysis is useful in determining how important large patches are compared to small patches in conservation planning.

To date, no formal study has assessed how best to conserve littoral forest bird diversity in south eastern Madagascar or the likely effectiveness of the conservation zones proposed by the mining company. Furthermore, to our knowledge, no study has combined nestedness and
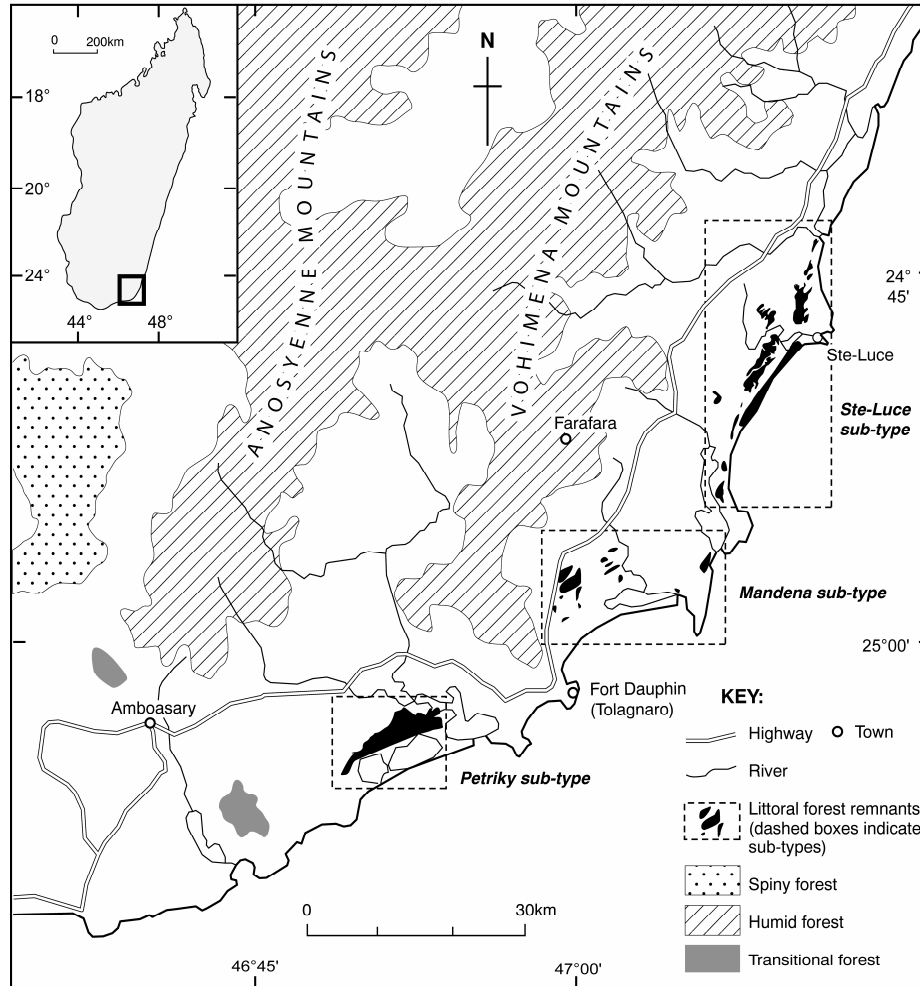
**Figure 1.** The location of littoral forest fragments surveyed in southeastern Madagascar. The matrix surrounding littoral forest fragments includes marécage swamp forest, *Melaleuca* forest, plantations of *Eucalyptus citriodora* and *Eucalyptus robusta*, and heath-type vegetation consisting predominately of *Erica* spp. Forest extent was based on the Figure presented in Ramanamanjato et al. (2002).

species accumulation analyses to asses the implications of conservation plans for threatened biodiversity in a fragmented landscape. The implications of this research with respect to the design of nature reserves in the littoral forest landscapes of southeastern Madagascar are explored in the discussion.

**MATERIALS AND METHODS**

**Study area**

The study was conducted in 30 stands of littoral forest located to the west and north of the township of Fort Dauphin, southeastern Madagascar (Figure 1 and Table 1). The littoral forest consists of a series of fragments sharply interspersed by a heath-type matrix consisting of *Erica* spp. (formerly Phillippia spp.) (Ramanamanjato and Ganzhorn, 2001). The abrupt boundary between dense humid forest and non-forest types is a puzzling feature of Madagascar's landscape. It is attributed to climate and prehistoric fires and it has been recently discovered that these fragments have been isolated

for many thousands of years, indicating they are islands of forest in a matrix of heath. The southeast of Madagascar has a subtropical climate with a regional mean annual minimum temperature of 15°C, mean maximum temperature of 28°C, and mean annual rainfall ranging from 500 - 3000 mm (Goodman and Patterson, 1997).

**Bird surveys**

Species presence within 30 littoral forest fragments and habitat-dependency of birds were determined using a combination of point-counts (Bibby et al., 1998) and the species-list census technique of MacKinnon and Phillips (1993). To analyse how well the mining conservation plan captures (that is represents) forest-dependent bird species, we had to be sure that we had obtained an accurate picture of which species occur in all 30 littoral forest remnants. Analyses of these data using rarefaction methodologies showed that the combined methodologies provided a highly accurate representation of the bird species present in the fragments (O'Dea et al., 2004). A full list of the birds found in each fragment and the detailed methodology of the bird census technique are provided in Watson et al. (2004).

**Table 1.** Geographic data, bird species richness and number of endemic bird species per littoral forest fragment. Island endemic was defined as species endemic to Madagascar while regional endemic was defined as species endemic to Madagascar, Comoros and Mascarenes. Sources for status and endemism were from Wilmé and Goodman (2003).

| Fragment name | Sub-type | Latitude/Longitude | Area (ha) | Species number | Forest-dependent species number | Number of regional endemics | Number of island endemics |
|---|---|---|---|---|---|---|---|
| M1 | Mandena | 24° 45′ 01″ S  47° 10′ 55″ E | 126 | 42 | 22 | 15 | 19 |
| M4 | Mandena | 24° 57′ 37″ S  47° 01′ 01″ E | 47 | 30 | 11 | 10 | 12 |
| M5 | Mandena | 24° 56′ 49″ S  47° 06′ 17″ E | 25 | 25 | 5 | 8 | 9 |
| M6 | Mandena | 24° 56′ 07″ S  47° 01′ 51″ E | 17 | 21 | 4 | 9 | 5 |
| M7 | Mandena | 24° 56′ 57″ S  47° 01′ 33″ E | 13.7 | 15 | 1 | 6 | 4 |
| M15 | Mandena | 24° 58′ 01″ S  47° 00′ 33″ E | 116 | 45 | 22 | 17 | 19 |
| M16 | Mandena | 24° 59′ 21″ S  46° 59′ 51″ E | 73 | 33 | 14 | 14 | 12 |
| M20 | Mandena | 24° 57′ 14″ S  47° 04′ 23″ E | 23 | 19 | 6 | 8 | 6 |
| MA | Mandena | 24° 56′ 36″ S  47° 01′ 02″ E | 0.8 | 7 | 0 | 2 | 2 |
| MB | Mandena | 24° 56′ 52″ S  47° 00′ 21″ E | 0.4 | 8 | 0 | 3 | 2 |
| MC | Mandena | 24° 56′ 32″ S  47° 00′ 52″ E | 0.9 | 11 | 0 | 4 | 3 |
| MD | Mandena | 24° 56′ 20″ S  47° 02′ 16″ E | 2.8 | 13 | 2 | 6 | 3 |
| ME | Mandena | 24° 58′ 01″ S  46° 59′ 33″ E | 5.9 | 14 | 2 | 6 | 4 |
| MF | Mandena | 24° 56′ 17″ S  47° 00′ 48″ E | 1.8 | 9 | 1 | 2 | 3 |
| MG | Mandena | 24° 58′ 02″ S  46° 59′ 09″ E | 4.1 | 16 | 2 | 7 | 3 |
| S1 | Ste-Luce | 24° 43′ 07″ S  47° 11′ 08″ E | 31 | 28 | 13 | 12 | 9 |
| S7 | Ste-Luce | 24° 47′ 17″ S  47° 09′ 12″ E | 254 | 42 | 28 | 15 | 20 |
| S8 | Ste-Luce | 24° 46′ 12″ S  47° 09′ 09″ E | 172 | 44 | 21 | 15 | 17 |
| S9 | Ste-Luce | 24° 45′ 39″ S  47° 10′ 19″ E | 464 | 58 | 35 | 17 | 30 |
| S10 | Ste-Luce | 24° 44′ 22″ S  47° 11′ 51″ E | 17 | 28 | 10 | 11 | 12 |
| S11 | Ste-Luce | 24° 44′ 20″ S  47° 10′ 44″ E | 35.3 | 36 | 19 | 11 | 18 |
| SH | Ste-Luce | 24° 46′ 41″ S  47° 09′ 47″ E | 0.4 | 10 | 0 | 1 | 3 |
| S17 | Ste-Luce | 24° 48′ 43″ S  47° 08′ 31″ E | 297 | 46 | 24 | 17 | 21 |
| SA | Ste-Luce | 24° 46′ 01″ S  47° 09′ 49″ E | 0.4 | 9 | 0 | 3 | 3 |
| SB | Ste-Luce | 24° 46′ 41″ S  47° 09′ 55″ E | 1.4 | 9 | 0 | 4 | 2 |
| SC | Ste-Luce | 24° 48′ 55″ S  47° 08′ 46″ E | 5.7 | 16 | 1 | 5 | 6 |
| SD | Ste-Luce | 24° 46′ 14″ S  47° 09′ 35″ E | 1 | 12 | 1 | 4 | 3 |
| SE | Ste-Luce | 24° 46′ 57″ S  47° 08′ 46″ E | 0.5 | 10 | 0 | 3 | 5 |
| SF | Ste-Luce | 24° 46′ 51″ S  47° 08′ 52″ E | 1.4 | 9 | 1 | 3 | 2 |
| SG | Ste-Luce | 24° 47′ 01″ S  47° 08′ 51″ E | 0.7 | 8 | 0 | 1 | 2 |

## Habitat complexity

Vegetation structural complexity of patches was measured using a rapid appraisal method that was first developed by Newsome and Catling (1979). For each fragment, a habitat complexity score (HCS) modified from that described by Catling and Burt (1995) was derived on the basis of five habitat attributes:

i) Canopy cover (percentage of crown cover of trees > 10 m high).
ii) Litter cover (percentage of leaf litter and fallen dead vegetation).
iii) Low shrub cover (percentage of shrub cover between 0 and 0.5 m high).
iv) Medium shrub cover (percentage of shrub cover between 0.5 and 2m high).
v) Tall shrub cover (percentage of shrub cover between 2 and 6 m high).

The five categories were chosen to represent a range of vertical structure and habitat complexity measurements, each of which can strongly influence the diversity of bird species (Ford  and Barrett,

1995) and may be affected when a habitat is degraded by human activity, such as fire-wood collection (Bentley and Catteral, 1997; Cadotte et al., 2002; Vallan, 2002). All habitat variables were recorded as continuous data and were collected at every point count station, using the same 25 m radius used for the bird sampling. Each attribute was rated as a percentage, and the scores for the five attributes were totalled to give an overall score for each point count. Each fragment habitat complexity score was the mean score for point counts conducted in each fragment.

## Patch and landscape attributes

We used a supervised, classified Landsat TM 7 satellite image acquired on 11 November 1999 and ArcView GIS software to measure each patch area (ha) and 'isolation'. The image was both geo-rectified and orthorectified. There has been criticism of the use of a single 'isolation' measure in fragmentation related research (Bender et al., 2003; Tischendorf et al., 2003). We therefore used three

measures of isolation: distance to nearest large (>1000 ha) block of forest (DS), distance to the nearest fragment > 100 ha (DR), and distance to nearest fragment (DRN). Measurements from the edge, rather than the centre of the patch, were used to calculate isolation measurements.

## Statistical analysis

Because spatial autocorrelation can influence results in spatial analyses, we conducted a spatial autocorrelation analysis using SAAP 4.3 software (Wartenberg, 1989; Hawkins and Pausas, 2004). We generated spatial correlograms at eight distance classes for the raw littoral species richness data, using Moran's I coefficients (Legendre, 1993).

Many methods are available to assess nestedness, and different methods have different limitations (Atmar and Patterson, 1993; Lomolino, 1996; Wright et al., 1998; Fischer and Lindenmayer 2005a, b; Ulrich et al., 2009). We used a combination of methods to overcome these limitations. Initially, a nested subset analysis was performed using the Nestedness Temperature Calculator (Atmar and Patterson, 1995). In this program the Temperature (T°) value is used to evaluate the degree of nestedness. The temperature may vary between 0 and 100°, and it is an absolute disorder index, based on the differences between a theoretical perfectly nested system (T° = 0°) and the observed system. This methodology has the advantage of being widely used in other nestedness studies for a wide range of taxa, including birds (Patterson and Atmar, 2000), amphibians (Ficetola and De Bernardi, 2004) and insects (Davidar et al., 2002). However, the significance of nestedness (T°) obtained using the Monte Carlo simulations in the Nestedness Temperature Calculator has been criticised because it can overestimate the actual nestedness level (Fischer and Lindenmayer, 2002b). This is because the null-model used by the nestedness calculator assumes that each cell of presence/absence has an equal probability of being occupied. Therefore, the null-model does not differentiate between species or patches, and only the total number of occupied cells in each simulated matrix is held constant in the simulations.

Following the methods described in Fischer and Lindenmayer (2005a), the discrepancy measure of Brualdi and Sanderson (1999) was used to measure the significance of nestedness. The null model used was the RANDNEST model (Jonsson, 2001). The RANDNEST model provides a suitable neutral background in this context because, for a given species, it assumes equal probabilities of occurrence between patches, but the probability of occurrence differs between species, and is directly proportional to the number of sites at which the species was detected in the original data matrix (Fischer and Lindenmayer, 2002b). The discrepancy measure, termed percent perfect nestedness (Kress et al., 2001), was derived as follows:

$$\%PN = 100 * (R - D) / R$$

Where; R is the mean matrix-wide discrepancy obtained from random simulations, and D is the observed matrix-wide discrepancy.

The matrix-wide discrepancy is the number of species presences that would have to be shifted to a different site to create a perfectly nested matrix. Nestedness may result from a number of possible mechanisms, including: selective extinction of species in deterministic order from sites too small to sustain them; deterministic patterns of colonisation of sites in relation to size and remoteness; nestedness of habitat types within littoral forest fragments; and passive sampling (Cook and Quinn, 1995; Lomolino, 1996; Whittaker and Fernández-Palacios, 2007). Passive sampling was effectively controlled for by using the RANDNEST null model (Jonsson, 2001). To assess the role of selective extinction, immigration or habitat nestedness in producing the nestedness patterns in birds of the littoral forests, we used the discrepancy measure when the matrix was sorted by area, HCS and the three measures of isolation described above.

One of the strongest criticisms of research examining nestedness is that organisms are often considered independently of their association with the habitat under consideration (Fischer and Lindenmayer, 2005a). To overcome this, we categorised species by their forest-dependence based on Watson et al. (2004). This research classified species as forest-dependent if they occurred in extremely low abundance in, or were absent from, the matrix habitat. All species that were not categorised as forest-dependent were considered 'habitat generalists'. We confirmed our classifications using the species accounts in Wilmé and Goodman (2003) and found a close match between our definitions of forest dependence and theirs. We repeated all nestedness analyses using only the forest-dependent species subset.

In addition to calculating the overall nestedness among the bird communities of the littoral forests, we also attempted to identify any idiosyncratic species and sites in the landscape and ascertain reasons why they did not follow the predicted nested pattern. The methodology employed followed Patterson and Atmar (2000), where species with a notably higher temperature than the matrix temperature were considered idiosyncratic [NB the term matrix here refers to the statistical properties of the data matrix rather than 'matrix habitat']. These species are of special interest because they follow a distribution that is not consistent with the pattern predicted by relaxation, and hence may not be conserved in a landscape that protects the largest fragments first.

Finally, cumulative species–area curves were used to assess the relative contribution made by small and by large patches to overall regional species richness. Patch areas were first ordered from large to small, and values for cumulative area and cumulative number of species were calculated; for comparison, the analysis was repeated with patches ordered from small to large (Quinn and Harrison, 1988; Fischer and Lindenmayer, 2002a). We also plotted the cumulative number of species against the number of patches, after sorting the patches from largest to smallest, and from smallest to largest. Under perfect nestedness, the single largest patch would capture 100% of species. To assess whether the contribution of small patches to species richness was caused by forest-dependent species we repeated all analyses after the exclusion of habitat generalist species. To assess the effectiveness of the proposed conservation zones, we followed Fischer and Lindenmayer (2005b) by choosing a minimalistic conservation target, defined as the number of patches required to capture 70% of the species in at least three patches.

## RESULTS

### Overview

Seventy-four bird species were found in the 30 littoral forest fragments, of which 41 species were identified as 'forest-dependent'. Of the species identified within the littoral forests, 40 were island endemic species (species that are endemic to Madagascar) and 21 were endemic to the biogeographic sub-region of Madagascar, Comoros and Mascarenes. The mean number of bird species detected in each point count was 15.4 (6.1 S.D.), of which 5.14 (5.08 S.D.) were considered forest-dependent. The seven most commonly encountered species were Madagascar bulbul *Hypsipetes madagascariensis*, souimanga sunbird *Nectarinia souimanga*, Madagascar coucal *Centropus toulou*, Madagascar turtle-dove *Streptopelia picturata*,

**Table 2.** Overview of the global nestedness tests conducted for the bird communities inhabiting littoral forests of southeastern Madagascar following 1000 runs using RANDNEST.  R is the mean matrix-wide discrepancy obtained from random simulations, D is the observed matrix-wide discrepancy and %PN is the percentage of perfect nestedness exhibited by the data (see materials and methods for details).

|  |  | All species | Forest dependent species |
|---|---|---|---|
| **Simulation** | R | 288.63 | 118.55 |
|  | Standard deviation | 10.6 | 7.2 |
| **Sorted by species richness** | D | 158 | 46 |
|  | %PN | 45.25 | 61.19 |
|  | p-value | <0.001 | <0.001 |
| **Sorted by area** | D | 166 | 51 |
|  | %PN | 42.48 | 56.9 |
|  | p-value | <0.001 | <0.001 |
| **Sorted by Habitat Complexity Score (HSC)** | D | 316 | 142 |
|  | %PN | -9.48 | -19.2 |
|  | p-value | 0.99 | 0.99 |
| **Distance to Source** | D | 297 | 99 |
|  | %PN | -2.89 | 16.4 |
|  | p-value | 0.78 | 0.003 |
| **Distance to fragment > 100 ha** | D | 304 | 136 |
|  | %PN | -5.3 | -14.7 |
|  | p-value | 0.92 | 0.99 |
| **Distance to nearest fragment** | D | 349 | 153 |
|  | %PN | -20.4 | -29.9 |
|  | p-value | 0.99 | 0.99 |

Crested drongo *Dicrurus forficatus*, Madagascar bee-eater, *Merops superciliosus* and common jery *Neomixis tenella*. Each of these species had > 50 % probability of detection in any point count and all were considered habitat generalists by Watson et al. (2004). The three most commonly encountered forest-dependent species were hook-billed vanga *Vanga curvirostris*, lesser vasa parrot *Coracopsis nigra* and Madagascar green pigeon *Treron australis*; each of which occurred in > 25% of point counts. No one remnant contained all the species found within the littoral forest system, with the number of bird species per fragment ranging from 7 to 58. The highest number of forest-dependent species per fragment was 35, and seven fragments contained no forest-dependent species (Table 1).

**Bird community dynamics in the littoral forest system**

There was no significant spatial autocorrelation between littoral forest species richness and the location of the fragments. There was also no statistical relationship between any of the landscape measures and the measure of habitat complexity.

The bird assemblage was highly ordered (T° = 15.95). The system also showed a significantly nested pattern using the RANDNEST null model (p<0.01; Table 2). When the forest-dependent communities were analysed as a separate subset, the data were again found to be significantly nested and the temperature was lower (T° = 3.21, that is more strongly nested) (Table 2). Ten forest-dependent species displayed clear idiosyncratic patterns in the nes-tedness analysis in that they did not conform to the nested pattern (Table 3). Although there was no obvious common pattern in the guild of the species that displayed idiosyncratic distributions, the majority were wide-ranging predators (e.g. *Accipter henstii*, *Accipter madagascariensis*, *Aviceda madagascariensis*) or gregarious (e.g. *Corocopsis vasa*, *Zosterops maderaspatana*) species (Table 3).  All idiosyncratic species are endemic to the island ex-cept for the Madagascar white-eye (*Z. maderaspatana*), which is a regional endemic.

Nestedness (% PN) was significantly associated with the size of littoral forest fragments for both the overall species assemblage and the forest-dependent species (Table 2). The number of departures from perfect nestedness (D) was significantly lower for the area-ordered matrices than for the three isolation-ordered matrices and habitat complexity score-ordered matrices. Selective extinction, rather than habitat patchiness or isolation (selective immigration), was therefore considered the most likely causal factor underlying nestedness of the bird com-

**Table 3.** The guild status of the idiosyncratic species identified in the Nestedness Analysis.

| Species | Stats | Body length (cm) | Body weight (g) | Edge-tolerance | Foraging Guild | Foraging substrate |
|---|---|---|---|---|---|---|
| Madagascar Brush Warbler *Nesillas typica* | C | 18 | 18 | ET | I | AR1 |
| Henst's Goshawk *Accipterhensti* | UC | 62 | 1140 | ET | V | AR2 |
| Gray-headed Lovebird *Agapornis cana* | C | 16 | 30 | EA | V | AR3 |
| Madagascar Cuckoo Falcon *Aviceda madagascariensis* | C | No data | No data | ET | V | AR2 |
| Madagascar Sparrowhawk *Accipter madagascariensis* | UC | 29 | 159 | ET | V | AR2 |
| Greater Vasa Parrot *Coracopsis vasa* | C | 50 | 525 | EA | VEG | AR3 |
| Madagascar Lesser Cuckoo *Cuculus rochii* | C | 28 | 59 | ET | I | AR3 |
| Madagascar Pygmy Kingfisher *Ispidina madagascariensis* | UC | 14 | 17 | EA | I, V | AR1 |
| Madagascar White-Eye *Zosterops maderaspatana* | C | 12 | 11 | EA | I | AR3 |
| Forest Fody *Foudia omissa* | UC | 15 | 19 | ET | I, VEG | AR3 |

Body length and weight data were obtained from Wilmé and Goodman, 2003.
Status describes the species' status in Madagascar (Hawkins and Goodman, 2003).
Edge tolerance is based on the species abundances at core and edge sites in a previous study (**ET**; edge-tolerant, **EA**; edge-avoiding, see Watson et al. 2004).
Foraging Guild describes the feeding habit of each species [**I**; Insects, **V**; vertebrates, **VEG**; nectar, fruit and/or seeds] (source: Wilmé and Goodman, 2003).
Foraging substrate describes the feeding habit of each species [**AR**; arboreal with **AR1** for lower strata, **AR2**; medium strata, **AR3**; higher strata].

munities in these forests.

The role of larger littoral forest fragments in capturing bird diversity was highlighted when the cumulative number of forest-dependent species was assessed against the cumulative area. When species richness was accumulated from the smallest to the largest fragment, the full set of forest dependent species was only achieved with the inclusion of the very largest fragment (Figure 2a).

This pattern was also highlighted when cumulative species richness was plotted against the number of patches added (Figure 3a). In contrast, when large patches were added first, it only took the first two patches to contain all forest-dependent species. The same trend became apparent when all species were assessed against cumulative area (Figure 2b). When cumulative bird species richness was plotted against patches added, starting from the smallest patch, it was not until the last fragment was added that all species were recorded (Figure 3b). When large patches were added first, it required 24 (80%) patches to be added before all species were recorded (Figure 3b).

## How effective are the proposed conservation zones?

Using our conservation target of capturing 70% of either forest-dependent or all species in at least three frag-

ments, the conservation zones did not adequately capture the assemblage of bird species. Less than 50% of forest-dependent species were recorded in more than two of the conservation zones (Figure 4a) and just over 50% of all species were recorded in more than two of the conservation zone fragments (Figure 4b). Thirteen forest-dependent species (Henst's goshawk *A. henstii*, Madagascar sparrowhawk *Accipter madagascariensis*, Madagascar cuckoo-falcon *Aviceda madagascariensis*, Madagascar wood rail *Canirallus kioloids*, Madagascar magpie-robin *Copsychus albospecularis*, greater vasa parrot *Coracopsis vasa*, Madagascar lesser cuckoo *Cuculus rochii*, red-fronted coua *Coua reynaudii*, Madagascar starling *Hartlaubius auratus*, Chabert's vanga *Leptopterus chabert*, Green jery *Neomixis viridis*, Madagascar scops owl *Otus rutilus* and Tylas vanga *Tylas eduardi*) were only found in one of the four conservation zones, and a further 10 species (Madagascar long-eared owl *Asio madagascariensis*, red-tailed vanga *Calicalicus madagascariensis*, blue coua *Coua caerulea*, forest fody *Foudia omissa*, *Ispidina madagascariensis*, cuckoo roller *Leptosomus discolor*, Lantz's brush warbler *Nesillas lantzii*, Archbold' newtonia *Newtonia archboldi*, Madagascar flufftail *Sarothrura insularis* and rufous vanga *Schetba rufa*) were found only in two of the four conservation zones. Notably,

a) Forest-dependent species data set in littoral forest remnants
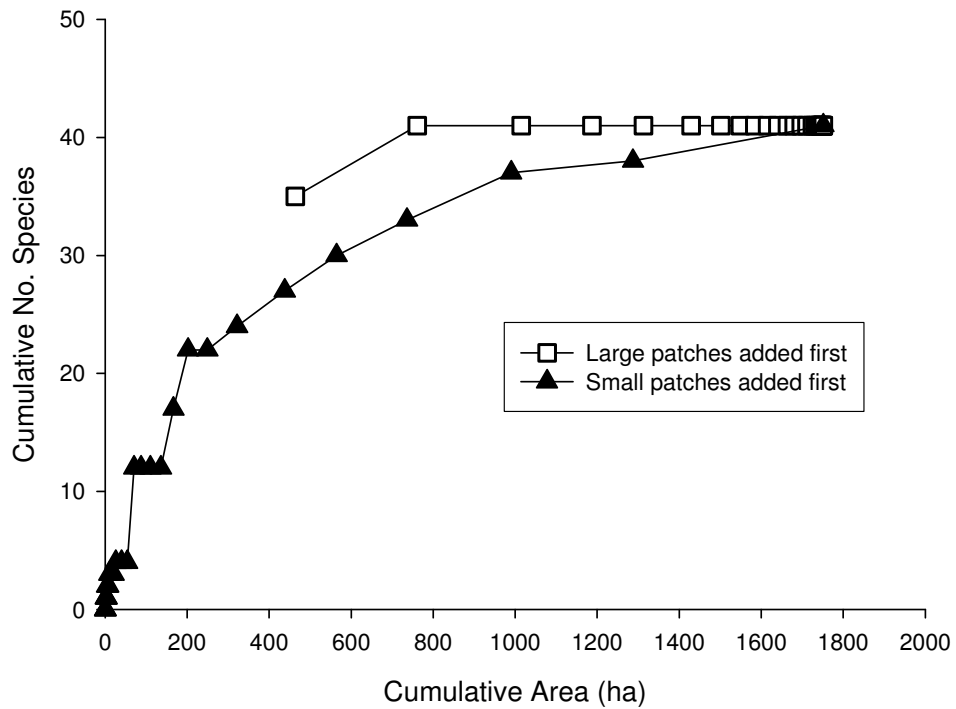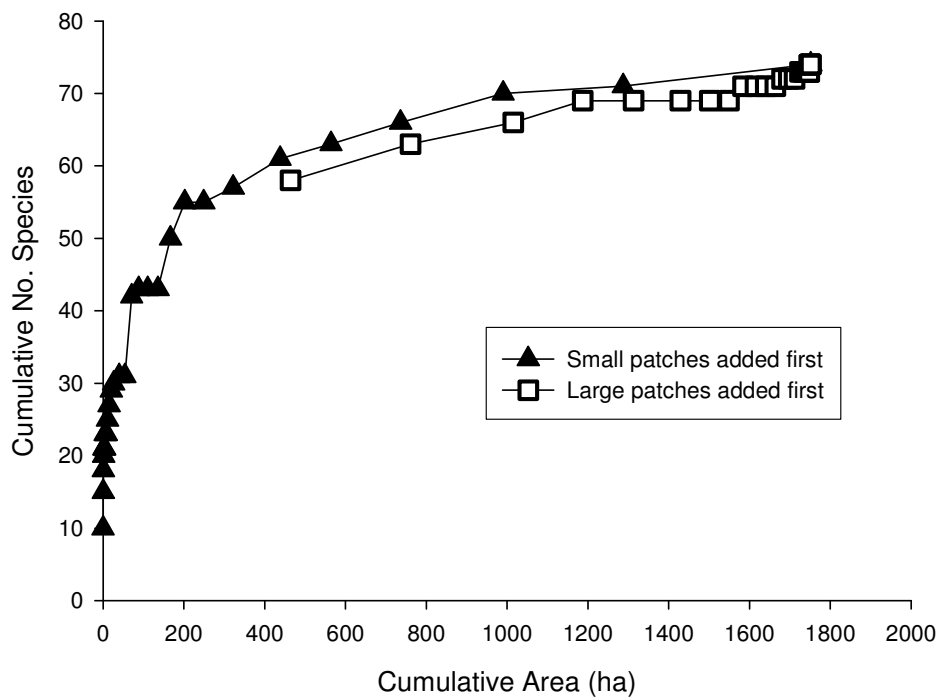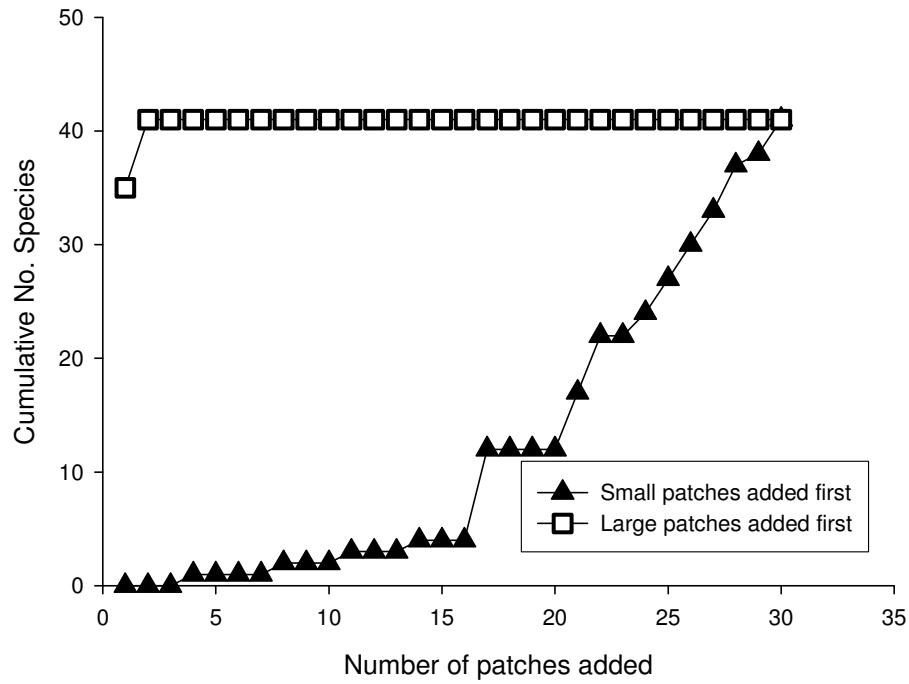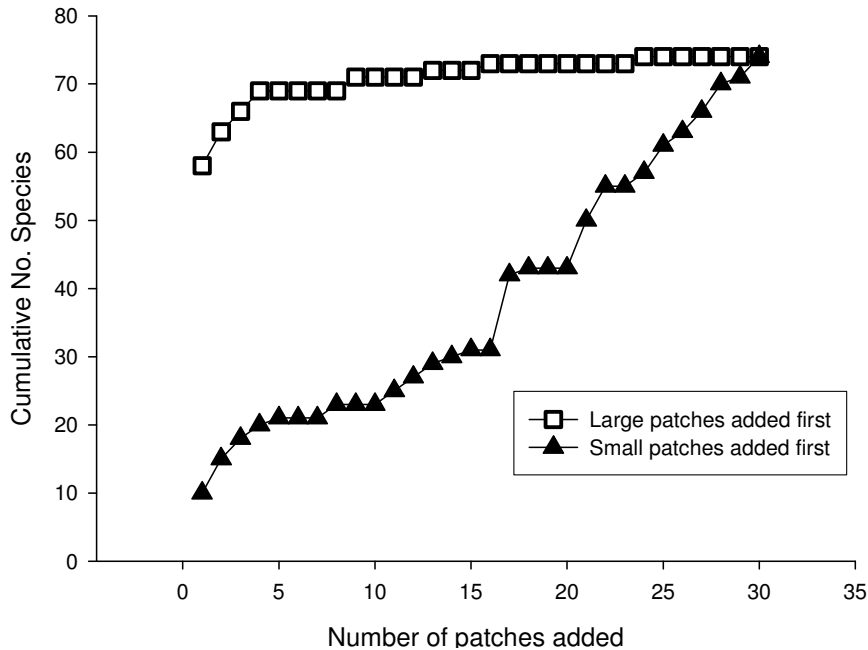


b) Total species data set in littoral forest remnants



**Figure 2**. Cumulative number of bird species versus cumulative patch area for a) forest-dependent species and b) all species. In both graphs, patches were added from large to small and from small to large fragments; respectively, then, corresponding cumulative species counts were obtained.

a) Forest-dependent species data set in littoral forest remnants



b) Total species data set in littoral forest remnants



**Figure 3.** Cumulative number of bird species versus number of patches added for a) forest-dependent bird species and b) all bird species. In both graphs, patches were added from large to small and from small to large fragments; respectively, then, corresponding cumulative species counts were obtained.

if the next four largest fragments were included in the conservation plan, then there will be an increase to 70% of species (regardless of habitat preference) captured in three fragments or more (Figure 4b).
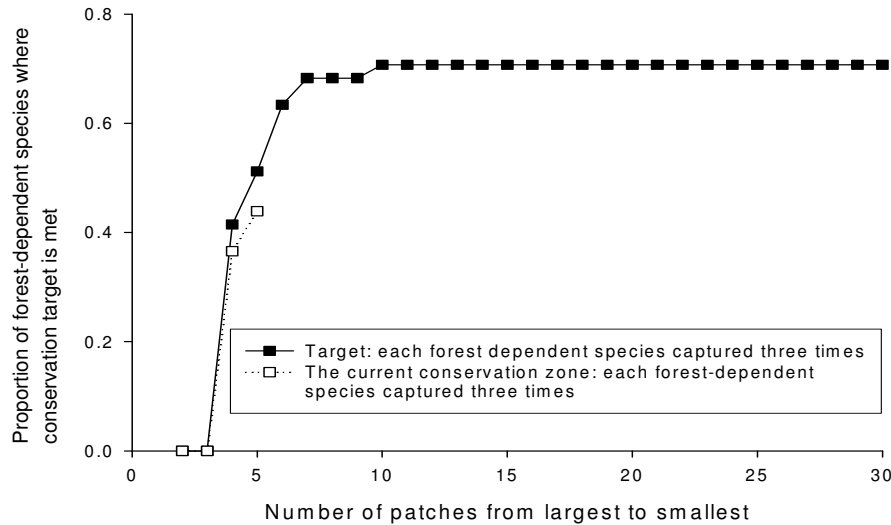
Figure 4a
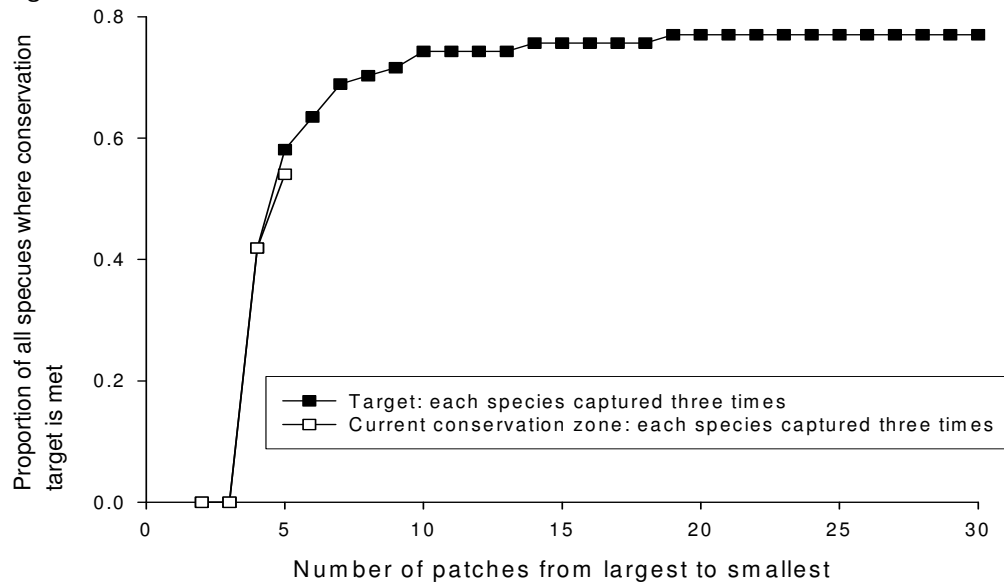


Figure 4b

**Figure 4.** Graphical illustration of how many of the largest sites were needed to capture a) forest-dependent species and b) all species, in at least three patches. Under perfect nestedness by-area the three largest patches would have captured 100% of species in the three locations. The two different curves highlight the proportion of species captured in at least three patches when all patches were considered and when the conservation zone was considered by itself.

## DISCUSSION

Combining nestedness and cumulative species–area analyses provided a simple and useful methodology in assessing the conservation plan for the bird diversity inhabiting littoral forest fragments in south-eastern Madagascar. Both methodologies have in the past been used independently to show different biotic community patterns in fragmented landscapes. By combining these techniques, we were able to identify emergent patterns of bird assemblages from the littoral forest landscapes and infer something of the mechanisms driving these patterns. As

a consequence, we are able to ascertain how effective proposed future conservation plans would be for bird conservation. Both nestedness and cumulative species–area analyses indicated that for birds at least, a number of large littoral forest fragments will be the necessary backbone of a successful conservation program. Therefore conserving four large fragments in Ste-Luce and Mandena is a logical first step to conserving birds inhabiting the southeastern littoral forests. When combined, the proposed conservation fragments contained all the forest-dependent species in the littoral forest zone. However, these fragments were found to be largely inadequate

when a modest conservation target was set because a large proportion (n=13, 33%) of the forest-dependent bird species were found in only one of the four fragments chosen as a conservation zone (Figure 4). We therefore propose that conserving only the four fragments could lead to a 'Noah's Ark' effect, where many species are apparently protected, but only for a short period of time (e.g. due to loss of resources or changes to metapopulation dynamics) (Pimm and Lawton, 1998).

An important finding of this research was that although the forest-dependent bird communities were highly nested when compared to other similar studies (compare $T° = 3.21$ with. $T° = 15.1$ from northern Australian rainforest patches, Williams and Pearson, 1997) $T° = 16.44$; Mexican montane patches, Watson, 2003) they were also imperfectly nested, with approximately a quarter of forest-dependent species distributed in an idiosyncratic manner (Table 3). These species are not generalists and are not widespread across many ecosystems, but within the region in which this research was undertaken are found only in littoral forest fragments (Watson et al., 2004). These findings have important ramifications for the identification and development of suitable conservation zones within the proposed mining zone. Although fragment size plays an important role in determining the composition of species within littoral forests, it shows that other processes are also important in determining species distribution. When traits found to be important to idiosyncratic species in other studies conducted in the tropics were examined (Terborgh, 1974; Gascon et al., 1999; Gaston and Blackburn, 2000), no common traits were found for these 10 species (Table 3). Although it is impossible to ascertain why these species were idiosyncratic, we hypothesise that these particular raptor, cuckoo, parrot, fody and white-eye species have either spatially or temporally dispersed resources which means that they are not dependent on remnant size. The territorial warbler and kingfisher species are likely to be affected by local-scale processes such as vegetation complexity, which may vary from fragment to fragment somewhat independently of size (Watson et al., 2004).

If a policy of conservation is based only on protecting a few large fragments, then it will, by definition, not capture the needs of other idiosyncratic forest-dependent species that require particular resources found in the smaller fragments. In this study, these species include large raptors and parrots that have food resources that are temporally and spatially patchily distributed and, as such, a small number of large fragments will probably not contain sufficient resources to sustain resident populations (Kattan et al., 1994; Bollen, 2003; Bollen et al., 2004b). As a conesquence, we argue that the successful long-term conservation of forest-dependent bird species in this region requires considerably more than the four remnant patches that are proposed in the conservation plan (Vincelette et al., 2003).

This research has shown that to adequately protect bird diversity adequately, there is a need to expand the number of large fragments conserved. We show that fragments S1, S9, S8, S17, S11, M1, M4, M15 and M16 should be given the highest conservation priority in the Ste-Luce and Mandena regions. These fragments have the highest species richness, and contain the largest numbers of regional and island endemic species (Table 1), and should be considered 'irreplaceable' (Margules and Pressey, 2000). Therefore, we encourage that all these large fragments be awarded some form of protected area status, to reduce the possibility of extinctions, and to preserve the diversity the littoral forests contain. With limited options and resources for reservation, a successful reserve network needs 'complementarity' (Pressey et al., 1993) to avoid the risk that extreme events ("disasters") or stochastic excursions in populations could lead to local extinctions within the littoral forest bird community.

It must be noted that conservation of biodiversity in the region depends not only on the ability to establish and manage a network of habitat fragments, but also on the cooperation of local people who utilize the forests for their day to day needs. As the majority of Madagascar's human population lives in poverty, conservation of the forest's unique biodiversity might be considered to be a luxury to local people, although this is to undervalue the significance of natural resources to the local population. Even if the mining actions are not to occur, it is clear that the greatest chance of conservation success in the region is to develop an integrated approach combining research, conservation, local participation and development aid in the region (Kremen et al., 2001; Bode et al., 2008).

## Caveats

This research addressed only the pattern of bird distribution across the landscape and has not provided quantitative insights on the processes that have determined these distributions. The presence of birds in a particular fragment does not mean that the sub-population is viable, nor does it mean that the particular fragment is making a positive contribution to the metapopulation (Donovan et al., 1995; Lens et al., 2002). Moreover, species incidence functions related to habitat patch area can vary between landscapes (Watson et al., 2005b) or through time if conditions change (Hinsley et al., 1994), thus future removal of some of the existing fragments will reduce the connectivity of the remaining fragments, possibly threatening the viability of populations of species in those patches. Autoecological studies should be conducted to understand minimum viable populations of particular species within this landscape. In addition to this, it is important to assess how different bird species use the matrix habitats, the small littoral forest fragments embedded within the matrix and the habitats that the mine intends to restore (Ramanamanjato and Ganzhorn, 2001). This type of research would be directly applicable to the development of con-

servation and reforestation programs within the region. Finally, any conservation plan based only on a single taxon, however charismatic or functionally significant it may be, has to be considered incomplete: further work should therefore aim to combine data and analyses for plant and other animal taxa to complement the analyses presented herein.

## Conclusion

This study has combined a number of different analytical techniques to show that the proposed conservation zones in this region may be inadequate, possibly leading to the local extinction of several species found within the littoral forests. We argue that a number of large fragments should be added to the currently proposed conservation zones, as well as a higher number of smaller fragments that are utilised by bird species not found in large fragments. Further research on the resource requirements of species would be useful to further refine conservation planning. This study assessed the characteristics and conservation potential for a single taxon embedded within a complex ecosystem, which is influenced on a day to day basis by human communities. Thus, effective conservation plans for the littoral forest must be combined with similar information on other vulnerable taxa and be developed in collaboration with the multiple stakeholders in the region.

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### REFERENCES

Andrianarimisa A, Bachmann L, Ganzhorn JU, Goodman SM, Tomiuk J (2000). Effects of forest fragmentation on genetic variation in endemic understory forest birds in central Madagascar. J. Fur Ornithologie 141: 152-159.

Atmar W, Patterson BD (1993). The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96: 373-382.

Baber MJ, Fleishman E, Babbitt KJ, Tarr TL (2004). The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. Oikos 107: 16-27.

Bender DJ, Tischendorf L, Fahrig L (2003). Using patch isolation metrics to predict animal movement in binary landscapes. Landsc. Ecol. 18: 17-39.

Bentley JM, Catteral CP (1997). The use of bushland, corridors, and linear remnants by birds in southeastern Queensland, Australia. Conserv. Biol., 11: 1173-1189.

Berglund H, Jonsson BG (2003). Nested plant and fungal communities; the importance of area and habitat quality in maximizing species capture in boreal old-growth forests. Biol. Conserv. 112: 319-328.

Bibby CJ, Jones M, Marsden SJ (1998). Expedition field techniques: bird surveys. Expedition Advisory Centre, London, UK.

Blake JG (1991). Nested subsets and the distribution of birds on isolated woodlots. Conserv. Biol.  5: 58-66.

Bode M, Watson JEM, Iwamura T, Possingham HP (2008). The cost of conservation. Science pp: 321- 340.

Bollen A (2003). Fruit-frugivore interactions in a Malagasy littoral forest: a community-wide approach of seed dispersal. Dep. Biol. Univ. Antwerpen, Antwerpen pp. 180.

Bollen A, Donati G (2006). Conservation status of the littoral forest of south-eastern Madagascar: a review. Oryx, 40: 57-66.

Bollen A, Elsacker L, Ganzhorn JU (2004a). Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). Oecologia 139: 604-616.

Bollen A, Van Elsacker L, Ganzhorn JU (2004b). Relations between fruits and disperser assemblages in a Malagasy littoral forest: a community-level approach. J. Trop. Ecol. 20: 599-612.

Cadotte MW, Franck R, Reza L, Lovett-Doust J (2002). Tree and shrub diversity and abundance in fragmented littoral forest of southeastern Madagascar. Biodivers. Conserv. 11: 1417-1436.

Catling PC, Burt RJ (1995). Studies of the ground-dwelling mammals of Eucalypt forests in south-eastern New South Wales: the effect of habtat variables on distribution and abundance. Wildl. Res. 23: 271-288.

Consiglio T, Schatz GE, McPherson G, Lowry II PP, Rabenantoandro J, Rogers ZS, Rabevohotra R, Robehvitra D (2006). Deforestation and plant diversity of Madagascar's littoral forests. Conserv. Biol. 20: 1799-1803.

Cook RR, Quinn JF (1995). The influence of colonization in nested species subsets. Oecologia 102: 413-424.

Davidar P, Yogananad K, Ganesh T, Devy S (2002). Distributions of forest birds and butterflies in the Andaman Islands, Bay of Bengal: nested patterns and processes. Ecography 25: 5-16.

Donovan TM, Lamberson R, Kimber A, Thompson III FR, Faaborg J (1995). Modelling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. Conserv. Biol. 9: 1396-1407.

Du Puy DJ, Moat J (1996). A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS map to map its distribution and to assess its conservation status, in: Lourenco WR (Ed), Biogeogragphy of Madagascar ORSTOM, Paris pp: 205-218.

Dufils JM (2003). Remaining forest cover, in: Goodman, S.M., Benstead, J.P. (Eds), The Natural History of Madagascar. The Univ. of Chic. Press, Chic. pp: 88-95.

Dumetz N (1999). High plant diversity of lowland rainforest vestiges in eastern Madagascar. Biodivers. Conserv. 8: 273-315.

Fernández-Juricic E (2002). Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. Oecologia 131: 269-278.

Ficetola GF, De Bernardi F (2004). Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. Biol. Conserv. 119: 219-230.

Fischer J, Lindenmayer DB (2005a). Nestedness in fragmented landscapes: a case study on birds, arboreal marsupials and lizards. J. Biogeogr. 32: 1737-1750.

Fischer J, Lindenmayer DB (2002a). Small patches can be valuable for biodiversity conservation: two case studies on birds in southeastern Australia. Biol. Conserv. 106: 129-136.

Fischer J, Lindenmayer DB (2002b). Treating the nestedness temperature calculator as a "black box" can lead to false conclusions. Oikos

99: 193-199.

Fischer J, Lindenmayer DB (2005b). Perfectly nested or significantly nested - an important difference for conservation management. Oikos 109: 485-494.

Fleishman E, Murphy DD (1999). Patterns and processes of nestedness in a Great Basin butterfly community. Oecologia 119: 133-139.

Ford HA, Barrett G (1995). The role of birds and their conservation in agricultural systems, in: Bennett SBA Clark T (Eds), People and nature conservation. Royal Zool. Soc. of New South Wales, Mosman, Aust. pp: 123–128

Ganzhorn JB, Lowry PP, Schatz GE, Sommer S (2001). The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. Oryx 35: 346-348.

Ganzhorn JU, Goodman SM, Ramanamanjato JB, Rakotondravony D, Rakotosamimanana, Vallan BD (2000). Vertebrate species in fragmented littoral forests of Madagascar, in: Lourenco WR, Goodman SM, (Eds) Diversity and endemism in Madagascar. Memoires de la Societe de Biogeographie Museum Histoire Naturelle, Paris pp : 155-164

Gascon C, Lovejoy T, Bierregaard RO, Malcolm JR, Stouffer PC, Vasconcelos HL, Laurance WF, Zimmerman B, Tocher M, Borges S (1999). Matrix habitat and species richness in tropical forest remnants. Biol. Conserv. 91: 223-229.

Gaston KJ, Blackburn TM (2000). Pattern and process in macroecology. Blackwell Science Ltd, Oxford.

Goodman SM, Patterson BD (1997). Natural change and human impact in Madagascar. Smithsonian Press, Washington D.C.

Gutzwiller KJ, Marcum HA (1993). Avian responses to observer clothing color: caveats from winter point counts. Wilson Bulletin 105: 628-635.

Hannson L (1998). Nestedness as a conservation tool: plants and birds of oak-hazel woodland in Sweden. Ecol. Letters 1: 142-145.

Hawkins BA, Pausas JG (2004). Does plant richness influence animal richness?: the mammals of Catalonia (NE Spain). Divers. Distrib. 10: 247-252.

Helzer CJ, Jelinski DE (1999). The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecol. Appl. 9: 1448-1458.

Hinsley SA, Bellamy PE, Newton I, Sparks TH (1994). Factors influencing the presence of individual breeding bird species in woodland fragments. English Nature Research Reports, pp: 99.

Ingram JC (2004). An exploration of forest change, condition and composition with implications for conservation in Madagascar. Sch. Geogr. and the Environ. Univ. of Oxford, Oxford.

Ingram JC, Dawson T (2005). Inter-annual analysis of deforestation hotspots in Madagascar from high temporal resolution satellite observations. Int. J. Remote Sensing 26: 1447-1461.

Jacquemyn H, Honnay O, Pailler T (2007). Range size variation, nestedness and species turnover of orchid species along an altitudinal gradient on Réunion Island: Implications for conservation. Biol. Conserv. 136: 388-397.

Jolly A, Jolly R (1984). Malagasy economics and conservation: a tragedy without villains, in: Jolly A, Oberle P, Albignac R (Eds), Key environments: Madagascar. Pergamon Press, Oxford.

Jonsson BG (2001). A null model for randomization tests of nestedness in species assemblages. Oecologia 127: 309-313.

Kattan G, Alavrez-lopez H, Giraldo M (1994). Forest fragmentation and bird extinctions: San Antonio eighty years on. Conserv. Biol. 8: 138-146.

Kistler P, Spack S (2003). Comparing agricultural systems in two areas of Madagascar in: Goodman SM, Benstead JP (Eds), The Natural History of Madagascar. The Univ. of Chic. Press, Chic. pp: 123-133.

Kremen C, Razafimahatratra V, Guillery RP, Rakotomalala J, Weiss A, Ratsisompatrarivo J (2001). Designing the Masoala National Park in Madagascar based on biological and socioeconomic Data. Conserv. Biol. 13: 1055-1068.

Kress WJ, Miller SE, Krupnick GA, Lovejoy TE (2001). Museum collections and conservation efforts Science, 291: 828-829.

Kull CA (2002). Madagascar aflame: landscape burning as peasant protest, resistance, or a resource management tool? Pol. Geogr. 21: 927-953.

Lazaro A, Mark S, Olesen JE (2005). Bird-made fruit orchards in northern Europe: nestedness and network properties. Oikos 110: 321-

329.

Legendre P (1993). Spatial autocorrelation: trouble of new paradigm? Ecol. 74: 1659-1673.

Lens L, Van Dongen S, Norris, K, Githiru, M, Matthysen, E., 2002. Avian persistence in fragmented rainforest. Science 298, 1236-1238.

Lomolino MV (1996). Investigating causality of nestedness of insular communities: Selective immigrations or extinctions? J. Biogeogr. 23: 699-703.

Lowry PP, Faber-Langendoen D (1991). Madagascar Minerals Project. Environmental impact assessment Study. Part 1: natural environment, appendix III: flora and vegetation study. Lewis Environ. Consultants, Montreal.

Lynan AJ, Billick I (1999). Differential responses of small mammals to fragmentation in a Thailand tropical forest. Biol. Conserv. 91: 191–200

Mac Nally R, Brown GW (2001). Reptiles and habitat fragmentation in the box-ironbark forests of central Victoria, Australia: predictions, compositional change and faunal nestedness. Oecologia 128: 116-125.

Mac Nally R, Horrocks G, Bennett AF (2002). Nestedness in fragmented landscapes: birds of the box-ironbark forests of south-eastern Australia. Ecography 25: 651-660.

MacKinnon S, Phillips K (1993). A field guide to the birds of Borneo, Sumatra, Java and Bali. Oxford Univ. Press, Oxford.

Margules CR, Pressey RL (2000). Systematic conservation planning. Nature 405: 243-253.

Mittermeier RA, Myers N, Thomsen JB, da Fonseca GAB, Olivieri S (1998). Biodiversity Hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conserv. Biol. 12: 516-520.

Newsome AE, Catling PC (1979). Habitat preferences of mammals inhabiting heathlands of warm, temperate montane and coastal and alpine regions of southeastern Australia in: Specht RL (ed), Heathlands and related shrublands of the world. Elsevier, Amsterdam.

O'Dea N, Watson JEM, Whittaker RJ (2004). Rapid assessment in conservation research: A critique of avifaunal assessment techniques illustrated by Ecuadorian and Madagascan case study data. Divers. Distributions 10: 55-63.

Patterson BD (1987). The principle of nested subsets and its implications for biological conservation. Conserv. Biol. 1: 323-334.

Patterson BD, Atmar W (2000). Analyzing species composition in fragments. Proceedings of the 4th International Symposium, in: Rheinwald, G. (ed.), Isolated vertebrate communities in the tropics. Museum Alexander Koenig, Bonn pp: 1-8.

Pimm SL, Lawton JH (1998). Planning for Biodiversity Science, 279: 2068-2069.

Pressey RL, Humphries CR, Margules CR, Vane-Wright RI, Williams PH (1993). Beyond opportunism: key principles for systematic reserve selection. Trends in Ecol. Evol. 8: 124-128.

Quinn JF, Harrison SP (1988). Effects of habitat fragmentation and isolation on species richness: evidence from biogeographic patterns. Oecologia 75: 132-140.

Ramanamanjato JB, Ganzhorn JU (2001). Effects of forest fragmentation, introduced Rattus rattus and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. Animal Conserv. 4: 175-183.

Saab V (1999). Importance of spatial scale to habitat use by breeding birds in riparian forests: A hierarchical analysis. Ecol. Appl. 9: 135-151.

Schatz GE (2000). Endemism in the Malagasy tree fauna, in: Lourenco, W.R., Goodman, S.M. (eds), Diversity and Endemism in Madagascar. Memoires de la Societe de Biogeogr., Paris pp: 1-9.

Smith AP (1997). Deforestation, fragmentation, and reserve design in western Madagascar in: Laurance WF, Bierregaard RO (Eds.), Tropical forest remnants: ecology, management and conservation of fragmented communities. Univ. of Chic. Chic. pp. 415-441

Terborgh J (1974). Preservation of natural diversity: the problem of extinction prone species. Biosci. 24: 715-722.

Tischendorf L, Bender DJ, Fahrig L (2003). Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist species. Landsc. Ecol. 18: 41-50.

Ulrich W, Almeida-Neto M, Gotelli NJ (2009). A consumer's guide to nestedness analysis. Oikos, 118: 3-17.

Vallan D (2002). Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. J. Trop. Ecol. 18: 725-742.

Vincelette M, Randrihasipara L, Ramanamanjato JB, Lowry PP, Ganzhorn JU (2003). Mining and environmental conservation: the case of QIT Madagascar Minerals in the southeast, in: Goodman SM, Benstead JP (Eds.) The natural history of Madagascar. The Univ. of Chic. Press, Chic. pp. 1535-1537

Wartenberg D (1989). SAAP 4.3: Spatial autocorrelation analysis program. Exeter Software, New York.

Watson DM (2003). Long-term consequences of habitat fragmentation— highland birds in Oaxaca, Mexico. Biol. Conserv. 11: 283-303.

Watson JEM (2005). Avifaunal responses to landscape-scale habitat fragmentation in the littoral forests of south-eastern Madagascar, in: Huber BA, Sinclair BJ, Lampe K (Eds.), Afr. Biodivers. Mol. Org. Ecosyst. Springer Sci. NY., pp: 253-260.

Watson JEM, Whittaker RJ, Dawson TP (2004). Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biol. Conserv., 120: 311-327.

Watson JEM, Whittaker RJ, Dawson TP (2005a). The importance of littoral forest remnants for indigenous bird conservation in southeastern Madagascar. Biodivers. Conserv., 14: 523-545.

Watson JEM, Whittaker RJ, Freudenberger D (2005b). Bird community responses to habitat fragmentation: how consistent are they across landscapes? J. Biogeogr., 32: 1353–1370.

Wethered R, Lawes MJ (2005). Nestedness of bird assemblages in fragmented Afromontane forest: the effect of plantation forestry in the matrix. Biol. Conserv. 123: 125-137.

Whittaker RJ, Fernández-Palacios JM (2007). Island Biogeography: Ecology, Evolution, and Conservation, 2nd edn. Oxford Univ. Press, Oxford.

Williams SE, Pearson SE (1997). Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rain-forests of Australia's wet tropics. Proc. of the Royal Soc. of Lond. Series B-Biol. Sci. 264: 709-716.

Wilmé L, Goodman SM (2003). Biogeography, guild structure, and elevational variation of Madagascar forest birds, in: Goodman SM, Benstead JP (Eds.) The natural history of Madagascar. The Univ. of Chic. Press, Chic. pp. 1045-1058

Wright DH, Patterson BD, Mikkelson GW, Cutler A, Atmar W (1998). A comparative analysis of nested subset patterns of species composition. Oecologia 113: 1-20.