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[1]Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA
Email: sgoodman@fieldmuseum.org
[2]Association Vahatra, BP 3972, Antananarivo 101, Madagascar
[3]Département Sciences de la Nature & Environnement, Université Nord Antsiranana, Antsiranana 201, Madagascar
Email: yasser.anbdou@hotmail.com
[4]Association Famelona, BP 3972, Antananarivo 101, Madagascar
[5]California Academy of Science, 55 Music Concourse Drive, San Francisco, California 94118, USA
Email: bfisher@calacademy.org
[6]Madagascar Biodiversity Center, Parc Botanique et Zoologique de Tsimbazaza, BP 6257, Tsimbazaza, Antananarivo 101, Madagascar
Email: tsiry91@gmail.com
[7]Bioculture, Senneville, Rivière des Anguilles, Mauritius
Email: owen@bioculturegroup.com
[8]Island Conservation, 2100 Delaware Ave, Suite 1, Santa Cruz, California 95060, USA
Email: brad.keitt@islandconservation.org
[9]Mention Biologie et Ecologie Végétales, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar
Email: patrick.ranirison@gmail.com
[10]Institut des Sciences et Techniques de l'Environnement, Université de Fianarantsoa, Fianarantsoa 301, Madagascar
Email: vsoarimalala@vahatra.mg
[11]Unité d'Entomologie Médicale, Institut Pasteur de Madagascar, BP 1274, Antananarivo 101, Madagascar
Email: lucinambi@pasteur.mg
[12]Université de La Réunion, CNRS UMR 9192, INSERM U1187, IRD UMR 249, Unité Mixte 134 Processus Infectieux en Milieu Insulaire Tropical (PIMIT), 2, rue Maxime Rivière, Plateforme Technologique CYROI, 97490 Sainte Clotilde, France
Email: pablo.tortosa@univ-reunion.fr
[13]Mention Zoologie et Biodiversité Animale, Université d'Antananarivo, BP 906, Antananarivo 101, Madagascar
Email: araselimanana@vahatra.mg

Résumé détaillé

Un inventaire biologique a été réalisé du 3 au 14 mars 2016 dans quatre petites îles de la Commune d'Ampisikinana, District de Vohémar : Nosy Ankao (365 ha), Nosy Manampao (29 ha), Nosy Ratsy (6 ha) et Nosiborona (6 ha). Ces îles font partie du Parc National de Loky-Manambato. Chacune des îles se distingue par sa superficie et par sa distance à la côte malgache. L'investigation menée sur le terrain et présentée ici inclut les groupes suivants : plantes ligneuses, moustiques, fourmis, reptiles, amphibiens, oiseaux et petits mammifères. En outre, des informations sur d'autres groupes, tels que les escargots terrestres, ont été collectées et sont présentées.

Plantes vasculaires – Une étude sur la flore et la végétation de l'archipel de Nosy Ankao a été menée en utilisant la méthode de relevé linéaire permettant de mettre en évidence les caractéristiques florisitico-structurales de la zone. Quatorze relevés ont été réalisés sur des unités de végétation jugées homogènes : 10 sur Nosy Ankao, deux sur Nosy Manampao et trois sur Nosy Ratsy. Par ailleurs, des récoltes botaniques ont été réalisées sur l'île de Nosiborona. L'étude a permis de recenser 81 espèces et morpho-espèces de plantes vasculaires réparties en 61 genres et 38 familles. Environ 72 % des espèces recensées sont endémiques de Madagascar. L'affinité phytogéographique des espèces rencontrées confirme la position géographique des îlots dans le Domaine phytogéographique de l'Ouest, plus précisément dans son Secteur Nord. Les îlots affichent chacun une diversité floristique liée à la variabilité des conditions écologiques rencontrées et à leurs paramètres de colonisation. Trois groupements végétaux ont été mis en évidence dans la zone : groupement à *Capurodendron greveanum* et *Eugenia* aff. *calciscopulasum*, groupement à

Goodman, S. M., Anbdou, Y., Andriamiarantsoa, Y., Fisher, B. L., Griffiths, O., Keitt, B., Rafanomezantsoa, J. J., Rajoelison, E. T. Rakotonirina, J. C., Ranaivoarisoa, L., Ranirison, P., Soarimalala, V., Tantely, M. L., Tortosa, P. & Raselimanana, A. P. 2017. Results of a biological inventory of the Nosy Ankao island group, Parc National de Loky-Manambato, northeastern Madagascar. *Malagasy Nature*, 11: 1-59.

Mystroxylon aethiopicum et *Diospyros erythrosperma* et groupement à *Mimusops coriacea* et *Ficus tiliifolia*. Ces groupements se présentent sous des variantes structurales différentes en fonction du type de substrat et d'autres facteurs écologiques moins apparents : variante à sous bois fermé, variante à sous bois clair, variante à canopée très ouverte. Les groupements végétaux des îlots s'individualisent, soulignant des particularités d'un îlot à un autre.

Moustiques – A l'aide de huit pièges lumineux, un total de 527 adultes de moustiques, appartenant à 11 espèces et quatre genres ont été identifiés, *Culex tritaentiorhynchus* (41,3 %) et *Aedes lambrechti* (36,8 %) représentant les espèces les plus abondantes. Le genre *Aedes* (sept espèces) prédomine (57,1 %) suivi par le genre *Culex* (42,3 %). Les genres *Anopheles* et *Aedeomyia* ne représentent que 0,6 % des adultes capturés. Les nombres maximums d'espèces (10) et d'adultes capturés (426) ont été enregistrés à Nosy Ankao, suivi par Nosiborona (cinq espèces, 50 adultes), Nosy Manampao (quatre espèces, 33 adultes) et Nosy Ratsy (trois espèces, 18 adultes). Des larves d'*Aedes* ont été trouvées dans des trous d'arbres, des noix de coco et dans la mangrove, ainsi que dans des gîtes artificiels tels que des containers métalliques, des puits et dans le fond d'embarcations de travail en polyester. Les larves de *Culex* ont été trouvées dans les puits et dans les embarcations, les larves du genre *Anopheles* dans les embarcations uniquement. Si huit des espèces recensées sont considérées comme vecteurs d'arbopathogène, seule la détection de *Plasmodium* a été réalisée chez *Anopheles arabiensis* et s'est avérée négative. Cette étude fournit la première liste des espèces de moustiques enregistrées dans les quatre îles du District de Vohémar.

Fourmis – La diversité des fourmis de l'archipel de Nosy Ankao, a été évaluée. Cinq sites ont été inventoriés, deux à Nosy Ankao et un site sur chacun des trois îles de Nosy Manampao, de Nosy Ratsy et de Nosiborona. Deux méthodes d'inventaire de la faune entomologique ont été choisies pour la capture des fourmis : une méthode non sélective qui consiste à échantillonner des fourmis de la litière par l'extracteur Winkler et une méthode sélective ou collecte générale. Nos résultats montrent une différence entre les compositions spécifiques des communautés de fourmis de l'archipel. L'île la plus grande et la plus proche de Madagascar, Nosy Ankao, héberge la plus haute diversité spécifique avec 33 espèces identifiées. Nosy Ratsy, sensiblement plus petite et légèrement plus éloignée de la grande île, comprend 25 espèces. Nosy Manampao est la plus éloignée des îles de l'archipel et, bien que de taille moyenne, elle héberge moins d'espèces (22 espèces) que les autres, tandis que 21 espèces ont pu être mises en évidence sur l'île la plus petite mais également la plus proche de Madagascar. Nos résultats semblent dont être en cohérence avec la théorie de la biogéographie insulaire. Les quatre îles ont montré une forte diversité quant à leur composition spécifique. Des genres rares tels que *Mystrium*, *Xymmer*, *Proceratium* et *Tanipone* ont été collectés. Il est à noter que la prédominance des espèces envahissantes menace la biodiversité de ces îles.

Reptiles et amphibiens – L'archipel de Nosy Ankao a fait pour la première fois l'objet d'une investigation herpétologique. La communauté herpétofaunique a été inventoriée en déployant trois méthodes standard qui ont déjà été utilisées et testées à Madagascar depuis plus d'une vingtaine d'années : observation directe sur un itinéraire-échantillon, fouille systématique des refuges et système de piégeage avec les trous-pièges. L'archipel héberge au moins 26 espèces herpétofauniques (une amphibien et 25 reptiles) dont trois espèces de reptiles sont inscrites sur la liste rouge de l'UICN, d'autres sont à aire de distribution restreinte et huit représentent probablement des formes nouvelles pour la science. Les écosystèmes insulaires jouent ainsi un rôle non négligeable dans la conservation de la biodiversité malgache. Malgré le faible rendement de piégeage avec le système de trou-piège, les résultats obtenus révèlent la complémentarité des trois techniques utilisées dans l'inventaire de l'herpétofaune. La taille, l'hétérogénéité écologique et la présence de micro-habitats particuliers jouent un rôle considérable dans la répartition de la composition spécifique au sein de la communauté herpétofaunique insulaire.

Oiseaux – L'inventaire des communautés d'oiseaux sur ces îles a été mené basé sur des observations directes et de vocalisation. Les oiseaux identifiés comportent en majorité des espèces qui ne sont pas strictement forestières mais ayant la capacité de traverser la distance séparant l'île principale de Madagascar et l'archipel de Nosy Ankao. Avec 24 espèces, l'avifaune de Nosy Ankao est la plus diversifiée, alors que les petites îles de Nosy Ratsy et de Nosy Manampao hébergent une diversité réduite. La colonie de sternes sur Nosy Manampao est l'une des plus importantes colonies dans l'océan Indien occidental, elle requiert une protection accrue et continue.

Petits mammifères – Un piégeage intensif des petits mammifères a été mené sur Nosy Ankao, Nosy Manampao et Nosy Ratsy en utilisant deux types de dispositifs de capture (des pièges standards et des trous-pièges). Les efforts de piégeage ont été concentrés dans les zones de végétation indigène et secondairement dans les milieux rudéraux à proximité des villages. Aucune espèce endémique de rongeurs Nesomyinae ou tenrecs Tenrecidae n'a été capturée. Tous les petits mammifères piégés sur ces îles sont introduits à Madagascar, incluant *Rattus rattus* et *R. norvegicus* ; ce dernier a été trouvé en une seule occasion et dans un village. En se basant sur les entretiens avec des membres âgés de communautés locales autochtones, personne ne se souvient de l'existence de lémuriens ou d'autres mammifères endémiques sur ces îles, y compris les tenrecs épineux (Tenrecinae). Les populations de rongeurs introduits posent un certain nombre de problèmes aux villageois par rapport à la consommation de denrées alimentaires et en tant que réservoirs potentiels de maladies. En outre, ils ont probablement un impact sur les animaux indigènes à travers la prédation, notamment sur les passereaux de Nosy Ankao et les sternes de Nosy Manampao.

Conclusions – D'après les résultats, il est clair que même si l'archipel de Nosy Ankao est relativement proche de la grande île de Madagascar, il présente des différences importantes vis-à-vis de la flore et de certains groupes d'animaux. En outre, la faune locale, en particulier les reptiles, comprend un certain nombre d'espèces mal connues, au degré de menace élevé (selon les critères de l'UICN), ainsi que des espèces qui sont inconnues de la science. Ces résultats soulignent l'importance de la conservation des îles composant le groupe Nosy Ankao, et stimulent la mise en place d'actions permettant de faire avancer leur protection biologique.

Introduction

The past decades have witnessed a dramatic increase in data on the ecology of native Malagasy terrestrial biota and the large-scale discovery of a remarkable number of organisms new to science and endemic to the island (Emberton, 1994; Goodman & Benstead, 2003; Vietes *et al.*, 2009). These projects have included multidisciplinary biological inventories within and outside protected areas (Ganzhorn & Sorg, 1996; Goodman, 1996, 2000; Ratsirarson & Goodman, 2000; Gautier & Goodman, 2002; Ranaivonasy *et al.*, 2016), including the collection of voucher specimens. This information has been paramount in providing a more detailed understanding of the island's biogeographic patterns and the formulation of different explanatory hypotheses (Wilmé *et al.*, 2006; Vences *et al.*, 2009), often in conjunction with the establishment of conservation priorities (Kremen *et al.*, 2001; Allnutt *et al.*, 2008) and forming baseline information to place in context aspects such as the impacts of climate change (Ingram & Dawson, 2005; Hannah *et al.*, 2008; Raxworthy *et al.*, 2008; Rasamimanana *et al.*, 2012). In short, major advances have been made in understanding the terrestrial organisms and ecology of many areas of Madagascar. This new information has had ramifications for many applied scientific fields, including conservation.

When considering Madagascar's biodiversity and unique ecosystems, most field biologists naturally focus on the principal island, which forms a vast and highly heterogeneous series of habitats. However, approximately 265 smaller islands and islets surround Madagascar and occur within Malagasy territory (Cooke, 1996) -- these smaller islands have received notably less attention concerning biodiversity research. The distribution of these islands around "mainland" Madagascar is not uniform, with some located on the Indian Ocean side and others in the Mozambique Channel. Further, some are isolated and others form archipelagos. Regardless of their geographic position, the smaller islands and islets are influenced by quasi-permanent solar radiation and very regular and often intense oceanic meteorological systems, which on a seasonal basis bring high levels of rain and salt laden humidity. Most islands within Malagasy waters are located within a few kilometers of the main island. In recent geological time, from a few million years to a few thousand years and during periods of fluctuating sea levels, many of these islands were sequentially attached and then separated from the principal island of Madagascar, which in most cases was the source of the native plants and animals. Subsequently, through seafaring and human establishment on some of the islands, different types of plants and animals have been introduced.

The soil types on these islands and islets show considerable variation, but with a preponderance of calcareous sediments associated with coral formations, as well as consolidated or non-consolidated sand and dune formations, and more complex alluvium deposits. Differences in substrate, as well as local climatic conditions, have major influences on the local flora and vegetation structure (Du Puy & Moat, 2003; Moat & Smith, 2007). These aspects in turn are directly related to the capacity of certain animal groups to maintain viable populations through time on islands separated from mainland Madagascar, as mentioned above, or their ability to colonize successfully via over-water dispersal. These complex ecological and life history factors help explain why certain organisms have viable populations on certain islands.

Some off-shore islands and islets of Madagascar have been the subjects of research projects focusing on terrestrial organisms, such as mosquitoes (Fontenille, 1989); land birds and nesting colonies of sea birds (Goodman, 1993; Cooke & Randriamanindry, 1996; Le Corre & Bemanaja, 2009); reptiles, including nesting sites for sea turtles, and amphibians (Rakotonirina & Cooke, 1994; Andreone *et al.*, 2003; Metcalf *et al.*, 2007; Allison, 2008; Roberts & Daly, 2014); and mammals, particularly lemurs (Birkinshaw, 2001; Andriantompohavana *et al., 2006*). However, few multi-disciplinary field studies have been conducted on a given island or across an archipelago. An important exception includes the Frontier Madagascar projects conducted in the Lokobe Forest on Nosy Be, in the northwest, which cover a wide range of organisms and focus on ecology and the impacts of habitat degradation (http://www.frontier.ac.uk/Publications/Publications.aspx).

Different organisms occurring on islands provide a good index of measuring changes in ecosystems across short-term or long-term timeframes. Groups such as ants (Agosti *et al.*, 2000), amphibians (Heyer, 1994), and mammals (Wilson, 1996) have all been analyzed as indicators of natural or anthropogenic environmental change. Detailed data concerning plants and animals derived from biological inventories form the baseline for future comparisons in the evolution of the biota of different sites, including Madagascar and its offshore islands. A good example

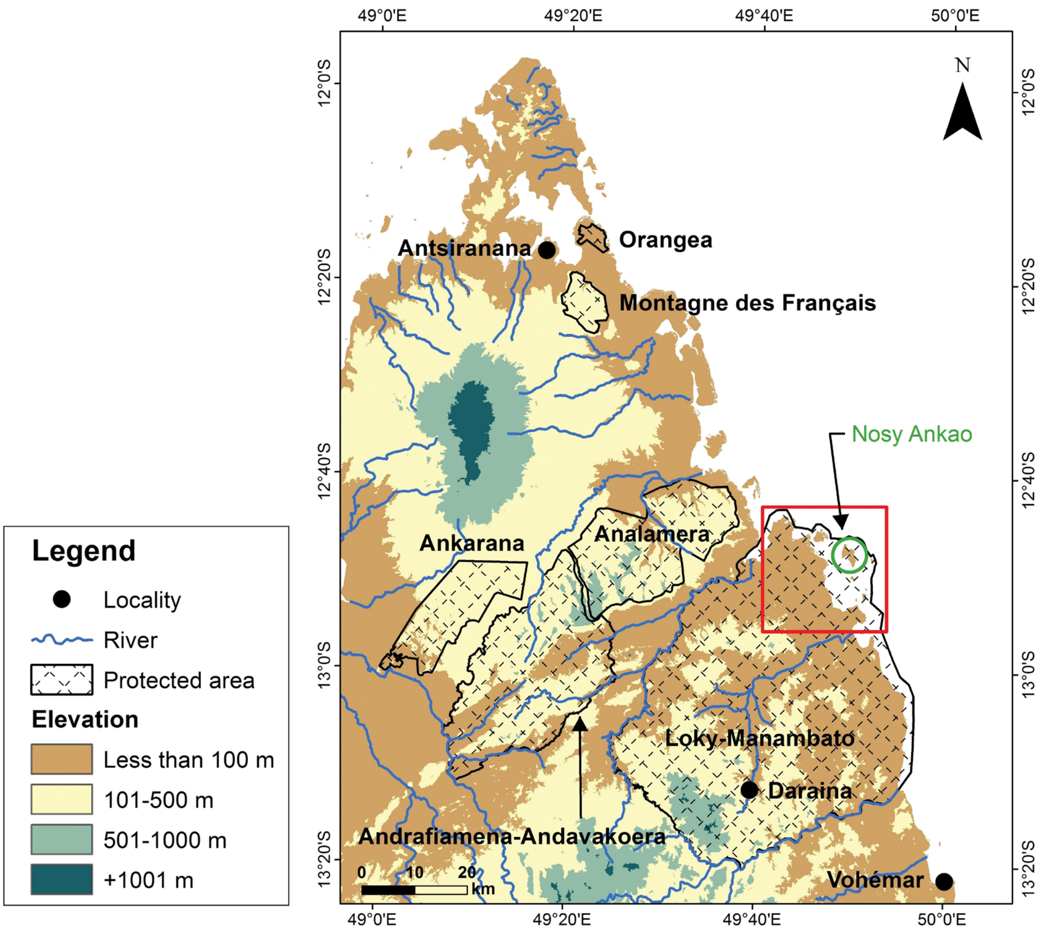

Figure 1. Map showing northern Madagascar and the islands in the Nosy Ankao group, which are part of Parc National de Loky-Manambato. Regional protected areas and elevational variation are also shown. The red-framed area to the northeast of Parc National de Loky-Manambato is detailed in Figure 2.

is how introduced species out compete native taxa, leading to major biotic shifts (Human & Gordon, 1996; Petren & Case, 1996; Stokes *et al*., 2009).

The focus of this paper is to report on the results of a multi-disciplinary study of plants, invertebrates, and vertebrates on islands in the Nosy Ankao Archipelago, northeastern Madagascar (Figure 1). The site is located about halfway between Vohémar (Iharana) and Diégo Suarez (Antsiranana) and part of the Parc National de Loky-Manambato. To our knowledge, this zone has not been the subject of a detailed biological inventory.

Historical exploration of the biological resources of the Nosy Ankao island group

In general, little historical or modern research has been conducted on the marine or terrestrial biota of the Nosy Ankao Archipelago. In contrast, the mainland areas adjacent to these islands, most notably the Parc National de Loky-Manambato and the Réserve Spéciale d'Analamera (Figure 1) have received considerable attention (Goodman & Wilmé, 2006; Nusbaumer *et al.* 2010); data and species lists from these sites provide a context to better understand aspects of the known biota of the Nosy Ankao island group.

One area within the archipelago that has been the site of some research is a zone historically known as Port Leven. This area is close to what is known today as Nosy Manambiby, one of the northern most islands in the Nosy Ankao group (Figure 2), which has also been referred to as the Leven Islands (Decary, 1963; Obura *et al*., 2011). The name Port Leven is derived from the boat H. M. Ship Leven and as gleaned from boat captain's accounts (Owen, 1833, p. 30) "*A fine bay on the north-east side of Madagascar, which was not known to the natives by any particular name, we called Port Leven, the islands between Andrava and Looké [=Loky] Bays…*". To our knowledge, the only published biodiversity work on the local biota of this archipelago includes information on land snails in the Port Leven area (Morelet, 1851, 1860) and recent surveys of the marine fauna off Nosy Ankao (Obura *et al*., 2011). Important unpublished data are included in reports on seaweed aquaculture and environmental assessments for a tourism project (Gilli & Gilli, 2007; Fanamby, 2014).

Figure 2. Map of the islands in the Nosy Ankao group, all of which are within the Parc National de Loky-Manambato. The yellow-framed area associated with Nosy Manampao is detailed in Figure 3. Nosiborona is also known as Nosimborona and Nosy Manampao as Nosy Manampaho.

Methods

Context of the 2016 biological inventory and study sites

During March 2016, a group of biologists (Table 1) was assembled to conduct a multi-disciplinary study of the biota of the Nosy Ankao Archipelago, within the ex-Province d'Antsiranana, Région Sava, Commune d'Ampisikinana. The island group is composed of about 10 small islands and islets, of which four were intensively surveyed in the context of this study (Figures 2 & 3): Nosy Ankao, Nosy Manampao, Nosy Ratsy, and to a lesser extent Nosiborona. The different characteristics of these four islands are given in Table 2.

The principal study organisms included in the March 2016 inventory were vascular plants, mosquitoes, amphibians, reptiles, birds, and small mammals, with some information collected on land snails and other invertebrates. Separate methods, results, and discussion sections are presented herein for each of the major study groups. The islands surveyed and the levels of study intensity were not the same for each group of organism; these details are summarized in Table 3. Nosy Ankao is the largest of the islands studied and with notable variation in habitat, geology, and hydrology (Figures 4 & 5). Two separate forest blocks occur on Nosy Ankao and these are generally referred to herein as 1) "dune forest", which is at the southern end of the island, and to the east of the village Antafondro, and 2) what is referred to herein as "large forest block" or "Nosy Ankao forest" and more precisely the parcel between the villages of Andasibe and Andrangana (Figure 4).

Table 1. Researchers who participated in the field portion of the biological inventory of islands in the Nosy Ankao group, Parc National de Loky-Manambato, in March 2016.

Name	Study group	Home institution
Yasser Anbdou	Small mammals	Université Nord Antsiranana
Steven M. Goodman	Small mammals and birds	Field Museum of Natural History and Association Vahatra
Eric T. Rajoelison	Ants	California Academy of Sciences - Madagascar
Luc Ranaivoarisoa	Vascular plants	Association Famelona and Université d'Antananarivo
Achille P. Raselimanana	Reptiles and amphibians	Association Vahatra and Université d'Antananarivo
Voahangy Soarimalala	Small mammals	Association Vahatra and Université de Fianarantsoa
Michaël L. Tantely	Mosquitoes	Institut Pasteur de Madagascar
Pablo Tortosa	Small mammals and associated zoonoses	Université de La Réunion

Table 2. Characterization of the different islands in the Nosy Ankao group surveyed in March 2016 (see Figure 2 for the location of each of these islands).

	Nosy Ankao	Nosy Manampao	Nosy Ratsy	Nosiborona
Total surface area (ha)	365	29	6	6
Nearest distance to mainland (km)	3.4	8.6	7.1	0.5
Latitude S (centroid) (°)	12.79594	12.80995	12.81626	12.81682
Longitude E (centroid) (°)	49.82695	49.86853	49.85388	49.79185
With native woody vegetation	Yes	Some	Yes	Some
Permanent human habitation	Yes	No[1]	No[2]	No
Freshwater sources (wells)	Yes	Yes	No	No
Landing sites for fishermen or people traveling by boat	Yes	Yes	Yes	Yes

[1]In the latter portion of 2015 to early 2016, there was a guard hut on Nosy Manampao and with permanent staff engaged by the Nosy Ankao Development Company. The role of these individuals was to limit access to the island in the context of Nosy Manampao being part of the Parc National de Loky-Manambato.

[2]In March 2016, a house built by fishermen was present in the northeastern portion of the island and apparently unused for at least several months

Table 3. Groups surveyed on islands in the Nosy Ankao group and the relative work intensity invested in each group. - = not surveyed, + = superficially surveyed, ++ = sufficiently surveyed.

Taxonomic group	Nosy Ankao	Nosy Manampao	Nosy Ratsy	Nosiborona
Vascular plants	++	++	++	+
Land snails	+	+	+	-
Mosquitoes	++	++	++	++
Ants	++	++	++	++
Reptiles	++	++	++	+
Birds	++	++	++	-
Small mammals	++	++	++	-

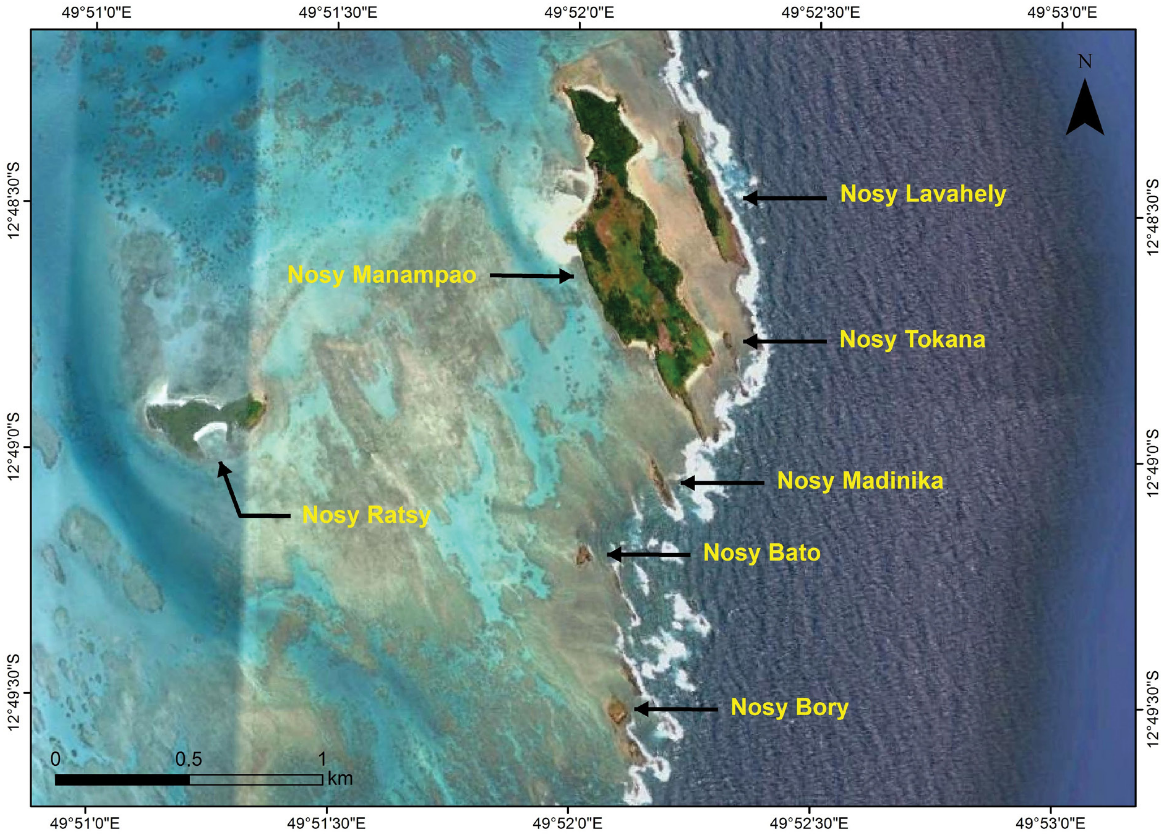

Figure 3. Map of Nosy Manampao and its surrounding islands. According to interviews with older people on Nosy Ankao, the two islands nearest to Nosy Manampao were traditionally unnamed. On the advice of a Nosy Ankao resident, we have named these two islands Nosy Lavakely and Nosy Tokana. Nosy Manampao is also known as Nosy Manampaho.

Study sites

The researchers that conducted surveys on the different islands generally worked independently. Information for each represented discipline associated with the placement of transects, traps, etc. are presented separately in the methods sections below. Generalized localities used for the four different islands and some villages where collections were made are presented below.

Villages on Nosy Ankao

Nosy Ankao, Andasibe (village), 12°47’25”S [12.790139°S], 49°49’17”E [49.821375°E], 5 m,

Nosy Ankao, Analabozaka (village), 12°47’44”S [12.795639°S], 49°49’59”E [49.833167°E], 12 m,

Nosy Ankao, Ampasimangidy (village), 12°47’57”S [12.799417°S], 49°49’53”E [49.831389°E], 5 m,

Nosy Ankao, Antafondro (village), 12°48’48”S [12.813556°S], 49°50’07”E [49.835417°E], 5 m,

Nosy Ankao, March 2016 research base camp, 12°47’24”S [12.790194°S], 49°49’17”E [49.821389°E], 10 m.

Islands (geographical coordinates based on centroid positions)

Nosy Ankao, 18 km S Ampisikinina, Nosy Ankao forest, 12°47’31”S [12.791944°S], 49°49’27”E [49.824167°E], 6 m,

Nosiborona, 14.5 km S Ampisikinina, 12°49’01”S [12.816828°S], 49°47’30”E [49.7917°E], 18 m,

Nosy Manampao, 17 km SW Ampisikinina, 12°48’32”S [12.808889°S], 49°52’06”E [49.868333°E], 15 m,

Nosy Ratsy, 16 km SW Ampisikinina, 12°48’58”S [12.816111°S], 49°49’11”E [49.819722°E], 12 m.

Weather data

Meteorological information during the inventory was obtained using a minimum-maximum thermometer and a rain gauge installed near the research base camp on Nosy Ankao (see above). A HOBO data logger (model U10-003, Onset Computer Corporation, Bourne, Massachusetts) was also used on three islands during the mosquito surveys to measure hourly variation in temperature and relative humidity.

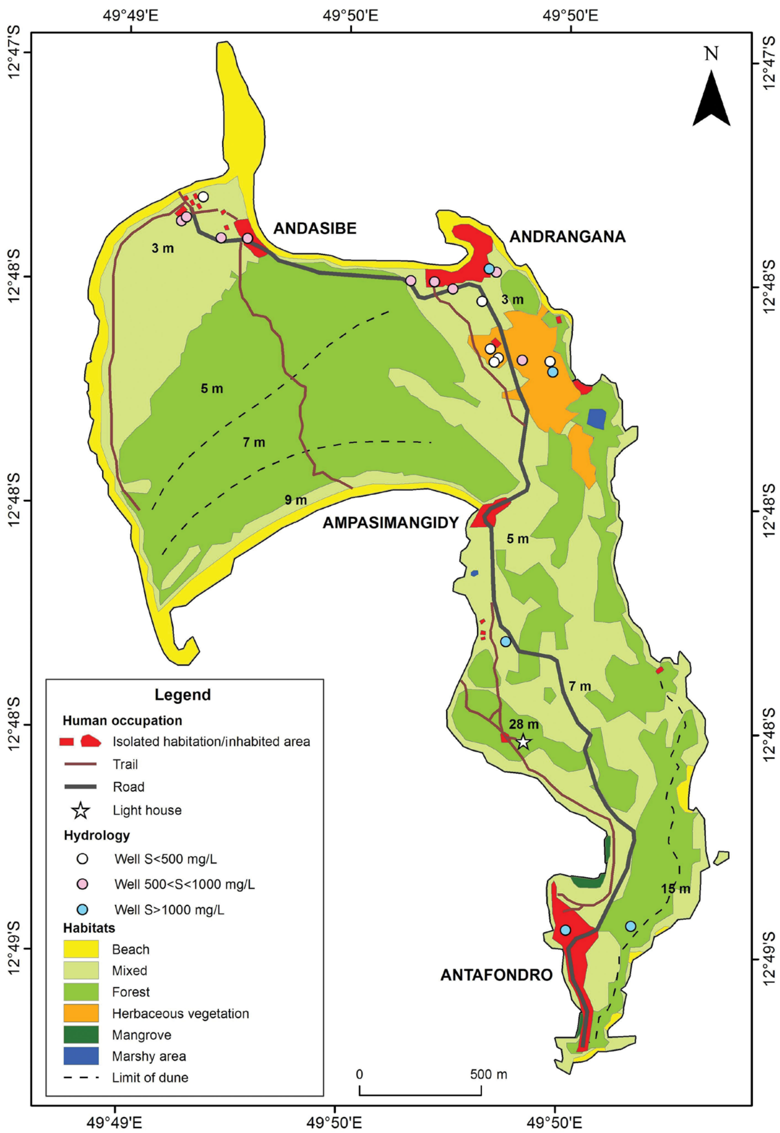

Figure 4. Map of different vegetation types and areas of human occupation on Nosy Ankao. Map adapted from Gilli & Gilli (2007).

Vascular plants (fieldwork conducted by Luc Ranaivoarisoa and assisted by Yannie Andriamiarantsoa and Patrick Ranirison with identifications and analysis)

The principal objective of this study was to characterize the major vegetation formations on islands in the Nosy Ankao group, specifically their floristic and physiognomic aspects. The islands associated with the botanical study are presented above in the introduction to the methods section; the details are summarized in Table 2. To our knowledge, other than the work of Fanamby (2014), which is associated with an environmental impact study, no previous botanical research has been conducted on these islands. The intensity of field collections and quantitative measures used differed between islands (Table 3).

Data collection

Three different techniques were employed to collect data on the flora and vegetation: linear transects, surface area sampling, and general collections. Collected voucher specimens obtained during the inventory have been deposited in the FOFIFA Herbarium (TEF), Ambatobe, Antananarivo.

Linear transects

Linear transects followed the methods of Gautier *et al*. (1994), with each transect being either 50 or

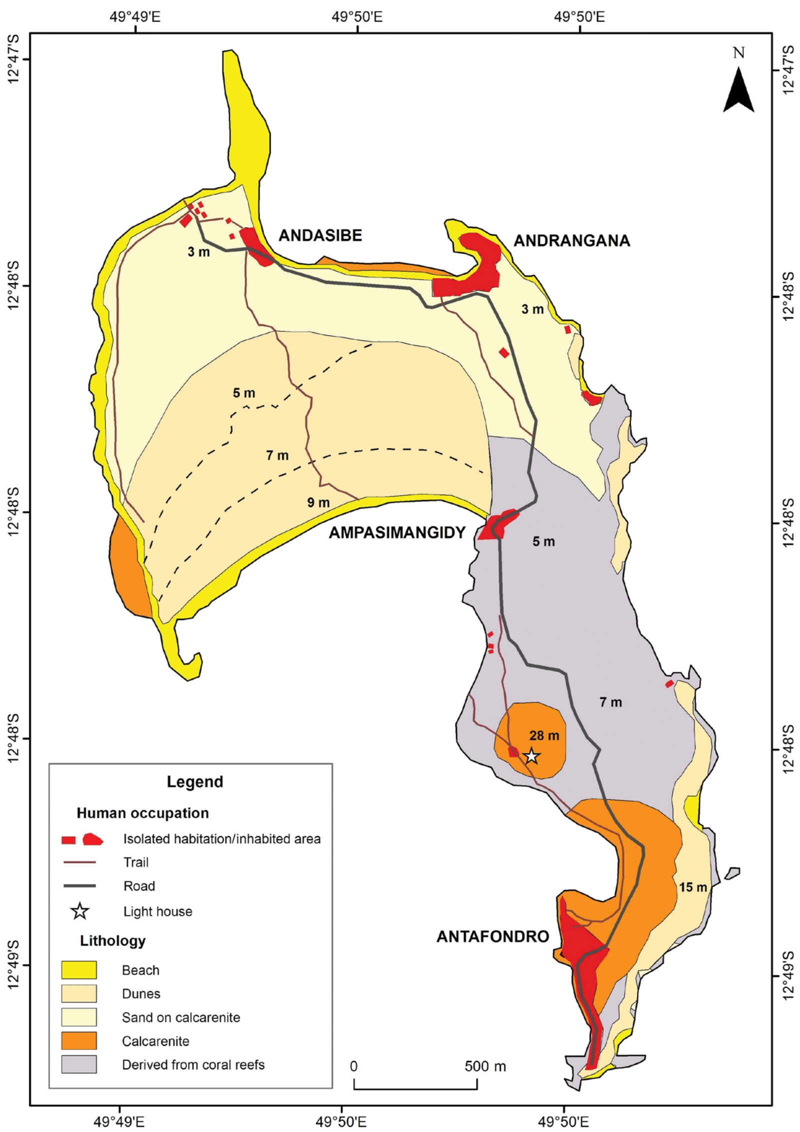

Figure 5. Map of geological and hydrological aspects of Nosy Ankao. Map adapted from Gilli & Gilli (2007).

100 m in length and measurements made every 2 m along each transect (see Table 4). Site transects were installed in zones that showed notable levels of homogeneity with respect to physiognomy, floristic composition, and ecological conditions. Every 2 m along a given transect line, all plants coming in contact with a vertical and graduated pole 8 m in length were included, voucher specimens collected, and information recorded on their minimum and maximum point of contact and, when possible, scientific name. The following parameters were noted for each of these points: GPS coordinates, altitude (based on GPS), slope, orientation, and type of substrate. This methodology allows an assessment of qualitative aspects of vegetation structure along the transect.

Surface area sampling

Surface area sampling followed the technique of Braun-Blanquet (1965) and used the standard area of 0.1 ha (minimal biological area) at sites along the transect lines and meeting the above mentioned three criteria of homogeneity. The following parameters were recorded at each sampled area: diameter at breast height, height of the bole, and total maximum height. This technique provides insights into dendrometrics.

General botanical collections

In addition to the two methods mentioned above, general plant inventories were also conducted on each island. More specifically, fertile plants were

Table 4. Summary of ecological profiles of vegetation groups on the Nosy Ankao island group.

	Floristic group	**Group *Capurodendron greveanum* and *Eugenia* aff. *calciscopulasum***		**Group *Mystroxylon aethiopicum* and *Diospyros erythrosperma***		**Group *Mimusops coriacea* and *Ficus tiliifolia***
	Occurrence on islands	Only on Nosy Ankao		Only on Nosy Ratsy		Only on Nosy Manampao
	Number of transects	9		3		2
	Transects	Tr 1, Tr 2, Tr 3, Tr 4, Tr 5, Tr 6, Tr 9, Tr 13, Tr 14		Tr 10, Tr 11, Tr 12		Tr 7, Tr 8
Ecological parameters	Substrate	Sandy soils		Sandy soils		Sandy soils
Florisitic parameters	Number of species	51		22		7
	Number of genera	38		19		6
	Number of families	28		15		4
Structural parameters	Structural variation	Closed understory	Open canopy	Open understory	Open canopy	Open understory
		Tr 1 to Tr 5, Tr 9, Tr 13, Tr 14	Tr 6	Tr 11, Tr 12	Tr 10	Tr 7, Tr 8
	Mean linear density (individuals/100 m)	110	97	127	138	99
	Maximum height (m)	3.8 ± 0.23	4.0 ± 2.31	2.8 ± 0.80	2.4 ± 0.76	2.8 ± 0.48
Spatial parameters	Phytogeographical affinities	Dominance of Western Domain plants		Mixed affinities between Western, Eastern, Central, and Southern domains		Mixed affinities between Western and Eastern domains

collected as herbarium specimens in different areas of each island. For each collection, information was recorded on the provisional scientific name, GPS position, a brief description of their biology, and local habitat characteristics. In the field, these specimens were conserved in newspaper saturated with alcohol and then transported to Antananarivo, where they were dried and then compared to herbarium specimens in the TEF herbarium. In most cases, the collected plants could be identified to species, but in some cases only to genera. In the later case, they were considered as a morphospecies and named as sp. 1, sp. 2, etc.

Data analysis

Floristic richness

In the context of this field study, collected plants were conserved as pressed specimens and the dried material was subsequently compared to previously identified herbarium material. A list of taxonomic names of identified plants served as the basis of subsequent analyses and comparisons.

Geographic range of plant species

The ranges of identified taxa were established based on published documents (Mabberley, 1997) and different online sources (Tropicos -- http://www.tropicos.org/, Sonnerat -- https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form). This information was used to determine the phytogeographic origin of plants found on the different islands in the Nosy Ankao Archipelago.

Phytogeographic affinities relative to Madagascar

The distribution patterns of plants found on the islands of the Nosy Ankao group with respect to phytogeographic domains of Madagascar (sensu Humbert, 1955) were used to determine their associated affinities.

Plant life-forms

We employ here the definitions of different plant life-forms proposed by Raunkiaer (1905) and then adapted by Lebrun (1966) for tropical regions of the world:

- mesophanerophytes (me) = plants growing between 8 and 16 m in height;
- microphanerophytes (mi) = plants growing between 2 and 8 m in height;
- nanophanerophytes (na) = plants growing between 0.5 and 2 m in height;
- therophytes (th) = annual plants;
- vines (V) = creeping or climbing on forest floor or other types of support; and
- epiphytes (E) = attached to another plant.

Identification of vegetation groups

The linear transects documented during the surveys were first classified based on the floristic similarities between transects calculated by the Horn index (referred to herein as "floristic group" and classified as Group 1 to Group 3). They were also classified based on their structural characteristics (referred to herein as "structural group" and classified as Group A to Group C) using several different parameters. The vegetation groups (referred to herein as Group I to Group III) were obtained by comparing the floristic and structural groups, giving priority to the floristic classification and using the structural classification to identify subgroups.

Identification of indicator species within vegetation groups

The indicator species of a given vegetation group were identified by calculating their frequency and abundance between the different transects. A species is considered indicative of a vegetation group when its relative frequency and relative abundance are equal to or greater than 25%, following the INDVal formula (Dufrêne & Legendre, 1997).

Phytogeographic affinities of vegetational groups

The phytogeographic affinities of each vegetational group were tabulated with respect to the recognized domains of Madagascar (Humbert, 1955) and more specifically as a percentage of the floral affinity of the indicator species within a group relative to that of the different domains. The different descriptions of a vegetational group were based on data obtained from the linear transects.

Snails (Owen Griffiths identified material collected principally by Steven M. Goodman)

The collection of land snails was not the primary research interest of any of the individuals that took part in the field inventory. Specimens were obtained from the ground or low vegetation in a non-standardized manner on three different islands: Nosy Ankao, Nosy Ratsy, and Nosy Manampao (Table 3). Specimens were identified using the monographs of Fischer-Piette *et al.* (1993, 1994) and the reference collection of Owen Griffiths.

Ants (fieldwork conducted by Eric Tsiriniaina Rajoelison and specimens identified by Brian Fisher, Jean Jacques Rafanomezantsoa, Eric Tsiriniaina Rajoelison, and Jean Claude Rakotonirina)

Five sites were extensively sampled, two on Nosy Ankao, and single sites on Nosy Manampao, Nosy Ratsy, and Nosiborona. In Table 5, the specific coordinates of each site inventoried for ants and other aspects are presented.

Inventory methods

Two different techniques were employed to inventory ants: 1) non-selective methods involving leaf litter sampling and associated Winkler extractions, and 2) a selective method, specifically hand collecting.

Non-selective method

This method involved the collection of insects living on the ground surface, particularly ants found in soil litter. This technique is particularly suitable for inventorying the soil fauna of forest habitats with abundant litter (Nadkarni & Longino, 1990; Olson, 1991; Fisher, 1996a, 1999). Ground litter within a plot of approximately 1 m² was collected, hashed with a machete to disrupt ant nests in fallen small branches and dead wood, and then filtered through a 1 cm sieve. About 2 l of sieved litter was collected from each 1 m² plot (also referred to as station). Arthropods found in litter samples were separated

Table 5. Details on the five transects conducted for ants on islands in the Nosy Ankao group.

Island	Elevation	Latitude south (°)	Longitude east (°)	Period	Habitat type	Distance to nearest point on mainland (km)
Nosy Ankao	25 m	-12.791639	49.823778	3-6 March 2016	Dry forest	4.70
Nosy Manampao	20 m	-12.809417	49.869028	4-8 March 2016	Sparse woodland	8.79
Nosy Ankao	15 m	-12.811389	49.837639	9 March 2016	Dune forest	5.50
Nosy Ratsy	22 m	-12.816139	49.853833	11-14 March 2016	Mixed scrub	7.46
Nosiborona	18 m	-12.817000	49.792278	13-14 March 2016	Lowland humid forest	0.60

from the collected organic material using a Winkler extractor over a 48 h period.

Two forms of Winklers were employed: a "mini-Winkler" with the capacity to accommodate a single sack of ground litter, and a "maxi-Winkler" which can hold up to four bags of litter. The choice of Winkler used during an inventory was based on transect length. The standard protocol was for 25 mini-Winkler samples to be collected along a 250 m transect, sampling every 10 m. Two sites did not meet this criterion because of limited habitat: Nosiborona and the dune forest on Nosy Ankao. At these two sites, litter samples were collected at 20 points every 10 m and grouped in five maxi-Winklers. The transects at the forest site on Nosy Ankao, on Nosy Ratsy, and on Nosy Manampao followed the standard protocol.

Selective method

The selective method, also referred to here as hand collecting, focused on obtaining specimens associated with ant colonies (Figure 6). It was based on prospecting different microhabitats at a site, such as dead stems, rotten wood, and dead roots, as well as under moss, lichen, and rocks, and systematically collecting any ants encountered. This technique was effective to provide an overview of the local ant species and was used on all four of the islands inventoried and the five surveyed sites (Table 5).

Sample processing and data analysis

Standard processing protocols were followed in the laboratory of the California Academy of Sciences, Tsimbazaza, Antananarivo, for the identification of sampled ants to the level of species. The process involves different phases: 1) sorting all ants to morphospecies and, when possible, using published keys to identify the specimens to genus and species, and 2) the unidentified species were compared to images on the website Antweb (https://www.antweb.org*), which has up-to-date summaries of what is known about the taxonomy of Malagasy ants,* including unnamed taxa, and the associated species codes from this database were used (e.g. mg02, mg06, fas-12, fas-23). In the case when a taxon was previously unknown based on the images presented on Antweb, it was given the name "ankao X". Only identified individuals of the worker caste were used in the faunistic analyses. It is important to mention that the presence of males or queens within a sample does not necessarily mean the presence of a colony along the respective transect.

Species abundance was calculated. Since ants are social, the abundance of each species was measured as the proportion of stations where the species occurred (frequency), using the following formula:

Figure 6. Eric Tsiriniaina Rajoelison employing the selective method to collect ants. (Photograph by Voahangy Soarimalala.)

Abundance (A) = x / X

with x = the number of times or number of stations a species was found along a transect and X = the number of stations on a transect.

From a faunistic perspective, the sites are compared using the Jaccard Index of similarity to better understand differences in the species represented at the surveyed sites based on pairwise comparisons. This index was calculated based on the following equation:

$$C_{AB} = j/(a+b-j)$$

with j = the number of species in common to the two sites, a = the number of species at site A, and b = the number of species at site B.

As the value of C increases, the number of species in common between two sites increases, indicating lower inter-site differences; as the value of C decreases, there is greater turnover in species composition between the two sites (De Bello *et al.*, 2007).

Antweb was used as the primary source of ant taxa known from northeastern Madagascar. For biogeographical comparisons, the following two nearby mainland sites were employed: (1) Analabe Forest -- 30.0 km 72° ENE Daraina and 30 km from the Nosy Ankao group, 13.08333°S, 49.90833°E, 30 m, wooded grassland-bushland and littoral rainforest; (2) Réserve Spéciale d'Analamera -- 28.4 km 99° Anivorano-Nord and 38 km from the Nosy Ankao group, 12.74667°S, 49.49483°E, 60 m, tropical dry forest (Figure 1).

Mosquitoes (Michaël Luciano Tantely)

Field surveys were conducted on four separate islands: Nosiborona, Nosy Ankao, Nosy Ratsy, and Nosy Manampao (Table 3). Each island had different features related to variation in microclimate and vegetational cover, all characteristics having a direct impact on the natural history of mosquitoes. The vegetation of these islands is discussed in the botanical portion of this paper, but a few points are important to note with regards to mosquitoes and associated ecological aspects of collection sites: Nosiborona is the closest to the main island of Madagascar, is 6 ha in size, has little human activity, is partially covered by woody vegetation, and features a small mangrove area; at 362 ha, Nosy Ankao is notably larger, has several villages and human habitations, including houses constructed on stilts (Figure 7), and includes a considerable

Figure 7. View of the village of Ampasimangidy on Nosy Ankao. The island in the distant background is Nosiborona and behind this are the hills of the northern portion of the Parc National de Loky-Manambato. (Photograph by Achille P. Raselimanana.)

Figure 8. View of mangrove on Nosy Ratsy and associated exposed old coral. Both of these habitats are potential breeding sites for mosquitoes. (Photograph by Achille P. Raselimanana.)

block of native forest habitat; Nosy Ratsy is 6 ha in size, covered in low scrub, with a small mangrove area (Figure 8), and little human activity; and Nosy Manampao is 29 ha in size, located furthest away from the coast of the main island, sees little human activity, and is mostly covered by open grassland habitat, with a small area of woody vegetation.

Inventory methods

Capture of preimaginal stages

Preimaginal stages were collected in natural or artificial cavities (tree trunks, tires, and bamboo) using a flexible plastic hose and a siphoning technique (Tantely, 2013). Other individuals were captured following the methods of Robert *et al*. (2002) with different size dip nets used in small, open water sources (puddles, small marshy areas) or larger water sources (ponds, canoes, wells); collected material was sorted on a white plate (Figure 9). Collected larvae were separated, preimaginal stages obtained using a pipette, and preserved in 70% ethanol.

Capture of adult stages

Eight light traps, CDC type (CDC miniature light trap, BioQuip Products, Inc, Rancho Dominguez, California, USA) were employed on Nosy Ankao, Nosy Manampao, and Nosy Ratsy. These devices were powered with rechargeable 6-volt batteries. The traps were opened after 15h00 and closed the following morning at around 7h00. Two different CDC trapping sessions were conducted on each of these three islands. On all four islands, mosquitoes were captured on people; these cases are referred to as "human landing catch" (HLC) according to Maquart *et al*. (2016).

Handling of mosquitoes

Live mosquitoes were anesthetized in a closed box filled with chloroform vapor. The morphological identification of adults was conducted with a binocular microscope and using the keys of Grjebine (1966), Ravaonjanahary (1978), Fontenille (unpublished, 1989), and Brunhes *et al*. (2011). To confirm species identification, the genitalia of male specimens belonging to the genus *Aedes*, subgenus *Skusea*, were dissected. Determinations were based on morphological characters defined by Brunhes (1977) and Ravaonjanahary (1978). Diagnosis of species belonging to the *Anopheles gambiae* complex was based on DNA extractions from specimen leg tissue following the method of Scott *et al*. (1993) and the protocol of Musapa *et al*. (2013).

Figure 9. Luciano Tantely using a white plate to isolate mosquito larvae collected from a natural tree cavity. Preimaginal stages were collected with a pipette and preserved in a tube with 70% ethanol. (Photograph by Voahangy Soarimalala.)

Possible Plasmodium *infection of mosquitoes*

Examination of possible mosquito *Plasmodium* infection was carried out through an ELISA immunological technique using monoclonal antibodies following Wirtz *et al*. (1987) and specifically targeting *P*. *falciparum* and *P*. *vivax*, both species being most common on Madagascar.

Reptiles and amphibians (Achille P. Raselimanana)

The field mission to the Nosy Ankao island group took place during the end of the warm and rainy season in northeastern Madagascar. This is a period that is favorable for herpetological inventories and when the majority of the local fauna is presumed to be active (Glaw & Vences, 2007). Further, this is the period when it is possible to encounter the highest density of reptiles and amphibians that depend on local ambient temperatures associated with their activity. Survey efforts were concentrated on Nosy Ankao, Nosy Manampao, and Nosy Ratsy, and the fourth island, Nosiborona, was the subject of a rapid and incomplete visit.

Inventory techniques

Three principal standard and complimentary methods have been employed on Madagascar for several decades to inventory the herpetofauna (Raxworthy & Nussbaum, 1994; Nussbaum *et al*., 1999; Raselimanana *et al*., 2000; Raselimanana, 2013). These include: 1) direct observation and inventory along transects or trails, 2) systematic searching in different microhabitats in a non-systematic manner, and 3) capture with pitfall traps.

Direct observations

This technique involves searching for reptiles and amphibians along pre-established trails or transects in different habitats or microhabitats. The principal objective was to capture individuals in the habitats they occur, which in turns provides insights into their ecology and biology. As reptiles and amphibians are poikilotherms, warmer periods in the late morning and early afternoon are the most favorable to observe diurnal species. In the case of nocturnal species, the period from just after sunset to about 10 p.m. works best for finding these animals. With the use of a headlamp, animals active at night can be located based on eye shine. Some diurnal species that rest at night on accessible branches and other types of vegetation can be readily seen with a headlamp, particularly those taxa that have bright or very light body coloration and stand out from the surrounding vegetation. In some cases, finding animals can be facilitated by their position (e.g. elongated or partially folded body, rolled up tails, spread legs, etc.).

Systematic searching

This method is used during daylight hours and consists of exploring a variety of habitats where different species might occur, particularly special habitats such as decomposing fallen or standing wood, dead or exfoliating tree bark, crevices between rocks, holes in trees, and areas with standing water-filled cavities in trees such as *Pandanus* and *Ravenala* (known as phytotelmic leaf axil). Termite mounds, soil litter, and thick humus at the base of standing trees were examined in detail. Such sites were the objects of systematic searching and, when appropriate, were excavated to extract animals. This technique provides insights into the microhabitats of certain species, including taxa that in many cases are not obtained with the other two described field techniques.

Pitfall traps

This method consists of a line of unbaited pitfall traps 100 m in length, with a 15 l plastic bucket placed every 10 m, and the line starting and ending with a bucket, hence n = 11 buckets per line (Figure 10). Each bucket was dug into the ground to rim level. Along the complete length of the line, a black plastic drift fence about 0.6 m in height was stapled to stakes in a vertical position, so that the plastic bisects the central portion of each bucket. An additional 0.2 m of drift fence was in contact with the ground and covered with soil or organic debris; this barrier acts to block the passage of terrestrial animals, guiding them towards the buckets. The bottom of each bucket was pierced with small holes, allowing drainage of rainwater and preventing captured animals from drowning. Each pitfall line was in place for a minimum of five days, and visited at least twice each day, once early in the morning and once in the late afternoon, to remove captured animals. One bucket in place for a 24-hour period is considered one "bucket-night".

In our standard utilization of this technique, three lines of pitfalls should have been employed on each island, each placed in different habitats. However, given the size of some of the surveyed islands, time constraints, and the generally low degree of variation in habitats, the number of pitfall lines installed on certain islands deviates from this standard methodology.

Species identification

Preliminary field identifications were conducted using the guide of Glaw & Vences (2007), as well as recent scientific publications describing new species from northeastern and northern Madagascar

Figure 10. Example of a pitfall line installed in an open area on Nosy Manampao. (Photograph by Voahangy Soarimalala.)

(Glaw *et al*., 2001, 2012) and systematic revisions of certain groups (Miralles & Vences, 2013; Wegener *et al*., 2013; Nagy *et al*., 2010, 2015). Definitive identifications were based on comparisons of the samples to specimens held in the collections of the Mention Zoologie et Biodiversité Animale, Domaine Sciences et Technologie, Université d'Antananarivo (UADBA, formerly called Département de Biologie Animale), and different scientific publications. Specimens collected during the Nosy Ankao Archipelago survey were deposited in this same collection.

Other aspects

In order to have a context of how common certain species were with respect to the different communities or islands they were found, an estimation of relative abundance was used; this was derived from frequency observations of a given taxon during a fixed period of five days of field surveys using the three complementary herpetological methods outlined above. Effectively, the period of investigation at each site was approximately five days, with the exception of Nosy Ankao, which was distinctly larger than the other surveyed islands (Table 2). On this island, efforts were divided into two parts; the first was to explore the large forest parcel near the village of Andasibe, and the second to investigate the dune forest near Antafondro. Following these frequency measures, a species was classified, based on the three different field techniques employed, as not abundant (=relatively rare), relatively abundant (=relatively frequent), abundant (=frequent) or very abundant (=common). It is important to mention that these measures are only relative to the period of the inventory. The conservation status of each species cited herein follows the IUCN (2016) Red List. In cases when the species determination was uncertain, but with an affinity to a known taxon, the species name is preceded by "aff."; in cases when species identity was uncertain, the species name was designated as "sp.". In any case, the species designated in this manner, probably represent undescribed taxa, some of which have already been verified by genetic analyses (e.g., *Liophidium* aff. *torquatum*).

Birds (Steven M. Goodman)

Lists of the landbirds from three islands, Nosy Ankao, Nosy Manampao, and Nosy Ratsy, were derived from direct observation or vocalizations. No mist netting was conducted. This survey did not take place during the period in which different species of seabirds, specifically terns, were breeding and information about seabirds has been extracted from the literature.

Small mammals (Yasser Anbdou, Steven M. Goodman, Voahangy Soarimalala, and Pablo Tortosa)

We employed two different trapping techniques commonly used on Madagascar in past decades: live traps, described below, and pitfall traps, described above under reptiles and amphibians. Trapping devices were installed on Nosy Ankao, Nosy Manampao, and Nosy Ratsy. The duration of the trapping sessions on each of these islands was proportional to island size (see results), with the most intensive efforts focused on the forested areas of Nosy Ankao. Interviews were also conducted with older villagers living on the island to provide insights into possible mammals occurring locally that are rare or recently extirpated.

Live traps

Two different live trap types were employed: National traps, 39.2 x 12.3 x 12.3 cm (Tomahawk Trap Company, Hazelhurst, Wisconsin, USA) and Sherman traps, 22.5 x 8.6 x 7.4 cm (H.B. Sherman Traps Inc., Tallahassee, Florida, USA). Traps were not installed at fixed distances, but rather at sites that appeared to have possible evidence of small mammal activity, such as in front of burrows, along fall tree trunks, and arboreal positions on branches and lianas. All traps were visited in the early morning and in the late afternoon; during the latter period fresh peanut butter bait was added, and the previous bait removed. We use the term "trap-night" which indicates the utilization of one of these trap devices over a 24-hour period, typically from 7h00 to 7h00.

Specimens

Voucher specimens of small mammals captured during this survey were deposited in the Field Museum of Natural History (FMNH) and Mention Zoologie et Biodiversité Animale, Domaine Sciences et Technologie, Université d'Antananarivo (UADBA, formerly called Département de Biologie Animale). Tissues were collected from each captured small mammal associated with different zoonotic disease studies, as well as future phylogeographic work.

Results

Weather data

During our inventory, daily information was obtained on the minimum and maximum daily temperatures, as well as precipitation on Nosy Ankao (Table 6) in the immediate vicinity of our camp. In general, there was little variation in daily minimum and maximum temperatures, with the average measures being 23.5°C ± 0.65 (range 23-25°C) and 32.8°C ± 0.87 (range 31-34°C), respectively. We recorded rainfall on six days of the 11 days the rain gauge was installed, and the heaviest recorded precipitation during a 24-hour period was 6 mm.

Table 6. Weather data obtained during biological inventories of the Nosy Ankao group from 4 to 14 March 2016. The station was set up next to the research camp on Nosy Ankao.

Date	Minimum temperature (°C)	Maximum temperature (°C)	Rainfall (mm)
4 March	25	33	1
5 March	25	32	1.5
6 March	25	33	1
7 March	24	33	0
8 March	23	33	0
9 March	24	34	0
10 March	24	34	6
11 March	24	33	0
12 March	24	31	4
13 March	24	32	0
14 March	25	33	4
	23.5 ± 0.65 23-25, n = 11	32.8 ± 0.87 31-34, n = 11	1.6 ± 2.11 0-6, n = 11

Data were obtained over the course of a 48-hour cycle using the HOBO loggers. Hourly variation in temperature and relative humidity on three different islands (Nosy Ankao, Nosy Manampao, and Nosy Ratsy) showed rather stable patterns. Daily temperatures varied from a high of slightly less than 25 to 36°C, with the coolest temperatures occurring at night through the post-dawn period and daily maximum temperatures recorded between the late morning to the early evening (Figure 11A).

Relative humidity varied from about 60% to 90%, with the lowest values occurring during the cooler early morning hours and increasing towards mid-afternoon and through the night (Figure 11B).

Vascular plants

General aspects

The known flora of vascular plants collected in March 2016 on islands in the Nosy Ankao group (Nosy Ankao, Nosy Manampao, Nosy Ratsy, and Nosiborona) comprised 81 species or morphospecies in 61 genera, and 38 families; the identifications are presented in Table 7.

In total, 14 vegetational transects were conducted, including nine on Nosy Ankao, two on Nosy Manampao, and three on Nosy Ratsy. For Nosiborona, only general botanical collections were made, as the flora of this island was largely herbaceous. The study sites showed little elevational variation, falling between near sea level to about 15 m above sea level. The soil substrates on these different islands were composed of sands or derived from coral, both of which retain little water.

Global vegetational characteristics

Floristic diversity

In total, 81 plant species and morphospecies were identified based on botanical inventories on islands in the Nosy Ankao group. A few specimens could not be identified to species, but it is too early to know whether any of these might be new to science. The most represented families were Rubiaceae, Asclepiadaceae, Euphorbiaceae, and Celastraceae.

Biogeographic affinities

Among the 81 plant species identified from the Nosy Ankao island group, about 72% are endemic to Madagascar (Figure 12A, B), 23% native, and 5% introduced. A number of these species also occur in tropical Africa, on other western Indian Ocean islands, or in other areas of the world (cosmopolitan species).

Life-forms spectrum of the vegetation

The documented plant species were classified into different life-forms following Raunkiaer's (1905) classification adapted by Lebrun (1966) (Figure 13). These results indicate that of the different life-forms, microphanerophytes dominate (55%), which means that most vascular plants occurring on these islands were small in stature, a characteristic associated with the local climatic conditions.

Synthesis of general floristic aspects

Different parameters associated with the collected data showed that at the inter-island level, each site had different floristic characteristics. Further, about 74% of the inventoried species were restricted to a single island, 24% were found on two islands, and 3%

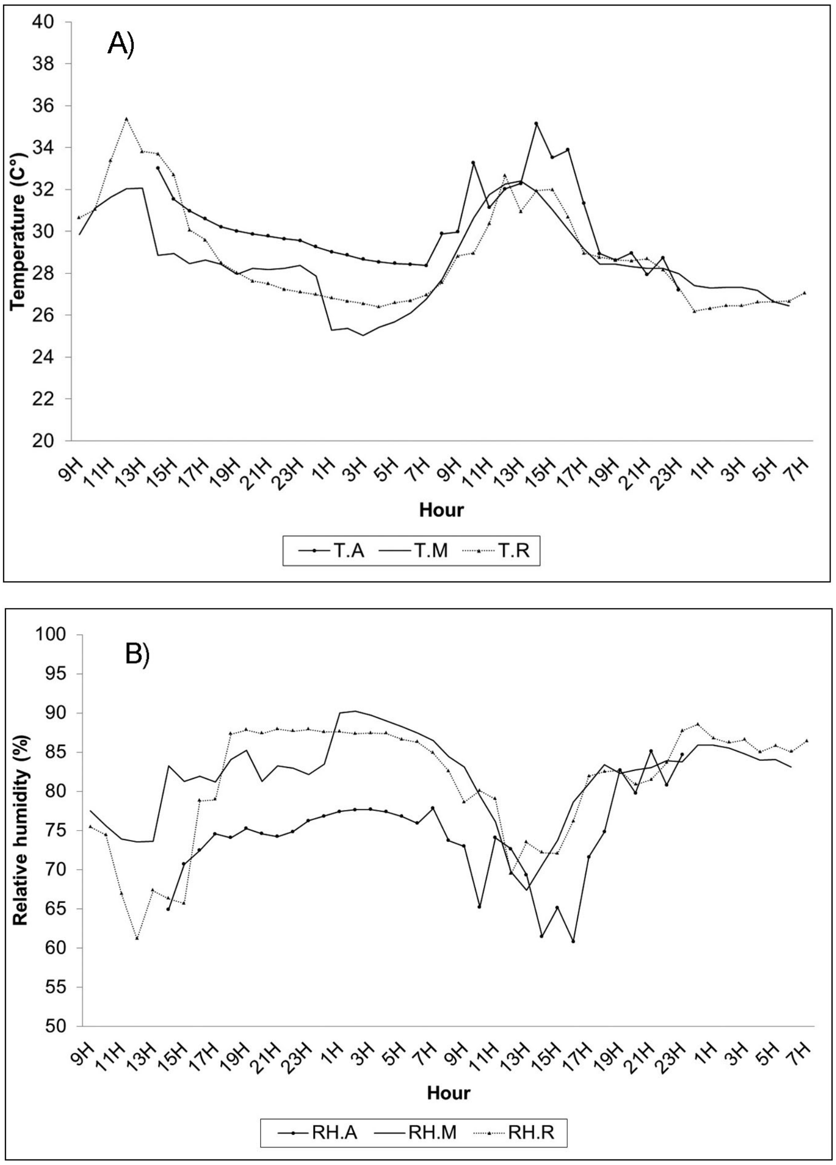

Figure 11. Patterns of temporal variation over 48 hours: A) temperature (T.) and B) relative humidity (RH) on Nosy Ankao (A), Nosy Manampao (M), and Nosy Ratsy (R).

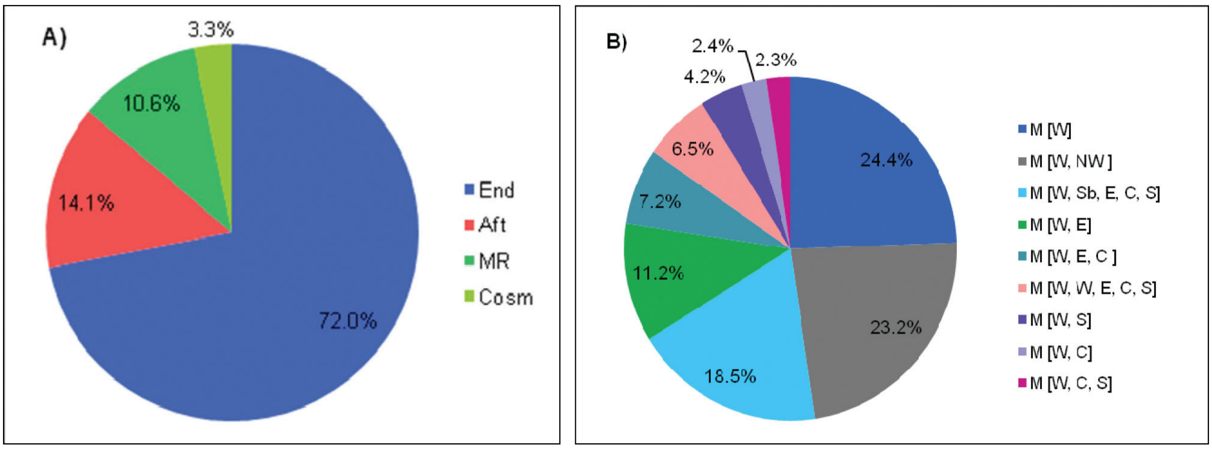

Figure 12. Phytogeographic aspects of flora of the islands of the Nosy Ankao Archipelago, including A) range of indicator species: Malagasy endemic (End), tropical Africa (Aft), Malagasy Region (MR), and Cosmopolitan (Cosm) and B) phytogeographic affinities of native Malagasy species (following Humbert, 1955): Sambirano (Sb), Eastern (E), Western (W), Northwest (NW), Center (C), and Southern (S).

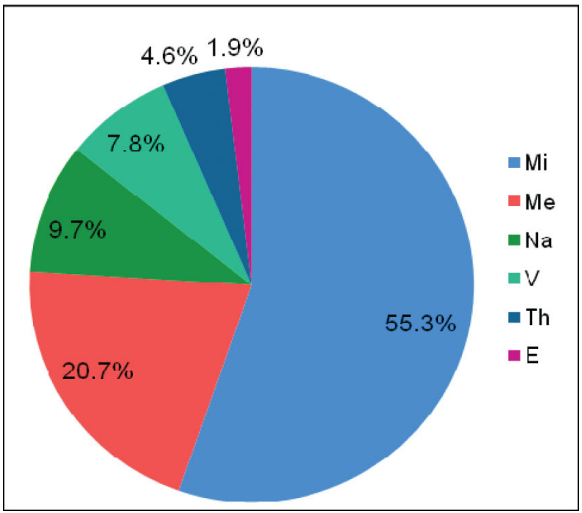

Figure 13. The relative diversity of plant life-forms occurring on islands in the Nosy Ankao group. Mesophanerophytes (me), microphanerophytes (mi), nanophanerophytes (na), therophytes (th), vines (V), and epiphytes (E).

occurred on three or more islands. The combination of the small size of these islands, with Nosy Ankao being the largest at 365 ha (Table 2), presumed extended dry season, and their lack of topographic variation, probably best explain why these sites have low species richness and diversity at different taxonomical levels (species, genus and family).

The dominant phytogeographic affinity of the plant species encountered on these islands was that of the Western Domain and more specifically its Northern Sector. This is associated with the local climatic regime and geographical position of the islands in the Nosy Ankao group.

The life-forms identified indicate a dominance of microphanerophytes, which is also characteristic of the Northern Sector of the Western Domain. This is most likely associated with ecological conditions such as the strong, desiccating, and salt saturated winds

Table 7. The known flora of the Nosy Ankao island group. All three survey techniques were employed on Nosy Ankao, Nosy Ratsy, and Nosy Manampao; only general botanical collections were made on Nosiborona. + = present, - = not found on a given island.

Family	Genus and species	Nosy Ankao	Nosy Ratsy	Nosy Manampao	Nosiborona
Acanthaceae	*Hypoestes strigata* Benoist	-	+	+	-
Amaranthaceae	*Lagrezia ambrensis* Cavaco	-	-	-	+
Anacardiaceae	*Abrahamia pauciflora* (Engl. ex H. Perrier) Randrian. & Lowry	+	-	-	-
	Poupartia gummifera Sprague	-	-	-	+
Annonaceae	*Monanthotaxis pilosa* (Baill.) Verdc.	-	-	-	+
Apocynaceae	*Cynanchum arenarium* Jum. & H. Perrier	+	+	-	+
	Landolphia gummifera (Poir.) K. Schum.	+	-	+	-
	Gonocrypta sp. 1	+	-	-	-
	Pervillea sp. 1	+	-	-	-
	Secamone aff. *grandiflora* Klack.	+	-	-	-
	Secamone capitata Klack.	+	-	-	-
Bignoniaceae	*Rhodocolea racemosa* (Lam.) H. Perrier	+	-	-	-
Boraginaceae	*Cordia myxa* L.	-	-	-	+
Capparaceae	*Crataeva excels* Bojer.	-	-	-	+
Celastraceae	*Brexia* aff. *humbertii* H. Perrier	+	-	-	-
	Brexia madagascariensis (Lam.) Ker Gawl.	+	-	-	-
	Loeseneriella rubiginosa (H. Perrier) N. Hallé	-	-	-	+
	Maytenus undata (Thunb.) Blakelock	+	-	-	-
	Mystroxylon aethiopicum (Thunb.) Loes.	+	+	-	-
Combretaceae	*Combretum coccineum* (Sonn.) Lam.	-	-	-	+
Commelinaceae	*Commelina* aff. *madagascarica* C.B. Clarcke	-	+	+	-
Convolvulaceae	*Ipomoea rubens* Choisy	-	-	-	+
Cyperaceae	*Cyperus betafensis* Cherm.	-	-	+	+
	Cyperus longifolius Poir.	-	-	-	+
Asparagaceae	*Dracaena reflexa* var. *lanceolata* H. Perrier	+	-	-	+

Table 7. (continued)

Family	Genus and species	Nosy Ankao	Nosy Ratsy	Nosy Manampao	Nosiborona
Ebenaceae	*Diospyros erythrosperma* H. Perrier	+	-	-	-
	Diospyros aff. *ferrea* (Willd.) Bakh.	+	-	-	-
	Diospyros pervilleana (Baill.) G.E. Schatz & Lowry	+	-	-	-
	Diospyros platycalyx Hiern	-	+	-	-
	Diospyros pruinosa Hiern	+	+	-	-
	Diospyros quercina (Baill.) G.E. Schatz & Lowry	-	-	-	+
	Diospyros squamosa Bojer ex A. DC	+	+	-	-
Erythroxylaceae	*Erythroxylum retusum* Baill. ex O.E. Schulz	+	-	-	-
	Erythroxylum cf. *sphaeranthus* Bojer	-	+	-	-
	Erythroxylum platyclados Bojer	+	-	-	-
	Erythroxylum rignyanum Baill.	+	-	-	-
Euphorbiaceae	*Euphorbia tetraptera* Baker	+	+	-	-
	Margaritaria anomala (Baill.) Fosberg	+	+	-	-
	Thecacoris aff. *perrieri* Leandri	-	-	-	+
Fabaceae	*Albizia arenicola* R. Vig.	+	+	-	-
	Dichrostachys richardiana Baill.	+	+	-	-
	Senna occidentalis (L.) Link	-	-	+	-
Loganiaceae	*Strychnos* sp. 1	+	-	-	-
Lythraceae	*Capuronia benoistii* (Leandri) P.E. Berry	-	+	-	-
Malvaceae	*Grewia* aff. *barorum* Capuron	+	-	-	-
	Grewia betulaefolia Baill.	+	-	-	+
	Hibiscus megistanthus Hochr.	+	-	-	-
Meliaceae	*Malleastrum boivinianum* (Baill.) J.-F. Leroy	+	-	-	-
Moraceae	*Ficus lutea* Vahl	+	-	-	-
	Ficus tiliifolia Baker	-	-	+	-
Myrtaceae	*Eugenia* aff. *calciscopulorum* N. Snow	+	+	-	-
	Eugenia aff. *oligantha* Baker	+	+	-	-
Ochnaceae	*Ochna ciliata* Lam.	+	-	-	-
Oleaceae	*Jasminum greveanum* Danguy ex H. Perrier	-	+	-	-
	Noronhia seyrigii H. Perrier	+	-	-	-
Orchidaceae	*Angraecum* aff. *magdalenae* Schltr. & H. Perrier	+	+	-	-
Primulaceae	*Oncostemum* sp. 1	+	-	-	-
	Oncostemum sp. 2	+	-	-	-
Rhamnaceae	*Scutia myrtina (*Burm. f.) Kurz	+	-	-	-
Rhizophoraceae	*Cassipourea microphylla* Tul.	+	-	-	-
Rubiaceae	*Coffea boiviniana* (Baill.) Drake	+	-	-	-
	Coptosperma sp. 1	+	-	-	-
	Empogona ovalifolia (Hiern) J. Tosh & Robbr.	-	+	-	-
	Ixora aff. *ripicola* De Block	+	-	-	-
	Ixora emirnensis Baker	+	-	-	-
	Pyrostria sambavensis (Cavaco) Razafim., Lantz & B. Bremer	-	+	-	-
	Tarenna grevei (Drake) Homolle	-	+	-	-
	Tricalysia ambrensis Randriamb. & De Block	+	-	-	-
Rutaceae	*Vepris* aff. *arenicola* H. Perrier	+	+	-	-
Salicaceae	*Casearia nigrescens* Tul.	+	-	-	-
Sapindaceae	*Allophylus cobbe* (L.) Raeusch.	+	-	-	-
	Macphersonia gracilis var. *hildebrandtii* (O. Hoffm.) Capuron	+	+	-	-
Sapotaceae	*Capurodendron greveanum* Aubrév.	+	-	-	-
	Mimusops coriacea (A. DC.) Miq.	+	-	-	-
	Sideroxylon aff. *saxorum* Lecomte	+	-	-	-
Vitaceae	*Cissus microdonta* (Baker) Planch.	+	+	+	+

that come off the sea, low precipitation, and sandy, water-porous soils.

Identified vegetation groups

The data obtained from the plant transects on islands in the Nosy Ankao group provide insights into their floristic and structural affinities.

Floristic groups

Among the 14 plant transects (Tr) conducted on the different islands, three different floristic groups were identified (Figure 14): Group 1 (nine transects, restricted to Nosy Ankao), Group 2 (three transects, restricted to Nosy Ratsy), and Group 3 (two transects, restricted to Nosy Manampao). Even though a few plants were common to different islands, each island should be considered floristically distinct.

On the basis of the linear transect data, each of the three islands form a unique group, indicating distinct floral differences. The nomenclature for these floristic groups and the two species in each group with the highest indicator values (INDVal formula) are presented in Table 8.

Structural groups

Three structural groups were identified based on the linear transect data and with respect to their physiognomic characteristics (Figure 15): Group A (eight transects, restricted to Nosy Ankao), Group B (four transects, found on Nosy Ratsy and Nosy Manampao), and Group C (two transects, found on Nosy Manampao and Nosy Ankao). The structural groups are identified based on the dominant physiognomic aspects for each and include:
Group A: Low-growing forest with dense understory;
Group B: Low-growing forest with open understory;
Group C: Low-growing forest with open canopy.

Identification of vegetation groups

The classification of the vegetation groups was derived from combination of floristic and structural groups (Table 9). The details and nomenclature for these vegetation groups are presented (Table 10).

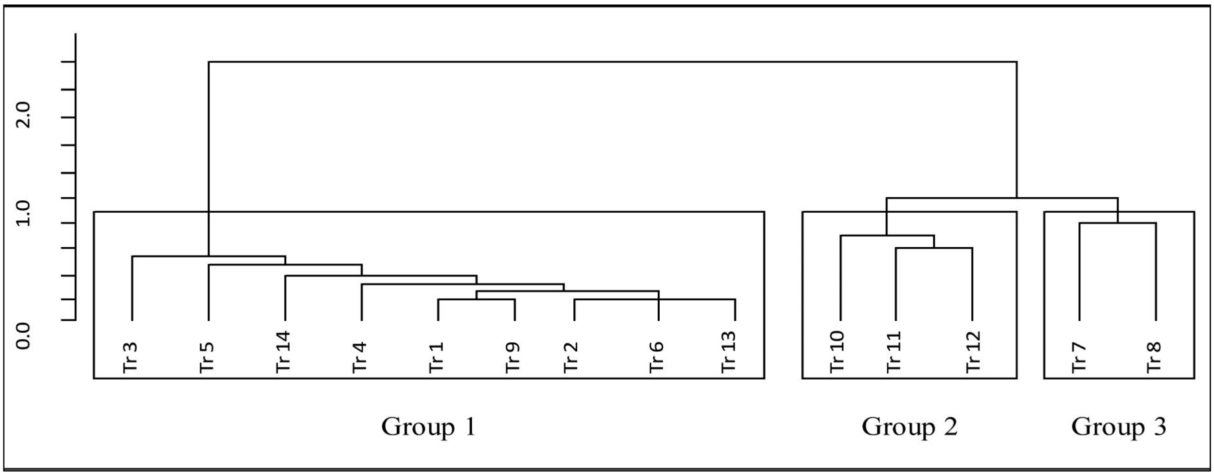

Figure 14. Classification of the 14 transects (Tr) based on floristic similarity and fall into three distinct groups.

Table 8. Details and associated nomenclature of the three recognized floristic groups based on data obtained during the linear transects.

Group	Family	Taxa	Indicator value (%)	Group designation	Island
1	**Sapotaceae**	*Capurodendron greveanum*	96.8	Group *Capurodendron greveanum* and *Eugenia* aff. *calciscopulasum*	Nosy Ankao
	Myrtaceae	*Eugenia* aff. *calciscopulasum*	66.7		
2	**Celastraceae**	*Mystroxylon aethiopicum*	100.0	Group *Mystroxylon aethiopicum* and *Diospyros erythrosperma*	Nosy Ratsy
	Ebenaceae	*Diospyros erythrosperma*	88.9		
3	**Sapotaceae**	*Mimusops coriacea*	50.0	Group *Mimusops coriacea* and *Ficus tiliifolia*	Nosy Manampao
	Moraceae	*Ficus tiliifolia*	50.0		

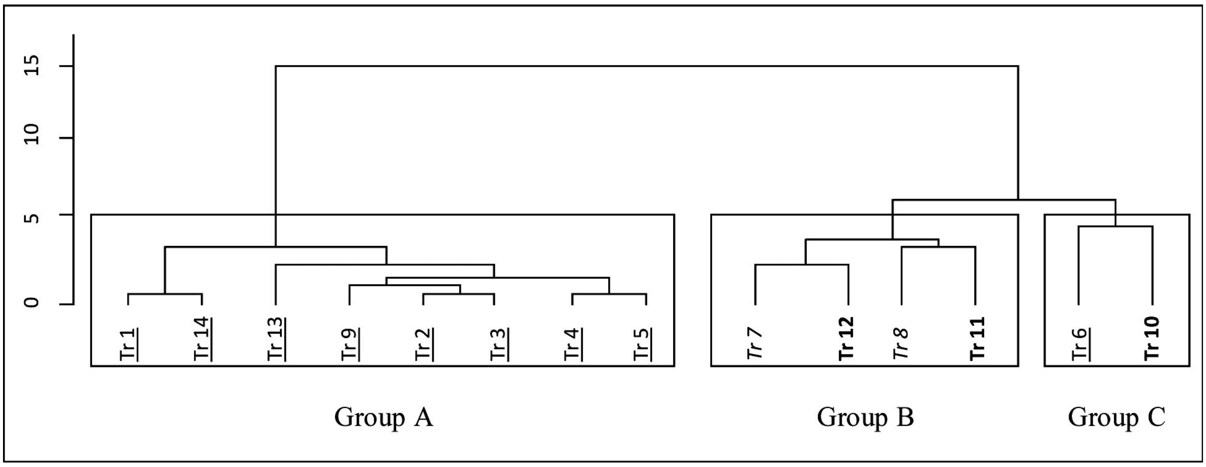

Figure 15. Classification of the 14 transects (Tr) based on structural data; these fall into three distinct groups. Transect numbers underlined are from Nosy Ankao, those in italics are from Nosy Ratsy, and those in bold are from Nosy Manampao.

Table 9. Relationships between the two different types of groups, floristic and structural, associated with linear transects (Tr) conducted on islands in the Nosy Ankao group, and used to determine the vegetation group classification.

Transects	Floristic group	Structural group	Vegetation group
Tr 1, Tr 2, Tr 3, Tr 4, Tr 5, Tr 9, Tr 13, Tr 14	1	A	I
Tr 6		C	
Tr 11, Tr 12	2	B	II
Tr 10		C	
Tr 7, Tr 8	3	B	III

Table 10. Nomenclature used for the vegetational groups and associated variation in structural form.

Group	Name of vegetational group	Structural form	Island
I	*Capurodendron greveanum* and *Eugenia* aff. *calciscopulasum*	Low-growing forest with dense understory Low-growing forest with open canopy	Nosy Ankao
II	*Mystroxylon aethiopicum* and *Diospyros erythrosperma*	Low-growing forest with open understory Low-growing forest with open canopy	Nosy Ratsy
III	*Mimusops coriacea* and *Ficus tiliifolia*	Low-growing forest with open understory	Nosy Manampao

Description of vegetation groups

Group Capurodendron greveanum *and* Eugenia *aff. calciscopulasum (Group I)*

This vegetation group is represented by nine different linear transects, all conducted on Nosy Ankao. The group has a distinct appearance with emergent *Capurodendron* trees (Figure 16).

Floristic characteristics of Group I

In this group, 51 species occurring in 38 genera and 28 families were identified. The phytogeographic affinities of the indicator species of this group are nearly 82% endemic (Figure 17A). The phytogeographic relationships of this group indicate that 40% of the indicator species are shared with the Western Domain and 20% with the Northern Sector of this domain (Figure 17B).

Structural characteristics of Group I

The vegetation groups of Nosy Ankao present two distinct variants, largely due to substrate.

Structural variant 1: Low-growing forest with closed understory -- This first variant was found on flat sandy soils and is formed by a multi-layered plant community, with an average height of 3.7 m (Figures 16 & 18). This variant has a density of 110 plants per 100 m of transect. The formation is open with an average canopy cover of 63% (Figure 19). The

Figure 16. View of the *Capurodendron greveanum* and *Eugenia* aff. *calciscopulasum* forest on Nosy Ankao, considered Group I, structural variant 1. The dominant large tree is *Capurodendron greveanum.* The dense lower portion of the formation is associated with the image taken at the forest edge and does not represent understory structure within the forest. (Photograph by Achille P. Raselimanana.)

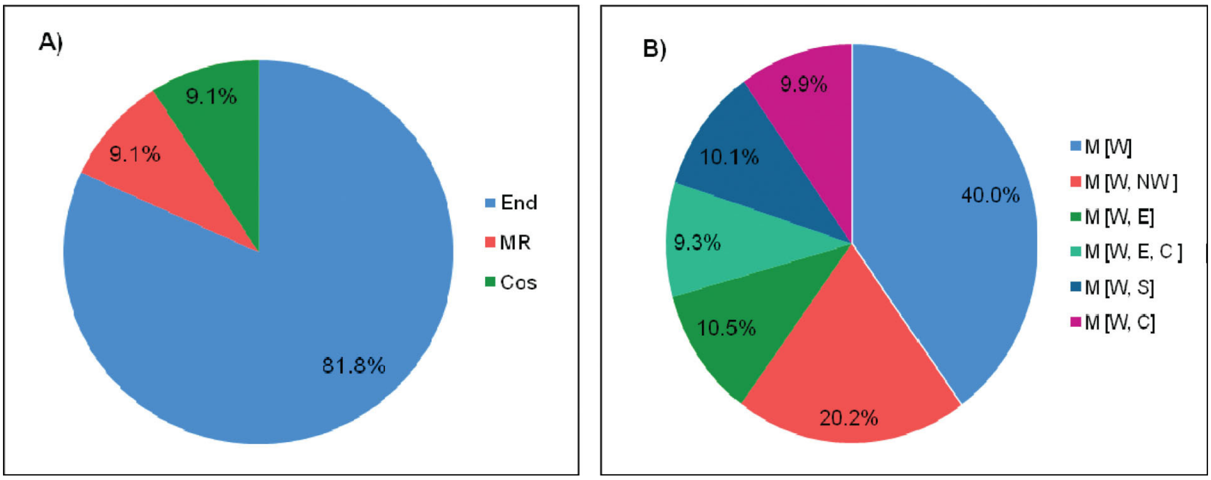

Figure 17. Aspects of the Nosy Ankao island Vegetation Group I flora, including A) range of indicator species: Malagasy endemic (End), tropical Africa (Aft), Malagasy Region (MR) and Cosmopolitan (Cosm) and B) phytogeographic affinities of native Malagasy species (following Humbert, 1955): Sambirano (Sb), Eastern (E), Western (W), Northwest (NW), Center (C), and Southern (S).

analysis of the vertical structure indicates that each stratum was characterized by particular species:

1) The lower stratum (ground to 4 m) is largely dominated by *Dracaena reflexa* var. *lanceolata* (Agavaceae), *Strychnos* sp 1. (Loganiaceae), and *Diospyros pervilleana* (Ebenaceae).
2) The middle stratum (4 to 8 m) is composed of different trees; the most frequently encountered groups are *Macphersonia gracilis* var. *hildebrandtii* (Sapindaceae), *Maytenus undata* (Celastraceae), *Vepris* aff. *arenicola* (Rutaceae), and *Eugenia* aff. *calciscopulasum* (Myrtaceae).

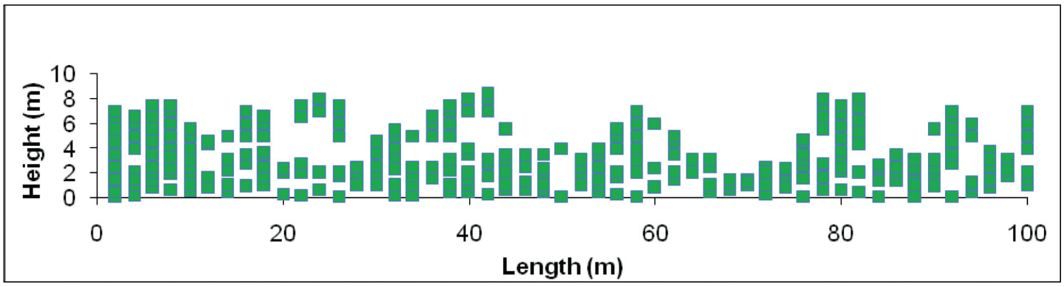

Figure 18. Profile of Group I, structural variant 1, on Nosy Ankao. For a photograph of this formation, see Figure 16.

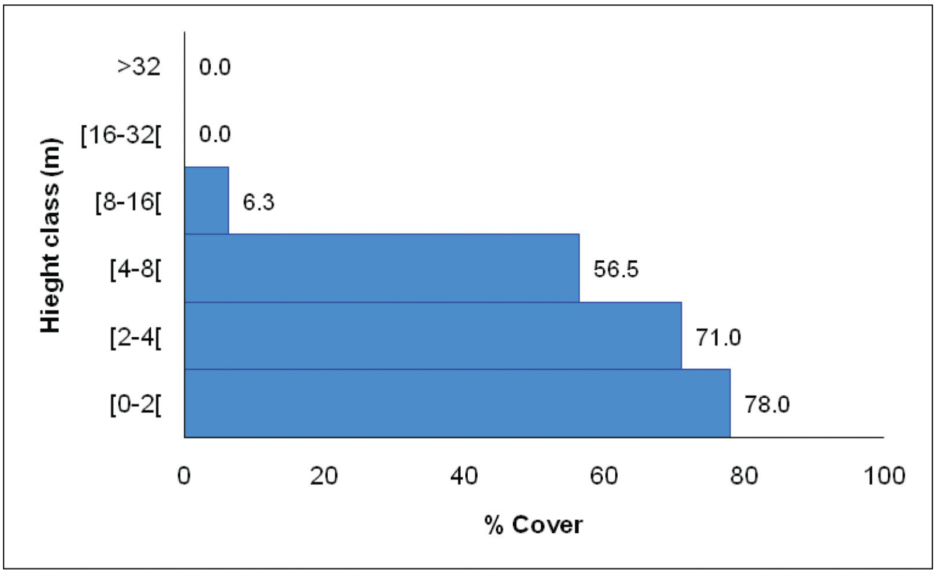

Figure 19. Diagram of forest canopy cover associated with Group I, structural variant 1, on Nosy Ankao. For a photograph of this formation, see Figure 16.

3) The upper stratum (starting at 8 m), which is not continuous, is formed by the canopy cover of *Capurodendron greveanum* (Sapotaceae) and *Eugenia* aff. *calciscopulasum*.

Structural variant 2: Low-growing forest with open canopy -- The second variant was found on sandy soils, associated with a coastal dune formation, and is formed by a multi-layered plant community, made up by species with an average height of 4.0 m (Figures 20 & 21). This variant has an average density of 97 plants per 100 m of transect. It is an open formation with an average measure of canopy cover of 40% (Figure 22). The different vegetational strata are composed of:

1) The lower and middle strata (ground to 4 m), dominated by *Vepris* aff. *arenicola* and *Maytenus undata*.
2) The common canopy elements (4 to 8 m), occupied by *Capurodendron greveanum* and *Diospyros erythrosperma* (Ebenaceae).

Group Mystroxylon aethiopicum *and* Diospyros erythrosperma *(Group II)*

This vegetational group has been defined based on three linear transects conducted on Nosy Ratsy. It is composed of vegetation growing on sand and with a low canopy reaching an average height of 2.4 m. The physiognomic aspect of this vegetation formation would appear to be that of considerable former disturbance and in an advanced stage of regeneration.

Floristic characteristics of Group II

In this group, 22 species occurring in 19 genera and 15 families were identified. The phytogeographic affinities of the indicator species showed that nearly 78% plants are endemic to Madagascar (Figure 23A). The phytogeographic relationships of this group indicate that 42.9% of the species are shared with the Western, Eastern, Central, and Southern domains; among the endemic taxa, 28.6% are in common with

Figure 20. View of the *Capurodendron greveanum* and *Eugenia* aff. *calciscopulasum* forest on Nosy Ankao, considered Group I, structural variant 2. This is the dune forest formation on the eastern side of Nosy Ankao located in close proximity to the village of Antafondro. (Photograph by Achille P. Raselimanana.)

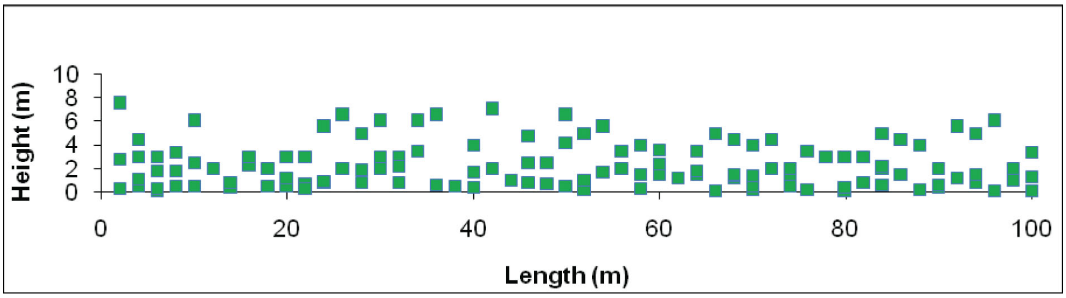

Figure 21. Profile of Group I, structural variant 2, on Nosy Ankao.

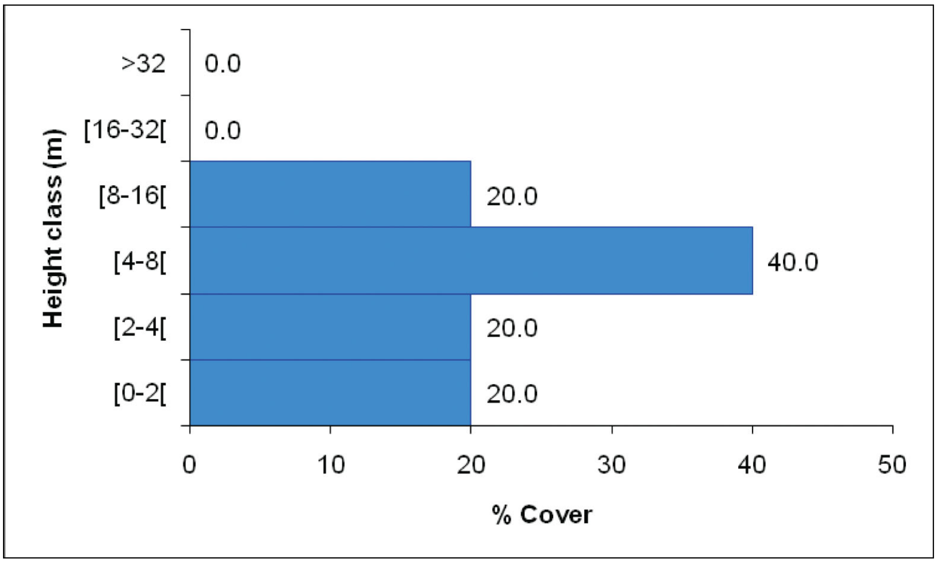

Figure 22. Diagram of forest canopy cover associated with Group I, structural variant 2, on Nosy Ankao.

the Western Domain and 14.3% with the Eastern Domain (Figure 23B).

Structural characteristics of Group II

This low-growing formation (Figure 24) has two structural variants, the second of which was only represented by one linear transect.

Structural variant 1: Low-growing forest with open understory -- This structural variant has an average canopy height of 3 m (Figure 25) and an average density of 127 plants per 100 m of transect. The vertical structure of the vegetation consists of two distinct layers (Figure 26):

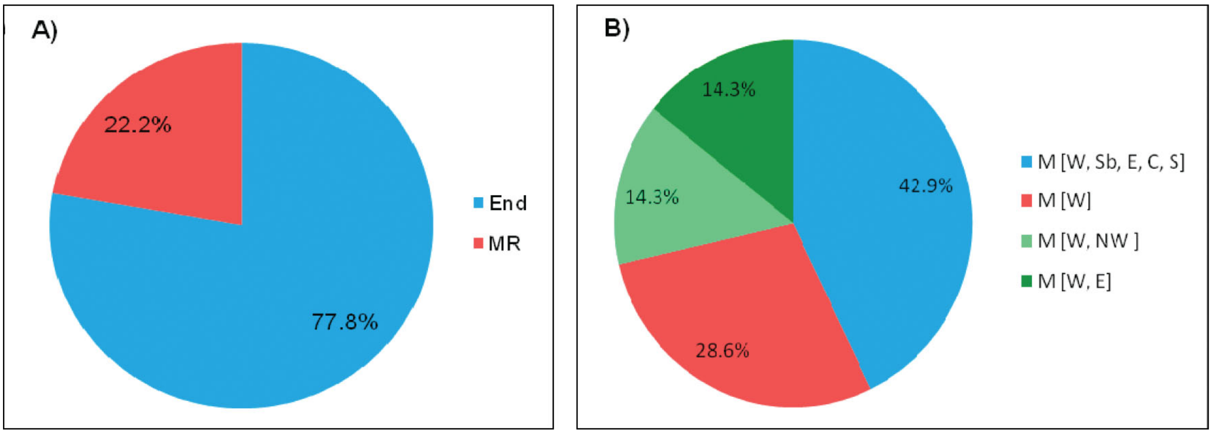

Figure 23. Aspects of the Nosy Ratsy flora represented by Group II, including A) range of indicator species: Malagasy endemic (End), tropical Africa (Aft), Malagasy Region (MR) and Cosmopolitan (Cosm) and B) phytogeographic affinities of native Malagasy species (following Humbert, 1955): Sambirano (Sb), Eastern (E), Western (W), Northwest (NW), Center (C), and Southern (S).

Figure 24. View of the *Mystroxylon aethiopicum* and *Diospyros erythrosperma* formation on Nosy Ratsy. (Photograph by Voahangy Soarimalala.)

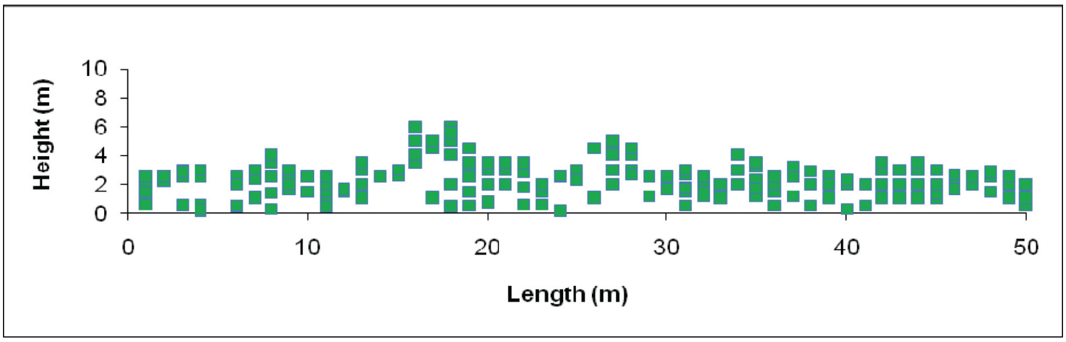

Figure 25. Profile of Group II, structural variant 1, on Nosy Ratsy.

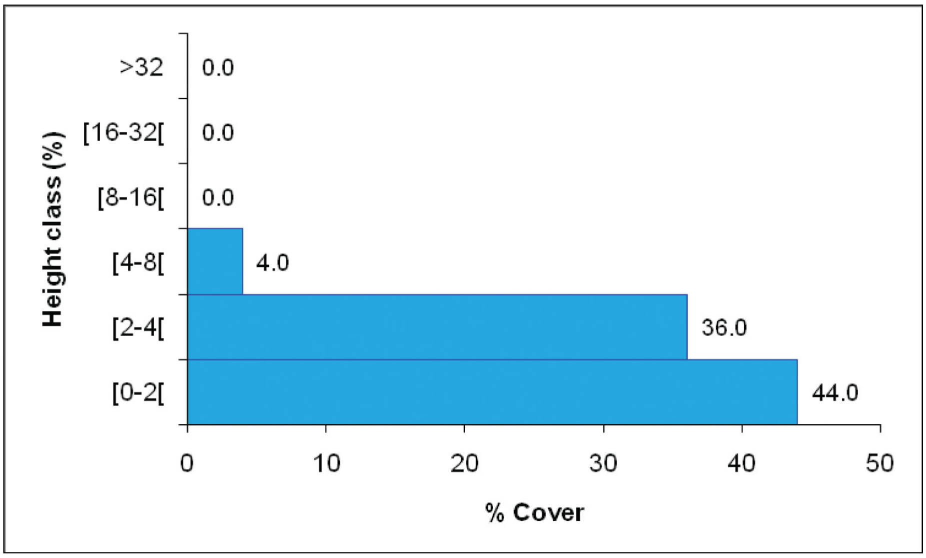

Figure 26. Diagram of forest canopy cover associated with Group II, structural variant 1, on Nosy Ratsy.

1) A lower stratum (ground to 4 m), dominated by *Cynanchum arenarium* (Apocynaceae) and *Grewia* aff. *barorum* (Malvaceae).
2) An upper stratum (starting at 4 m), notably open, and discontinuous, dominated by *Margaritaria anomala* (Euphorbiaceae) and *Mystroxylon aethiopicum* (Celastraceae).

Structural variant 2: Low-growing forest with open canopy -- This structural variant, based on a single transect, has an average canopy height of 2.4 m (Figure 27) and an average density of 138 plants per 100 m of transect. The vertical structure of the vegetation consists of two distinct layers (Figure 28):

1) The lower stratum (ground to 2 m) is not extensively vegetated, with canopy cover of 42% (Figure 28). The dominant species are *Grewia betulaefolia* (Malvaceae) and *Grewia* aff. *barorum*.
2) The upper stratum (2 to 4 m) is very open, with 22% canopy cover (Figure 28). The vegetation is dominated by *Margaritaria anomala* (Euphorbiaceae) and *Mystroxylon aethiopicum* (Celastraceae).

Group Mimusops coriacea *and* Ficus tiliifolia *(Group III)*

This group is based on two linear transects conducted on Nosy Manampao. The physiognomic aspects of this vegetational formation would appear to be that of considerable former disturbance and in a stage of regeneration (Figure 29).

Floristic characteristics of Group III

The vegetation community within this group is dominated by two woody plants, *Mimusops coriacea* and *Ficus tiliifolia*, and comprised seven species in total. The phytogeographic affinities of the indicator species show a level of endemism of about 60% with respect to the Malagasy Region (Figure 30A). The phytogeographic relationships of this group indicate that 40% of the species are shared with the Western and Eastern Domains (Figure 30B).

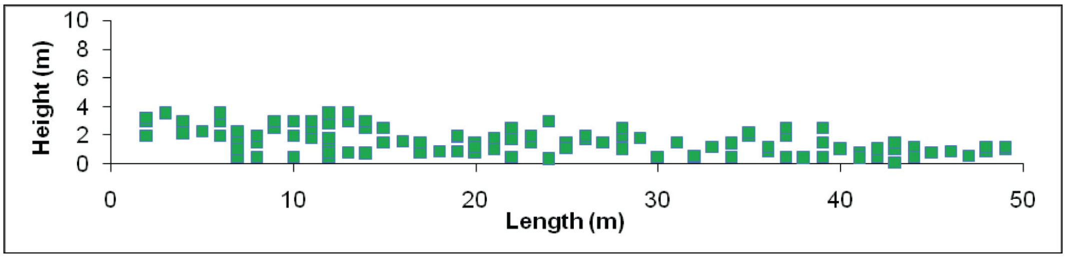

Figure 27. Profile of Group II, structural variant 2, on Nosy Ratsy.

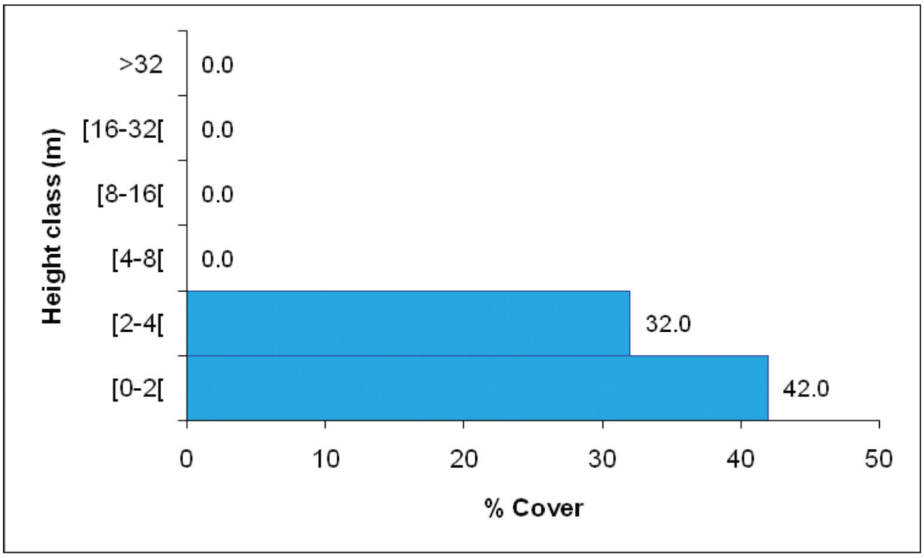

Figure 28. Diagram of forest canopy cover associated with Group II, structural variant 2, on Nosy Ratsy.

Figure 29. View of the *Mimusops coriacea* and *Ficus tiliifolia* formation on Nosy Manampao. (Photograph by Voahangy Soarimalala.)

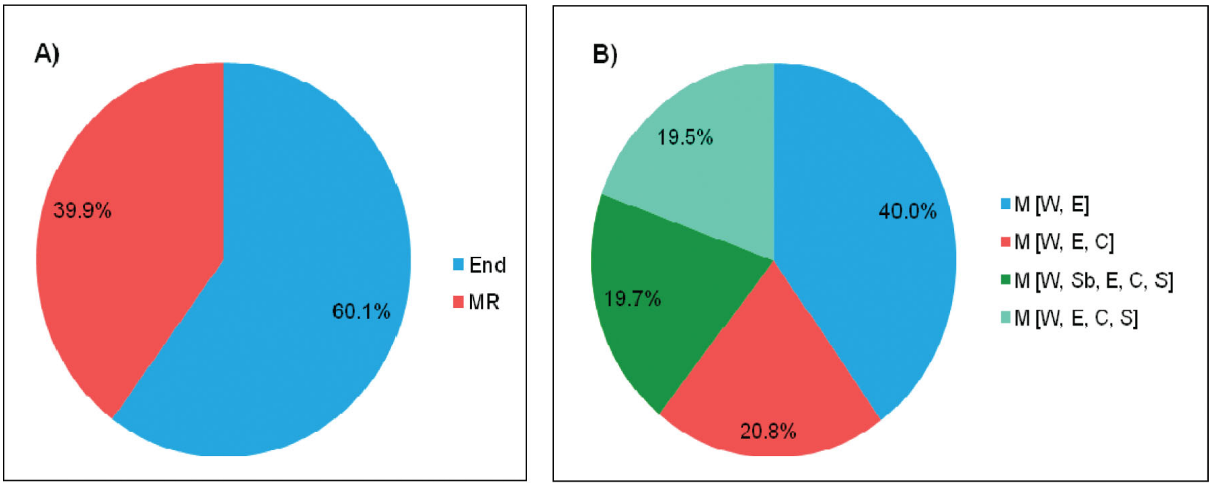

Figure 30. Aspects of the Nosy Manampao flora represented by Group III, including A) range of indicator species: Malagasy endemic (End), tropical Africa (Aft), Malagasy Region (MR) and Cosmopolitan (Cosm) and B) phytogeographic affinities of native Malagasy species (following Humbert, 1955): Sambirano (Sb), Eastern (E), Western (W), Northwest (NW), Center (C), and Southern (S).

Structural characteristics of Group III

This group has a structure characterized by an open understory with distinct vertical stratification, and an average canopy height of 2.8 m; in some areas, the emergent trees reach 4 to 8 m (Figure 31). In general, the canopy is slightly flat, and regular. This vegetation group has an average density of 99 individuals per 100 m length of transect. The vertical structure can be divided into two different strata:

1) The lower stratum (ground to 4 m) is generally dense and with a closed structure (Figure 32), with understory dominated by *Landolphia gummifera*

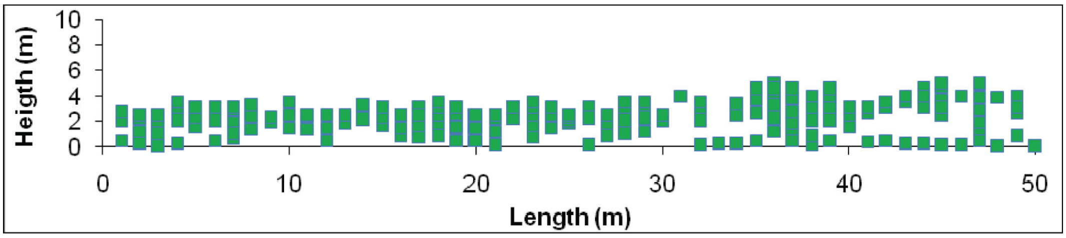

Figure 31. Profile of Group III on Nosy Manampao.

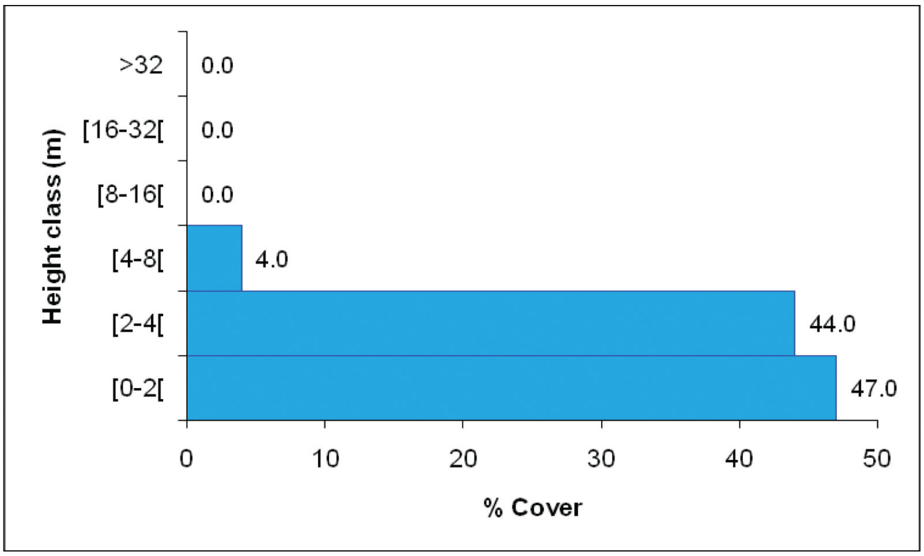

Figure 32. Diagram of forest canopy cover associated with Group III on Nosy Manampao (Humbert, 1955).

(Apocynaceae), *Cissus microdonta* (Vitaceae), *Mimusops coriacea* (Sapotaceae), and *Ficus tiliifolia* (Moraceae).

2) The upper layer (4 to 8 m) is notably open with canopy cover of only 4%. It is dominated by *Mimusops coriacea*, *Ficus tiliifolia*, and *Commelina* aff. *madagascarica* (Commelinaceae).

Snails

The land snails of the Nosy Ankao region are comparatively well known based on the descriptive work of Morelet (1851, 1860) using specimens sent to the Muséum national d'Histoire naturelle, Paris, from "Port Leven and the sandy islets nearby." Port Leven is presumably in close proximity to what is known today as Nosy Manambiby (see Historical exploration section above), one of the northern islands of the Nosy Ankao group (Figure 2).

A total of eight native and one introduced species of land snails were collected. The species list is as follows:

1) *Tropidophora vittata* (Sowerby, 1842). This species is known from "Port Leven" and one record from Nosy Be, a large island off the northwestern coast. It was found in the Nosy Ankao dry forest.
2) *Tropidophora vesconis* (Morelet, 1860). Type locality - Port Leven. Range: northeastern Madagascar. Found during the survey in the Nosy Ankao dry forest.
3) *Omphalotropis* sp. Found during the survey on Nosy Ratsy under dense bushes.
4) *Ampelita vesconis* (Morelet, 1851). Type locality - Port Leven, under dead leaves at the base of large trees growing among the dunes of Port Leven. Range: northeastern Madagascar. Found in the Nosy Ankao dry forest.
5) *Edentulina* sp. (juvenile). Probably *Edentulina intermedia* (Morelet, 1851). Type locality - Port Leven. Range: northeastern Madagascar. Found in the Nosy Ankao dry forest.
6) *Conulinus vesconis* (Morelet, 1851) Type locality - Port Leven. Range: northeastern Madagascar. Found in the Nosy Ankao dry forest.
7) *Microcystis* sp. Found during the survey of the Nosy Ankao dry forest and under dense bushes on Nosy Ratsy.
8) *Opeas soulaianus* Fischer-Piette & Testud, 1973. Range: northeastern Madagascar. Found on Nosy Ratsy under dense bushes.
9) *Lisachatina immaculata* (Lamarck, 1822). Native to southeastern Africa. Pre-colonial introduction to Madagascar. Found during the survey on Nosy Manampao in a grassy area and a specimen had been extensively fed upon by *Rattus.*

Ants

Faunistics

A total of 26 genera and 66 species placed in eight subfamilies were collected on the four surveyed islands in the Nosy Ankao group. The list of ant species obtained based on hand collecting and leaf-litter sampling is presented in Table 11. The composition of the ant fauna at each site varied based on habitat differences, and, excluding common species, the uniqueness of each island is determined by the number of taxa only known from that site and relative to the other surveyed islands. With the exception of two morphospecies, all of the recorded taxa occur on mainland Madagascar.

Unique species found at the different inventoried sites include seven in the dry forest on Nosy Ankao, six on Nosy Ratsy, five on Nosy Manampao, four on Nosiborona, and four in the dune forest on Nosy Ankao. Several remarkable and poorly known taxa were found, which include *Xymmer* mg02 on Nosiborona and the endemic Malagasy genus *Malagidris* in the dune forest on Nosy Ankao. *Xymmer* is a poorly known genus documented in the Afrotropics, Madagascar, and southeastern Asia. Moreover, Nosy Ankao was the only island with *Mystrium oberthueri* (a specialized predator on centipedes) and shares rare species such as *Proceratium* ankao 1 (a presumed specialist on spider eggs) with Nosiborona. Ant diversity at the five inventoried sites includes two genera endemic to Madagascar, 57 endemic species (86%), and nine introduced species (14%).

Variation in species richness between sites

The patterns of variation in richness of native species at the five surveyed sites is presented in Figure 33. There appears to be correlations between distances from mainland Madagascar, island size, and ant species richness. The two most distant sites, Nosy Ratsy and Nosy Manampao have the lowest species diversity, with 21 and 17 species, respectively. Nosy Ankao, the largest in the island group, has the greatest diversity with 33 species. The island closest to the mainland and the smallest in surface area is Nosiborona with 21 species.

Table 11. List of all ant species inventoried at five sites on the four different islands in the Nosy Ankao group. G = general collections, w = mini-Winkler, and W = maxi-Winkler. The names of endemic genera are presented in bold, endemic species are indicated (E), and introduced are denoted (In). + = the presence of a species at a given site and EL = locally endemic species. Site names include forested site on Nosy Ankao (A), dune forest site on Nosy Ankao (a), Nosy Ratsy (r) Nosy Manampao (m), and Nosiborona (b). Undescribed species (known unnamed species) are identified by species code (e.g. mg02, mg03, fas-12, fgh-lagi, etc) and the unknown species was labeled “ankao 1”.

	Status	Dry forest Nosy Ankao		Nosy Manampao		Nosy Ratsy		Nosiborona		Dune forest Nosy Ankao	
		w	G	w	G	w	G	W	G	W	G
Subfamily Amblyoponinae											
Mystrium oberthueri	E	+	+							+	
Xymmer mg02	E(b)							+			
Subfamily Dolichoderinae											
Tapinoma mg07	E	+	+								
Subfamily Dorylinae											
Lioponera mg06	E(A)		+								
Tanipone *subpilosa*	E(A)		+								
Tanipone ankao 1	EL(r)	+				+				+	
Subfamily Formicinae											
Camponotus alamaina	E (a)										+
Camponotus mg045	E	+									+
Camponotus grandidieri	E			+	+		+			+	
Camponotus hova	E(r)						+				
Camponotus repens	E(A)	+									
Nylanderia madagascariensis	E	+		+		+	+	+		+	+
Paratrechina longicornis	In	+	+		+	+	+				
Plagiolepis mg04	E(m)				+						
Plagiolepis mg03	E	+						+			+
Plagiolepis alluaudi	In	+	+	+		+	+	+		+	+
Plagiolepis madecassa	E(m)			+							
Tapinolepis mg01	E(A)	+									
Subfamily Myrmicinae											
Carebara fas-23	E	+		+	+						
Carebara grandidieri	E	+		+		+		+			
Carebara fas-12	E(b)							+			
Crematogaster hafahafa	E	+	+			+		+	+		+
Crematogaster maina	E	+				+	+				+
Crematogaster tricolor	E				+	+					
Crematogaster tavaratra	E(m)				+						
Crematogaster rasoherinae	E(r)						+				
Malagidris *jugum*	E(a)									+	
Monomorium termitobium	E		+								
Monomorium flavimembra	E		+	+		+	+				
Monomorium platynode	E	+		+		+		+		+	+
Monomorium micrommaton	E	+		+		+		+			
Monomorium lepidium	E			+		+		+			
Monomorium hanneli	E							+			
Nesomyrmex gracilis	E						+				
Pheidole mg028	E(a)										+
Pheidole mg019	E	+						+		+	
Pheidole megacephala	In	+	+	+	+	+		+		+	
Strumigenys inatos	E									+	
Strumigenys fanano	E	+								+	
Strumigenys sphera	E							+		+	
Strumigenys olsoni	E	+								+	
Strumigenys maxillaris	In	+				+		+		+	
Strumigenys emmae	In			+						+	
Terataner fgh-lagi	E							+	+	+	+
Terataner alluaudi	E(b)								+		
Tetramorium ryanphelanae	E	+	+								
Tetramorium sericeiventre	In		+								+
Tetramorium quasirum	E					+	+	+			
Tetramorium delagoense	In	+	+			+		+		+	
Tetramorium trafo	E							+		+	
Tetramorium scytalum	In			+		+	+				
Tetramorium fhg_isht	E(b)							+			
Subfamily Ponerinae											
Anochetus madagascariensis	E(r)					+					
Anochetus grandidieri	E(r)					+					

	Status	Dry forest Nosy Ankao		Nosy Manampao		Nosy Ratsy		Nosiborona		Dune forest Nosy Ankao	
		w	G	w	G	w	G	W	G	W	G
Bothroponera wasmanii	E		+					+	+	+	
Hypoponera mg045	E(A)		+								
Hypoponera mg011	E	+		+		+		+			
Hypoponera mg026	E(m)			+							
Hypoponera mg048	E			+				+			
Hypoponera mg106	E			+							
Leptogenys fasika	E(a)										+
Leptogenys fiandry	E(A)		+								
Leptogenys maxillosa	In(m)				+						
Plathytyrea arthuri	E(r)					+					
Subfamily Proceratiinae											
Proceratium ankao 1	E	+						+			
Subfamily Pseudomyrmicinae											
Tetraponera psw087	E (A)		+								
Total number of species per method		25	17	17	8	21	11	24	4	19	12
Number of unique species (w, W, and G)		17	9	14	5	14	4	21	1	15	8
Number of species in common per method		8		3		7		3		4	
Species richness per site		**33**		**22**		**25**		**25**		**27**	
Total number of species for the five sites		**66**									
Number of species unique to a site		**7**		**5**		**6**		**4**		**4**	

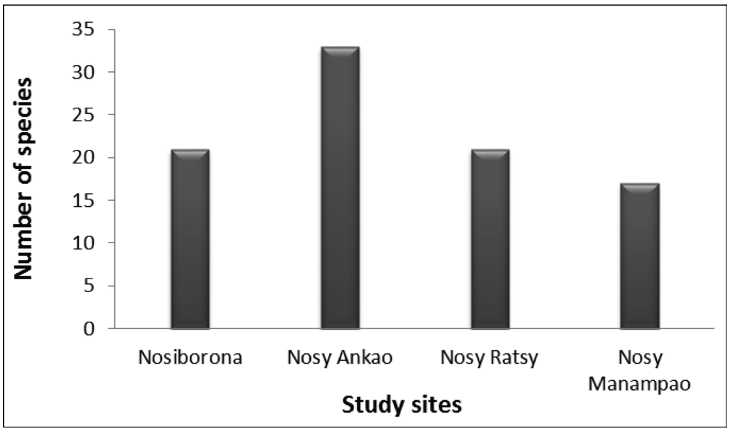

Figure 33. Variation in native ant species richness between the four surveyed islands, arranged from left to right in increasing distance from mainland Madagascar. See Table 2 for information on island size.

Faunistic similarities between sites

In Table 12, we present the Jaccard Index comparisons between sites for native ant species, which provides a measure of the level of faunistic similarity. For all sites, species overlap is low and the highest level of similarity (21%) is between Nosy Ratsy and Nosy Manampao.

Abundance of introduced species

In Table 13, we list abundance measures for introduced ant species on the surveyed islands, as measured by the frequency of such species along each sampled transect. At three sites (dry forest Nosy Ankao, Nosy Manampao, and Nosy Ratsy), data were obtained from 25 stations using mini-Winklers, as compared to two sites (dune forest Nosy Ankao and Nosiborona), where data were extracted from 20 stations and condensed into five maxi-Winklers. Introduced species were present at all sites but the species and their relative abundance differed. *Plagiolepis alluaudi* and *Pheidole megacephala* were present at all sites, but the latter has invaded Nosy Manampao. *Tetramorium delagoense* is very abundant on Nosiborona and at the dry forest site on Nosy Ankao.

Table 12. Faunistic comparisons of native ants between surveyed sites based on Jaccard's Index.

	Dry forest Nosy Ankao	Nosy Manampao	Nosy Ratsy	Dune forest Nosy Ankao	Nosiborona
Dry forest Nosy Ankao	-				
Nosy Manampao	0.10	-			
Nosy Ratsy	0.13	0.21	-		
Dune forest Nosy Ankao	0.20	0.07	0.12	-	
Nosiborona	0.15	0.15	0.16	0.16	-

Table 13. Measures of abundance based on frequency of introduced ant species at the five surveyed sites on islands in the Nosy Ankao group, based on 25 Winkler stations at the first three sites and 20 stations at the other two sites.

Taxa	Dry forest Nosy Ankao	Nosy Manampao	Nosy Ratsy	Dune forest Nosy Ankao	Nosiborona
Subfamily Formicinae					
Paratrechina longicornis	0.04	0.04	0.16		
Pheidole megacephala	0.24	1.00	0.60	0.20	0.20
Plagiolepis alluaudi	0.16	0.28	0.60	0.20	0.40
Subfamily Myrmicinae					
Tetramorium delagoense	0.52		0.32	0.80	1.00
Tetramorium sericeiventre	0.04				0.20
Tetramorium scytalum		0.08	0.32		
Strumigenys emmae	0.04	0.04			
Strumigenys maxillaris	0.20		0.40		0.40
Subfamily Ponerinae					
Leptogenys maxillosa		0.04			

Table 14. Comparison of all ant species occurring on islands in the Nosy Ankao group to two sites on the nearby mainland. Nosy Ankao (A), Nosy Manampao (M), Nosy Ratsy (R), and Nosiborona (B) to those at Daraina in the Analabe Forest (Analabe) and Réserve Spéciale d'Analamera (Anala). E = endemic to Madagascar, in = introduced to Madagascar, + = present. Endemic genera are highlighted in bold and EL = locally endemic species. The undescribed species were identified as a code (e.g. mg02, mg03, fas-12, fgh-lagi, etc.) and the unknown species were labeled "ankao 1".

		Nosy Ankao island group				Analabe	Anala
	Status	A	M	R	B		
Subfamily Amblyoponinae							
Mystrium oberthueri	E	+					
Xymmer mg02	E(B)				+		
Subfamily Dolichoderinae							
Tapinoma mg07	E	+					
Subfamily Dorylinae							
Lioponera mg06	E(A)	+				+	
Tanipone* *subpilosa	E(A)	+					+
Tanipone ankao 1	EL(R)	+		+			
Subfamily Formicinae							
Camponotus alamaina	E(a)	+				+	+
Camponotus mg045	E	+				+	
Camponotus grandidieri	E	+	+	+			
Camponotus hova	E(R)			+		+	
Camponotus repens	E (A)	+					
Nylanderia madagascariensis	E	+	+	+	+		
Paratrechina longicornis	In	+	+	+			
Plagiolepis mg04	E(M)		+				
Plagiolepis mg03	E	+			+		
Plagiolepis alluaudi	In	+	+	+	+	+	+
Plagiolepis madecassa	E(M)		+				
Tapinolepis mg01	E(A)	+				+	
Subfamily Myrmicinae							
Carebara fas-23	E	+	+				
Carebara grandidieri	E	+	+	+	+		
Carebara fas-12	E(B)				+		
Crematogaster hafahafa	E	+		+	+		
Crematogaster maina	E	+		+		+	+
Crematogaster tricolor	E		+	+			
Crematogaster tavaratra	E(M)		+				+

Table 14. (continued)

		Nosy Ankao island group				Analabe	Anala
	Status	**A**	**M**	**R**	**B**		
Crematogaster rasoherinae	E(R)			+		+	+
***Malagidris** jugum*	E(a)	+				+	+
Monomorium termitobium	E	+				+	+
Monomorium flavimembra	E	+	+	+		+	
Monomorium platynode	E	+	+	+	+		
Monomorium micrommaton	E	+	+	+	+		
Monomorium lepidium	E		+	+	+		
Monomorium hanneli	E				+		
Nesomyrmex gracilis	E			+			
Pheidole mg028	E(a)	+					
Pheidole mg019	E	+			+		
Pheidole megacephala	In	+	+	+	+	+	
Strumigenys inatos	E	+					
Strumigenys fanano	E	+				+	
Strumigenys sphera	E	+			+		
Strumigenys olsoni	E	+				+	
Strumigenys maxillaris	In	+		+	+		
Strumigenys emmae	In	+	+				
Terataner fgh-lagi	E	+			+		
Terataner alluaudi	E(B)				+	+	
Tetramorium ryanphelanae	E	+					+
Tetramorium sericeiventre	In	+				+	+
Tetramorium quasirum	E			+	+		
Tetramorium delagoense	In	+		+	+	+	
Tetramorium trafo	E	+			+	+	+
Tetramorium scytalum	In		+	+			
Tetramorium fhg_isht	E(B)				+		
Subfamily Ponerinae							
Anochetus madagascariensis	E(R)			+		+	
Anochetus grandidieri	E(R)			+			
Bothroponera wasmanii	E	+			+	+	+
Hypoponera mg045	E(A)	+				+	
Hypoponera mg011	E	+	+	+	+	+	
Hypoponera mg026	E(M)		+				
Hypoponera mg048	E		+		+	+	
Hypoponera mg106	E		+				
Leptogenys fasika	E(A)	+				+	
Leptogenys fiandry	E(A)	+					
Leptogenys maxillosa	In(M)		+				
Plathytyrea arthuri	E(R)			+		+	
Subfamily Proceratiinae							
Proceratium ankao 1	E	+			+		
Subfamily Pseudomyrmicinae							
Tetraponera psw087	E(A)	+					
All species shared with Analabe Forest		**18**	**5**	**10**	**8**	**25**	**-**
All species shared with Analamera		**10**	**2**	**3**	**3**	**-**	**12**

Comparison of the ant fauna of the Nosy Ankao island group to the mainland sites of Daraina and Analamera

The mainland sites of Daraina (Analabe Forest) and Réserve Spéciale d'Analamera were chosen for comparison to those on islands in the Nosy Ankao group, as they were previously inventoried for ants and are located relatively close to the islands (Figure 1). In comparison to these two mainland sites, the number of species recorded in the island group is lower (n = 66), as compared to Daraina (n = 114) and comparable with Analamera (n = 68). The degree of species overlap in taxa documented in the Nosy Ankao island group is higher when compared to Daraina, with 25 shared species (38%), and lower with respect to Analamera with 12 shared species (18%). For the surveyed islands, the number of species shared with the two mainland sites is highest on Nosy Ankao followed by Nosy Ratsy and Nosiborona, and is lowest on Nosy Manampao (Table 14). Two endemic genera of ants were found on the islands, which include *Malagidris*, also identified from Daraina, and *Tanipone*, also recorded from Analamera.

Mosquitoes

With all collection sites combined, 527 adult mosquitoes of four genera and 11 species were identified (Table 15). Seven species of the genus *Aedes* represent 57.1% (301/527) of the total captured mosquitoes, as compared to 42.3% (223/527) for the genus *Culex*. The balance of the taxa (0.6%) included two individuals of *Anopheles arabiensis* and a single female *Aedeomyia madagascarica*. These four genera were captured on Nosy Ankao, an island where 80.8% (426/527) of adult mosquitoes were obtained.

No statistically significant variation was identified between the number of mosquitoes, species of mosquitoes, and the types of traps employed (F = 0.008, df = 1, $P = 0.92$). Among the Culicidae captured using light traps, the most abundant species was *Culex tritaeniorhynchus* followed by *Aedes lambrechti*. Only *Aedes* was captured employing the two methods (human landing catches and light traps). In contrast, species diversity and abundance were notably different between the islands (F = 3.3, df = 10, $P < 0.001$). Nosy Ankao had the most diverse fauna with 10 species, followed by Nosiborona with five species, Nosy Manampao with four species, and Nosy Ratsy with three species.

Table 15. Distribution of mosquito species on the four islands in the Nosy Ankao group, based on collections made in March 2016. * = previously reported from Montagne des Français (Fontenille, 1989), µ = previously reported in the north of Madagascar (Tantely *et al*., 2016), £ = known vector species of arboviruses on Madagascar (Tantely *et al*., 2016), # = a principal vector of malaria to humans in Madagascar (Lèong Pock Tsy *et al*., 2003). HLC = human landing catch and LT = light trap.

	Nosy Ankao		Nosy Manampao		Nosy Ratsy		Nosiborona	Total
Genus and species	**HLC**	**LT**	**HLC**	**LT**	**HLC**	**LT**	**HLC**	
Aedeomyia								
madagascarica £		1						1
Aedes								
aegypti *µ£	5	2	3	15		6	6	37
albocephalus *µ		4						4
albopictus *µ£	4		1	2			1	8
fryeri	3	7	2	7		2		21
lambrechti µ	3	171					20	194
monetus *µ	13	1					10	24
tiptoni *µ							13	13
Anopheles								
arabiensis *#		2						2
Culex								
quinquefasciatus µ£		5						5
tritaeniorhynchus *µ£		205		3		10		218
Total	**28**	**398**	**6**	**27**		**18**	**50**	**527**

Larval breeding sites

A survey of potential breeding sites showed distinctly more diversity on Nosy Ankao (Table 16). One *Anopheles arabiensis* larva was found in a canoe near the hotel construction site and in association with the larvae of *Culex tritaeniorhynchus* and *Aedes albopictus.* On this same island, dug water wells and coconut husks often contained larvae of *A. aegypti*.

Table 16. Types of mosquito larvae sites found on different islands in the Nosy Ankao group. a = Nosy Ankao, m = Nosy Manampao, n = Nosiborona, µ = on all four islands.

	Breeding sites types					
Species	**Cement wells**	**Canoe**	**Coconut**	**Metallic container**	**Mangrove**	**Tree holes**
Aedes aegypti	++a	+a	++a	++a		++µ
Aedes albocephalus					+++a	
Aedes albopictus		+a		++a		
Aedes fryeri	+a				+++a	
Aedes lambrechti					+++a	+m
Aedes monetus	+a					+mn
Anopheles arabiensis		+a				
Culex tritaeniorhynchus	+a	+a				

This species was found exclusively in tree holes on the other islands; for example, on Nosy Ratsy, it was collected in a tree hole in a mangrove (Figure 8). On Nosy Ankao, larvae of *A. lambrechti*, *A. albocephalus*, and *A. fryeri* were primarily found at low tide in mangroves.

Reptiles and amphibians

A total of 26 species were identified during the survey of four islands in the Nosy Ankao group, which included one amphibian and 25 reptiles (Table 17). The overwhelming dominance of reptiles provides clear insights into the local ecology of these islands, particularly the lack of permanent surface water and certain temporary marsh areas or wells with slightly brackish water. The complete list of taxa found on the different islands, aspects concerning their ecology and biology, as well as IUCN conservation statutes, are presented in Table 17. The surface areas of the islands are given in Table 2. The majority of the documented reptile species are forest dwelling, although a few occur in open non-forested areas.

One striking aspect between the four surveyed islands was differences in species richness (Figure 34). Nosy Ankao had the highest species diversity. Nosiborona had the lowest measure of species richness as compared to the other three islands, but this island was only visited for a few hours and its apparent species paucity is almost certainly a function of survey effort. In contrast, the level of investigation of the other three islands was largely proportional to their surface area and the measured variation is presumed to reflect biological differences between the islands. No amphibian was found on any of the islands, with the exception of Nosiborona, where *Laliostoma labrosum* was documented. In any case, the frog fauna was poorly represented on these small islands, which lacked permanent running or standing surface water; the only source we located was a ground surface well on Nosy Manampao. Further, most of the water sources on these islands are moderately saline, which would also be a deterrent to most frog species associated with their successful colonization and continued existence.

A comparison of the three islands that were the principal focus of this inventory indicate that more than half of the reptile fauna (7/11) of Nosy Manampao also occurred on Nosy Ankao and/or on Nosy Ratsy; the remaining four species were only located on Nosy Manampao. The same general pattern also was found in pairwise comparisons to the other islands. For example, *Zonosaurus madagascariensis* was only found on Nosy Ratsy and a considerable number of species were restricted to Nosy Ankao. Expressed in a different manner, variation in species composition between these three islands is pronounced, particularly considering their relative close proximity to one another and the main island of

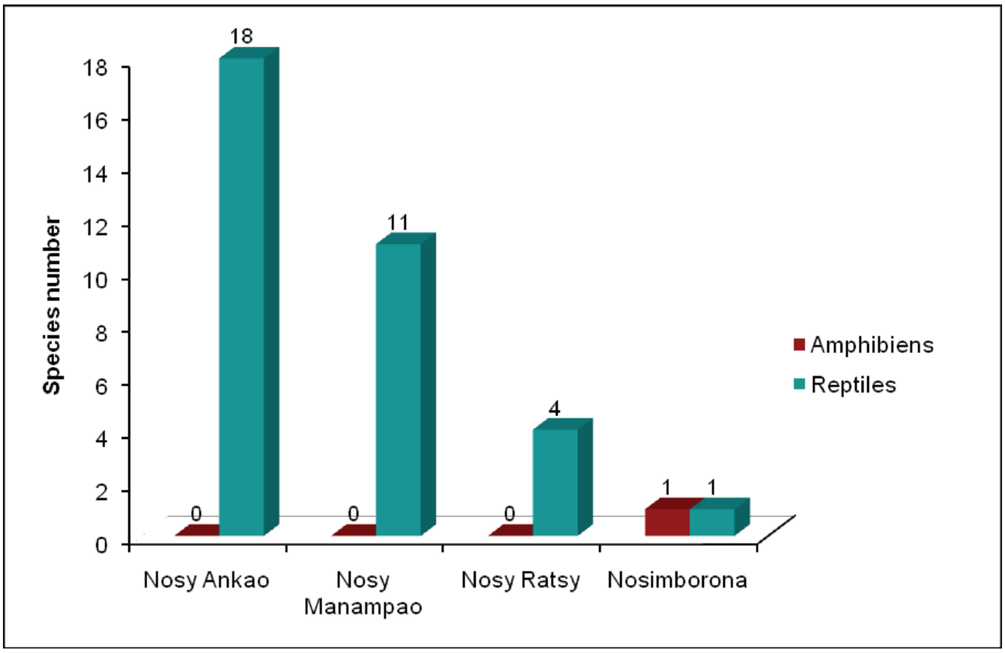

Figure 34. Graphical representation of herpetofauna species richness on the different study islands in the Nosy Ankao group.

Table 17. List of amphibian and reptiles known from islands in the Nosy Ankao group. IUCN statutes: LC = Least Concern, VU = Vulnerable, CR = Critically Endangered, DD = Data Deficient, and NE = Not Evaluated. Relative measures of abundance: NA = not abundant, SA = slightly abundant, A = abundant, and VA = very abundant.

Taxa	IUCN status	Habitat and biotope	Mode of displacement	Relative abundance	Island			
					Nosy Ankao 365 ha	Nosy Manampao 29 ha	Nosy Ratsy 6 ha	Nosiborona 6 ha
AMPHIBIANS								
Mantellidae								
Laliostoma labrosum	LC	Forest and open areas	Terrestrial	SA				+
Total amphibian: 1								**1**
REPTILES								
Gekkonidae								
Ebenavia inunguis	LC	Forest	Arboreal	NA	+	+		
Geckolepis maculata	LC	Forest	Arboreal	NA	+	+		
Hemidactylus frenatus	LC	Open areas	Arboreal	NA	+			
Paroedura lohatsara	CR	Forest	Terrestrial	NA	+			
Paroedura stumpffi	LC	Forest	Arboreal	NA	+			
Phelsuma abbotti	LC	Open area and forest	Arboreal	SA	+			
Phelsuma aff. *dorsivittata*	NE	Forest	Arboreal	SA		+		
Uroplatus ebenaui	VU	Forest	Arboreal	NA	+			
Gerrhosauridae								
Zonosaurus madagascariensis	LC	Forest and forest ecotone	Terrestrial	A			+	
Scincidae								
Amphiglossus sp.	NE	Forest	Burrowing	NA	+			
Cryptoblepharus boutonii	NE	Open area and coral reef	Rupicole	A		+	+	
Madascincus aff. *miafana*		Forest	Burrowing	A	+			
Paracontias aff. *hildebrandti*	LC	Forest and dunes with humid soils	Burrowing	VA		+		
Trachylepis elegans	LC	Forest ecotone and open areas	Terrestrial	VA	+			
Trachylepis gravenhorstii	LC	Forest and forest ecotone	Terrestrial	SA		+		
Chamaeleonidae								
Brookesia aff. *tristis*	NE	Forest, in leaf litter	Terrestrial	NA				+
Furcifer petteri	VU	Forest	Arboreal	VA	+			
Furcifer oustaleti	LC	Forest and forest ecotone	Arboreal	SA	+			
Boidae								
Acrantophis madagascariensis	LC	Forest and forest ecotone	Terrestrial	SA	+	+		
Lamprophiidae								
Liophidium aff. *torquatum*	NE	Forest and forest ecotone	Terrestrial	SA	+	+	+	
Lycodryas aff. *inopinae*	NE	Forest	Arboreal	NA	+			
Madagascarophis colubrinus	LC	Forest, forest ecotone, and open areas	Terrestrial	SA	+	+	+	
Mimophis mahfalensis	LC	Forest, forest ecotone, and open areas	Terrestrial	A	+	+		
Typhlopidae								
Madatyphlops microcephalus	DD	Forest	Burrowing	SA	+			
Xenotyphlops aff. *grandidieri*	NE	Forest and dunes with humid soils	Burrowing	NA		+		
Total reptiles: 25					**18**	**11**	**4**	**1**
Total amphibians and reptiles: 26					**18**	**11**	**4**	**2**

Madagascar, which presumably acted as the source area for reptile colonization. It is important to mention that three of the four species restricted to Manampao have specialized natural history requirements. For example, *Phelsuma* aff. *dorsivittata* occurred in a particular vegetation type (*Bismarckia* or *satrana*), *Paracontias* aff. *hildebrandti* and *Xenotyphlops* aff. *grandidieri* were found in non-compacted soils rich in organic material and leaf litter in the *Mimusops coriacea* and *Ficus tiliifolia* formation (see botanical section). In Figure 35, the relationships are illustrated of the different herpetofauna communities with respect to faunistic differences and similarities of these three islands.

Among the reptile species found in the archipelago, seven could not be identified with certainty (Table 17). These taxa show morphological characters (form and color) in common with described species, but display differences with respect to other characters, such as number or structure of different scales, which are often used to diagnose reptile species. These seven taxa may represent new forms to science or cases of isolated island populations in the course of differentiation. Examples include a gecko, named herein as *Phelsuma* aff. *dorsivittata*; a skink, *Amphiglossus* aff. *miafana*; a dwarf chameleon, *Brookesia* aff. *tristis*; and three snakes, *Liophidium* aff. *torquatum*, *Lycodryas* aff. *inopinae*, and *Xenotyphlops* aff. *grandidieri* (Figure 36). The discovery of these forms on islands in the Nosy Ankao group clearly underlines the biogeographic, ecological, and conservation importance of these islands.

Three species, including two geckos, *Paroedura lohatsara* and *Uroplatus ebenaui*, and a chameleon, *Furcifer petteri*, have elevated IUCN Red List status (Table 17); the first is classified as "Critically Endangered" and the latter two as "Vulnerable" (Figure 37). Hence, the archipelago represents an important refuge for these species and records documented herein represent notable extensions to their previously known distribution. All three species were found on Nosy Ankao.

The burrowing snake, *Xenotyphlops* aff. *grandidieri*, found on Nosy Manampao has a special importance. Morphologically it resembles *X. grandidieri*, a rare species known from only two specimens in the world's natural history museums, although the precise collection localities of these specimens are unknown. Hence, the single specimen obtained from the current study represents either a new species or the first known locality for *X. grandidieri* (Figure 38). Further research is needed to reach a conclusion about these two possibilities. The species *grandidieri* was the only representative of the endemic genus *Xenotyphlops* (Family Xenotyphlopidae, sensu Wallach & Ineich, 1996) in a recent revision based on morphology of blind snakes of the world. The molecular study of Nagy *et al.* (2015) showed that the other Malagasy typhlopids are monophyletic and best placed in the endemic genus *Madatyphlops* (Family Typhlopidae), and confirmed the validity of endemic genus *Xenotyphlops* and Family Xenotyphlopidae.

With a few exceptions, the majority of species found during this study where represented by few individuals. The age structure in a given population can be notably different between species. For example, only a single female adult of *Furcifer petteri* was found on Nosy Ankao, as compared to approximately 40 recent hatchlings or juveniles. This is in contrast to *Zonosaurus madagascariensis*,

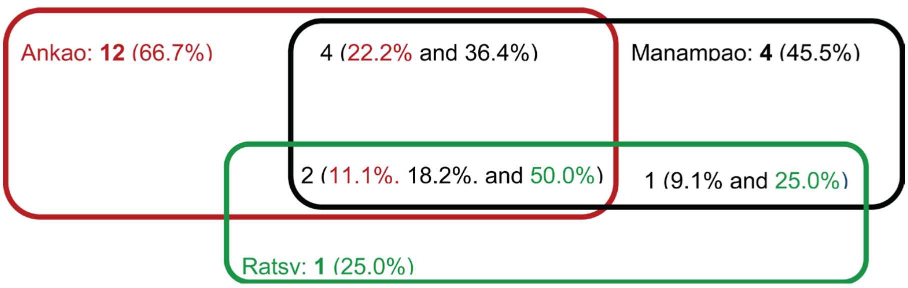

Figure 35. Schematic representation of the differences and similarities of the herpetofauna of three well-surveyed islands in the Nosy Ankao group, including Nosy Ankao (in red), Nosy Manampao (in black), and Nosy Ratsy (in green). The numbers should be interpreted as follows: for Nosy Ankao, 18 species were recorded of which 12 were unique to the island (in bold) and the associated values fall within the red rectangle, four were shared with Nosy Manampao, and two with Nosy Ratsy. The figure in parentheses indicates the percentage of species in common on a given island and in comparison to the other islands, following the same color codes.

Figure 36. Some reptile species found during the survey that could not be identified with confidence to the level of species and might represent previously undescribed taxa or isolated insular populations that have differentiated. A) *Amphiglossus* aff. *miafana* on Nosy Ankao; B) *Brookesia* aff. *tristis* on Nosy Nosiborona; C) *Phelsuma* aff. *dorsivittata* on Nosy Manampao, and D) *Lycodryas* aff. *inopinae* on Nosy Ankao. (All photographs by Achille P. Raselimanana.)

Figure 37. Reptiles occurring in the Nosy Ankao Archipelago with elevated IUCN Red List status: A) *Paroedura lohatsara* found on Nosy Ankao and considered "Critically Endangered"; this image is of an animal found at Orangea; B) *Uroplatus ebenaui* and C) *Furcifer petteri* from Nosy Ankao, both considered "Vulnerable." (All photographs by Achille P. Raselimanana.)

Figure 38. The burrowing snake *Xenotyphlops* aff. *grandidieri* found on Nosy Manampao is a rare species that was previously known from only two other specimens in all the world's natural history museums. (Photograph by Achille P. Raselimanana.)

which was only found during the survey on Nosy Ratsy, and of the tens of animals captured, all were adult. Another example is with *Paracontias* aff. *hildebrandti*, abundant on Nosy Manampao, with approximately equal ratios of juveniles and adults (males and females). For the latter species, about 10 gravid females were found during systematic examination of sandy and humid soil sites in the *Mimusops coriacea* and *Ficus tiliifolia* formation (see botanical contribution) with open understory and close canopy. In the case of other species, such as *Trachylepis elegans* and *T. gravenhorstii*, juveniles were more abundant than adults; individuals of the former still maintained traces of the umbilical cord and had not yet reached subadult stage. These different observations indicate notable differences in the reproductive cycles of reptile species occurring on different islands in the archipelago.

The results of pitfall trapping are presented in Tables 18-20. For the three different sites, capture rates for a given line varied between 5.5 and 11.8%, although one line on Nosy Manampao had a trap capture success of 20%. When the results for these traps are combined by island, trap success varied from 6.4% (Nosy Ratsy) to 12.7% (Nosy Manampao). The total number of accrued pitfall trap nights was different for certain islands -- 330 on Nosy Ankao and 110 on Nosy Manampao and Nosy Ratsy. Capture rates were not necessarily proportional to the amount of trapping effort, but a variety of factors may come into play. Even though the pitfall traps did not have high return with regards to the number of trapped animals, this type of device had considerable importance in our inventory of the local herpetofauna. To understand better the complementarities of the three techniques deployed during this inventory, the mode of capture for the different species, as well as period of activity, are given in Table 21.

Following the information presented in Table 21, even though direct observation represents the best survey technique to document a large percentage of the local herpetological fauna, a significant number of species would have been overlooked if the other two techniques had not been employed. Five species (*Phelsuma* aff. *dorsivittata*, *Paracontias* aff. *hildebrandti*, *Cryptoblepharus boutonii*, *Brookesia* aff. *tristis*, and *Xenotyphlops* aff. *grandidieri*) were only located by systematic searching in their biotopes, while three others (*Madatyphlops microcephalus*, *Amphiglossus* sp., and *Madascincus* aff. *miafana*)

Table 18. Pitfall captures on Nosy Ankao with three pitfall lines (each with 11 buckets) over the course of 10 nights and 330 accrued pitfall bucket nights. No small mammal was captured.

Characteristics	Pitfall line 1	Pitfall line 2	Pitfall Line 3	Total
Habitat type	Forest and compact sandy soil	Forest and compact sandy soil	Forest and slightly compact sandy soil	
Ground cover	Ground covered with moderate leaf litter	Ground covered with moderate leaf litter	Ground covered with leaf litter and moist	
Taxa				
Amphiglossus sp.	-	-	2	**2**
Madascincus aff. *miafana*	6	7	8	**21**
Trachylepis elegans	2	1	3	**6**
Madatyphlops microcephalus	1	-	-	**1**
Liophidium aff. *torquatum*	1	1	-	**2**
Number of captured animals	10	9	13	**32**
Number of buckets	11	11	11	**33**
Number of trapping nights	10	10	10	**10**
Total number of bucket nights	110	110	110	**330**
Trap capture rate (%)	**9.1**	**8.2**	**11.8**	**9.7**

Table 19. Pitfall captures on Nosy Manampao with two pitfall lines (each with 11 buckets) over the course of five nights and 110 accrued pitfall bucket nights. No small mammal was captured.

Characteristics	Pitfall line 1	Pitfall line 2	Total
Habitat type	Open non-forest, herbaceous vegetation, and compact sandy soil	Homogeneous forest fragment, non-consolidated sand dune, and moist	
Ground cover	Ground cover with Graminae	Non-compacted soil with humus, leaf litter, or herbaceous plants	
Taxa			
Paracontias aff. *hildebrandti*	-	1	**1**
Trachylepis gravenhorstii	8	3	**11**
Liophidium aff. *torquatum*	2	-	**2**
Number of captured animals	11	3	**14**
Number of buckets	11	11	**22**
Number of trapping nights	5	5	**5**
Total number of bucket nights	55	55	**110**
Trap capture rate (%)	**20.0**	**5.5**	**12.7**

Table 20. Pitfall captures on Nosy Ratsy with two pitfall lines (each with 11 buckets) over the course of five nights and 110 accrued pitfall bucket nights. No small mammal was captured.

Characteristics	Pitfall line 1	Pitfall line 2	Total
Habitat type	Dense secondary bush, a portion with compacted soil and balance with sandy soil	Less dense secondary bush with largely sandy soil	
Ground cover	Ground with little organic matter and rocky	Ground relatively rich in organic matter and somewhat moist	
Zonosaurus madagascariensis	3	2	**5**
Madagascarophis colubrinus	-	1	**1**
Liophidium aff. *torquatum*	1	-	**1**
Number of captured animals	4	3	**7**
Number of buckets	11	11	**22**
Number of trapping nights	5	5	**5**
Total number of bucket nights	55	55	**110**
Trap capture rate (%)	**7.3**	**5.5**	**6.4**

Table 21. Capture methods for various reptiles and an amphibian on islands in the Nosy Ankao group. ** = principal method used to collect a given taxon was obtained, * = method by which a taxon was occasionally found.

Taxa	Activity period	Mode of capture		
		Direct observation	Systematic searching	Pitfall traps
Laliostoma labrosum	Diurnal	**		
Ebenavia inunguis	Nocturnal	**	*	
Geckolepis maculata	Nocturnal	**		
Hemidactylus frenatus	Nocturnal	**		
Paroedura lohatsara	Nocturnal	**		
Paroedura stumpffi	Nocturnal	**		
Phelsuma abbotti	Diurnal	*	**	
Phelsuma aff. *dorsivittata*	Diurnal		**	
Uroplatus ebenaui	Nocturnal	**		
Zonosaurus madagascariensis	Diurnal	**		
Amphiglossus sp.	Diurnal			**
Cryptoblepharus boutonii	Diurnal		**	
Madascincus aff. *miafana*	Nocturnal			**
Paracontias aff. *hildebrandti*	Diurnal		**	
Trachylepis elegans	Diurnal	**		
Trachylepis gravenhorstii	Diurnal	**		
Brookesia aff. *tristis*	Diurnal		**	
Furcifer petteri	Diurnal	**		
Furcifer oustaleti	Diurnal	**		
Acrantophis madagascariensis	Nocturnal	**		
Liophidium aff. *torquatum*	Diurnal	**		**
Lycodryas aff. *inopinae*	Nocturnal	**		
Madagascarophis colubrinus	Nocturnal and crepuscular	**	*	**
Mimophis mahfalensis	Diurnal	**		
Madatyphlops microcephalus	Nocturnal			**
Xenotyphlops aff. *grandidieri*	Nocturnal		**	
Total		**18**	**8**	**5**

were only found with pitfall traps. These results clearly demonstrate the complementarity of these three techniques. While pitfall traps were not effective at capturing certain types of animals, such as frogs, they were very useful at detecting secretive terrestrial and burrowing reptiles (Andreone *et al*., 2001, 2003).

Birds

In Table 22, we list the landbirds observed on Nosy Ankao, Nosy Manampao, and Nosy Ratsy during our March 2016 field survey. Two other species have been reported from Nosy Ankao (Fanamby, 2014), but not recorded during our work: *Accipiter madagascariensis* and *Berniera* [sic for *Bernieria*] *madagascariensis*. A photograph referred to the first species (Fanamby, 2014, p. 38) is clearly *Buteo brachypterus* and no evidence of the second taxon, a forest-dwelling species, was found after many hours of observation in the Nosy Ankao forest. Until further evidence can be obtained, these two taxa are best considered as not occurring on the island. There are also observations of *Falco peregrinus* feeding on terns on Nosy Manampao during the breeding season of the latter (Sébastien Wohlhauser, pers. comm.).

Nosy Manampao has a considerable population of breeding terns, one of the most important sites in Madagascar waters. The following species were recorded on the island during a 8-9 July 2008 visit (Le Corre & Bemanaja, 2009): *Anous stolidus* and *A. tenuirostris*, each with five observed individuals; *Sterna caspia* with two individuals; *S. dougallii* with an estimated 135 individuals; *S. fuscata* with 21,800 ± 4790 breeding pairs; and *Thalasseus bergii* with three observed individuals. In 2012, on the basis of fieldwork conducted by researchers from the Centre National de Recherches Océanographiques, 900 pairs of *T. bergii* were found breeding on the island (Fanamby, 2014). During the 2008 visit to the island, considerable exploitation of tern eggs for regional markets was found, including that in Antsiranana, and this activity continued at least until 2010 (Fanamby, 2014). Over the past few years, the Association Fanamby in collaboration with the Nosy Ankao Development Company, have posted permanent guards on the island and such exploitation seems to have now ceased. Interviews with older people living in the region suggest tern eggs on the island have

Table 22. Observations of different landbirds on islands in the Nosy Ankao group. + = recorded from the respective island, * = introduced to Madagascar.

	Nosy Ankao	Nosy Manampao	Nosy Ratsy
Taxa	365 ha	29 ha	6 ha
Ardea cinerea	+		
Bubulcus ibis	+	+	
Butorides striata	+		
Egretta dimorpha	+		
Buteo brachypterus	+		
Falco newtoni	+		
Turnix nigricollis	+		
Dryolimnas cuvieri	+	+	+
Nesoenas picturata	+		
Centropus toulou	+	+	+
Caprimulgus madagascariensis	+		
Cypsiurus parvus	+		
Eurystomus glaucurus	+		
Upupa marginata	+		
Motacilla flaviventris	+		
Hypsipetes madagascariensis	+	+	+
Cisticola cherina	+		
Terpsiphone mutata	+		
Nectarinia souimanga	+	+	+
Nectarinia notata	+		
Zosterops maderaspatana	+		
Dicrurus forficatus	+		
Corvus albus	+	+	
**Acridotheres tristis*	+		
Foudia madagascariensis	+		
Total species	**25**	**6**	**4**

been exploited for several decades. One person who grew up on the main coast, directly across from the Nosy Ankao Archipelago, mentioned that when they were young, tern eggs were regularly sold in the local market during winter months, which is when the terns breed. The eggs were purported to have been collected on an island near Nosy Phare, known today as Nosy Ankao.

Small mammals

Live traps were installed in the forest of Nosy Ankao from 4 to 14 March (n = 100), in different habitats on Nosy Manampao from 5 to 10 March (n = 75), and in the dense ticket on Nosy Ratsy from 10 to 15 March (n = 75). The only species of small mammal captured in 1750 cumulative trap-nights in these standard lines on all three islands was *Rattus rattus* (Table 23), a species introduced to Madagascar. Notable differences were found in capture rates on the different islands, with trap success on Nosy Ankao during 1000 trap-nights being 6.3%, on Nosy Manampao during 375 trap-nights 2.9%, and on Nosy Ratsy during 375 trap-nights no animal was captured. The pitfall traps put in place on Nosy Ankao, Nosy Manampao, and Nosy Ratsy did not result in the capture of any small mammal (Tables 18-20).

The *R. rattus* captured on Nosy Ankao in the different standard trap lines placed in the principal forest block were captured in different types of sets, including traps on the ground and those in arboreal positions (Table 24). During the 10 night trapping session, a disproportionate number of adults as compared to subadults were captured. Further, there was a distinct tendency for this species to be obtained in traps placed off the ground. The same age structure pattern was also found on Nosy Manampao (Table 25), which in both cases is almost certainly related to the reproductive cycle of this introduced rodent.

On Nosy Ankao, we also placed live traps in and around human habitations to obtain more information on commensal small mammals. A small number of trap nights were accrued in the villages of Andasibe and the captured animals included *R. rattus* and a single individual of *R. norvegicus* (Table 23). On the basis of interviews with people living in the villages of Andasibe, Ampasimangidy, and Antafondro, it would appear that there is a population of *Suncus murinus* living on the island and in immediate proximity to human habitations.

Although not a small mammal per se, cats (*Felis silvestris*) also live on Nosy Ankao. Presumably some of this population represents domestic individuals and others feral animals. Evidence of this animal was found in the Nosy Ankao forest. Although cats would extensively prey upon *Rattus*, they are presumably also feeding on songbirds and their nest contents. The possibility of removing feral cats from the island should be considered to help boost songbird populations.

On the basis of interviews with elderly residents of Nosy Ankao who have spent all or most of their lives on the island, there is no historical memory of any spiny tenrecs (Family Tenrecidae, Subfamily Tenrecinae), specifically *Tenrec ecaudatus* or *Setifer setosus*, on the island. Based on the age of some of the interviewees, if a population of spiny tenrecs was formerly present on the island, it went extinct sometime before the 1940s or so. These same interviewees also mentioned that they have no memory of the existence of lemurs on the island. This is supported by the lack of observations of these animals during our biological inventory, even though tens of hours were spent during the day and night in the Nosy Ankao forest, and the lack of small nocturnal lemur species captured in the mammal traps.

Table 23. Total trapping effort and species of small mammals and reptiles captured in live traps installed on Nosy Ankao, Nosy Manampao, and Nosy Ratsy.

	Nosy Ankao	Nosy Manampao	Nosy Ratsy
Number of traps	100	75	75
Number of nights-traps in place	10	5	5
Total number trap-nights	1000	375	375
Reptile captures			
Zonosaurus madagascariensis	0	0	1
Small mammal captures			
Rattus rattus	56	11	0
Rattus norvegicus	1[1]	0	0
Trap success for small mammals (%)	**6.3**	**2.9**	**0.0**

[1]The single individual of this species was not captured in a standard trap line, but in the village of Andasibe and in some traps put in place to assess village commensal small mammals.

Table 24. Information on live trap distribution on Nosy Ankao and those traps which captured *Rattus rattus* analyzed by microhabitat, age, and sex.

	Position of trap		Localization for those on ground				Localization for those off ground		
	On ground	Off ground	In litter	Next to fallen and rotten wood	On roots	Other	Branch or trunk > 10 cm	Branch or trunk < 10 cm	Other
Trap distribution	61	39	42	1	8	10	15	20	4
Sex and age									
Female – adult	10	10	8	-	2	-	7	3	-
Male – adult	5	15	5	-	-	-	13	2	-
Female – subadult	6	1	6	-	-	-	1	-	-
Male – subadult	4	6	4	-	-	-	2	4	-

Table 25. Information on live trap distribution on Nosy Manampao and those traps which captured *Rattus rattus* analyzed by microhabitat, age, and sex.

	Position of trap		Localization for those on ground				Localization for those off ground		
	On ground	Off ground	In litter	Next to fallen and rotten wood	On roots	Other (mostly under grass)	Branch or trunk > 10 cm	Branch or trunk < 10 cm	Other
Trap distribution	74	4	1	-	1	70	3	1	-
Sex and age									
Female – adult	7	-	-	-	-	7	-	-	-
Male – adult	3	-	-	-	1	2	-	-	-
Female – subadult	-	-	-	-	-	-	-	-	-
Male – subadult	1	-	-	-	-	1	-	-	-

Discussion

Vascular plants

Three different plant community groups were identified, each found on different islands (Nosy Ankao, Nosy Ratsy, and Nosy Manampao). Although located within a few kilometers of one another, each island has its own particular vegetation, constituting three distinct vegetational groups notably different from one another with respect to their structure and florisitic components (Table 4). Nosiborona was not the subject of linear transects, but only general collecting, and details on its structural aspects are currently not available.

Nosy Ankao has the greatest plant diversity and structural variability in terms of its flora. The next most diverse island is Nosy Ratsy, followed by Nosy Manampao, and finally Nosiborona. The physiognomic aspects of these islands range from Nosy Ankao, with some distinct variation, followed by Nosy Ratsy, and then Nosy Manampao; this latter is characterized by low vegetation, although a small portion is dominated by *Ficus tiliifolia* (Moraceae). Nosy Ankao has distinctly more vegetational cover with respect to the other islands, is notably stratified, and has two structural variants that are associated with different types of soil substrates. In contrast, Nosiborona is dominated by herbaceous vegetation.

These islands have comparable ecological aspects, particularly with respect to local soil types and climatic conditions, at least based on the preliminary survey. Hence, the documented floral and structural differences between these islands must be due to other environmental factors and different anthropogenic disturbances. These islands, perhaps with varying frequency and intensity through time, represent transit sites for local people exploiting the rich marine resources of the area. Woody plants on Nosy Ankao represent the only existing local source for construction material to build houses and structures for drying fish catches. These factors, as well as previous exploitation associated with the Nosy Ankao seaweed farm, might explain the rarity of trees with a diameter greater than 10 cm. In the main forest block on this island, the vegetation shows characteristics of a pseudo-climax with respect to its species richness and multi-stratification.

Analysis of floristic and structural aspects on Nosy Ratsy and Nosy Manampao might indicate different types of external factors associated with human-induced habitat degradation and impacts on plant cover. On Nosy Ratsy, this is probably associated with human exploitation of the former vegetation or perhaps the impact of fire, while on Nosy Manampao these same factors might come into play, and influences from a large seasonal seabird colony and different aspects of soil chemical composition (Figure 39). These aspects are presumably accentuated by the long local dry season. Insufficient information is available from Nosiborona to provide insights into its current vegetation structure, but there it is presumed with an important anthropogenic component.

Snails

On the basis of information in the literature, the snails collected on islands in the Nosy Ankao group were what would be expected from the area based on the local coastal scrub and forest ecosystems and previous collections from the area. However, the collection technique focused mostly on larger snails (13 mm and over) with only a single exception. Four additional species recorded from Port Leven were not collected (Morelet 1851, 1860) and include: *Tropidophora thesauri* Fischer-Piette, 1949, *Edentulina minor* (Morelet, 1851), *E. arenicola* (Morelet, 1860), and *Gulella microdon* (Morelet, 1851). This suggests that a more detailed survey of the Nosy Ankao Archipelago would yield additional land snail records.

Ants

Ant diversity on islands in the Nosy Ankao group

A variety of factors can influence the presence of a given ant species in insular ecosystems. The local habitat type plus external factors such as island size, climate, and vegetation help determine what ant species survive in a given locality. At the sites where mini-Winklers were employed, considerable differences were found in the ant species documented on the different islands. Nosy Ankao, largest of the islands (365 ha) and located relatively close to the mainland (3.4 km), had the highest species diversity (33 taxa). Nosy Ratsy, notably smaller (6 ha), is slightly farther from the mainland (7.1 km) and showed lower diversity (25 taxa). Following this trend, Nosy Manampao is the farthest from the mainland (8.6 km), although of intermediate size (29 ha), and had even fewer species (22 taxa). Our results in general follow classical island biogeography theory (MacArthur & Wilson, 1967), with the species richness of an island related to its size and distance from the large landmass acting as the source area of

Figure 39. The area of Nosy Manampao occupied by a large seasonal breeding colony of different tern species. The large number of birds trampling the ground vegetation and the higher nitrogen content of the soil associated with accumulated fecal material may be responsible for the open nature of the vegetation. (Photograph by Achille P. Raselimanana.)

colonization, which in this case is the main island of Madagascar.

Aspects associated with the ant fauna in the island group and more specifically on each island provide insights into the biogeography of these insects. The finding that all eight subfamilies of ants known from Madagascar occur on these islands highlights two different issues: 1) their notable dispersal capacity and 2) the importance of the remaining local habitats. The results are useful for understanding the local distribution of ant taxa. Indeed, several particularly interesting species were inventoried. Among these are the genera *Mystrium*, *Xymmer*, and *Proceratium*, and the endemic genus *Tanipone*. The presence of amblyoponine ants in the archipelago is particularly noteworthy, as this subfamily is an old relictual group with unusual morphological and behavioral characteristics. In the context of this study, two species might be new to science and not yet recorded from mainland Madagascar: *Proceratium* ankao 1 and *Tanipone* ankao 1.

Introduced species

Several factors may be limiting native ant biodiversity, and our survey of the ants of the Nosy Ankao island group uncovered evidence of problems induced by introduced species. In the context of natural processes, fluctuations do occur in rates of immigration and extinction of species based on source populations, presumably in this case the main island of Madagascar. Given the reduced land area of these islands, introduced ant species pose a serious threat to the endemic taxa. The case of Nosy Manampao is a good example, where the introduced species *Pheidole megacephala* dominates the entire sampling transect, which largely covered grassland with a small patch of woody vegetation (*Mimusops coriacea* and *Ficus tiliifolia* formation). It is presumed that in these zones food resources are low, at least on a seasonal basis. We suggest that the native ant species are being outcompeted by introduced species, which in turn dominate. Further, our results also show that the introduced species *Plagiolepis alluaudi* has invasive characteristics on Nosy Ratsy. It is presumed that different forms of transport, such as canoes and small boats, between the mainland and the islands of the Nosy Ankao group facilitated the introduction of these exotic species, several of which have the capacity to be invasive.

Comparing the ant diversity on islands in the Nosy Ankao group to that of Daraina and Analamera

The level of endemism of native Malagasy ants is high; at the level of species and subspecies +90% of the taxa are endemic (Fisher, 1996b, 1997). This high rate of endemism is presumably associated with the isolation of the island in deep time and geographic space. For small islands in the Nosy Ankao Archipelago, an understanding of the origin of the native ant fauna needs to be evaluated with respect to the main island of Madagascar. The number of mainland Malagasy endemic species on these small islands indicates considerable faunistic overlap and strongly suggests that the islands were attached to the main island in very recent geological history. To illustrate this point, we have compared the ant faunas of Analabe Forest (Daraina), Analamera, and the islands of the Nosy Ankao group, which show considerable faunistic overlap, particularly with Analabe Forest. The Analabe Forest is closer to the Nosy Ankao group than the Analamera. Altitudes and types of forest habitat in the Nosy Ankao island group are more similar to those of Analabe than Analamera. Nosy Ankao is the largest in the island group and shows the greatest faunistic overlap with the two mainland sites.

Reptiles and amphibians

Faunistic and biogeographic considerations

The islands in the Nosy Ankao group are documented to have 25 species of reptiles and one species of amphibian (Table 17), of which eight reptiles (31%) could not be identified with certainty and might be new to science. These findings support the idea that these islands play an important role in the preservation of Malagasy biodiversity, and in this case specifically the herpetofauna. All four studied islands are small (Table 2), with Nosy Ankao (365 ha) and Nosy Manampao (29 ha) being the largest, and Nosy Ratsy and Nosiborona (each 6 ha) the smallest. The habitats on Nosy Ankao are the most varied, followed by Nosy Manampao, while Nosy Ratsy is notably homogenous and almost certainly the subject of human-induced habitat degradation (see vegetation section). The relationship between island surface area and species diversity clearly plays an important role in explaining patterns found in the Nosy Ankao Archipelago.

Surveys of reptiles and amphibians on six islands in the Nosy Hara group, off the northwestern coast of

Madagascar, showed the same relationship as that found in the Nosy Ankao group (Metcalf *et al.*, 2007; Glaw *et al*., 2012; Raselimanana, unpublished). Of the 24 species making up the herpetofauna of the Nosy Hara group, only one, a gecko (*Ebenavia inunguis*), was not found on Nosy Hara, which is the largest island (115 ha) in the archipelago, while the other islands range from 30 to 5 ha (Metcalf *et al*., 2007).

However, as the Nosy Hara islands show a nested relationship, with species forming subsets and increasing in species richness with the size of each island, this pattern was not found in the Nosy Ankao group. Ankao is the largest island within the complex, and the nearby islands possess at least two or three common species not present on Ankao. The islands in the Nosy Hara Archipelago share a considerable percentage of their herpetological taxa with the main island of Madagascar, but include a few species that are local micro-endemics, such as the smallest species of chameleon in the world, *Brookesia micra* (Glaw *et al*., 2012).

Taxonomic, ecological, and conservation considerations

In the case of the Nosy Ankao island group, a number of species remain unidentified. This lends credence to the idea that local insular populations are differentiating and could include endemic species. Further work needs to be conducted to verify this aspect, as these islands are located within a few kilometers of the main Madagascar coast and would have been attached to Madagascar during relatively recent periods in geological time, when sea levels were lower than today. In any case, many of the species recorded during our survey were previously unknown in the archipelago and are morphologically similar to taxa known from the northern portion of Madagascar, specifically at Montagne des Français, Orangea, and Ampombofofo (Figure 1) (D'Cruze *et al*., 2007; Megson *et al*., 2009). These zones presumably share aspects of their geological history, as limestone and coral reefs form a large portion of their exposed ground substrate.

The three principal islands (Nosy Ankao, Nosy Manampao, and Nosy Ratsy) which were the focus of this investigation occur within kilometers of each other (Figures 2 & 3). Counter to our initial expectations, they show notable differences in their represented herpetofauna. Given that each of these islands harbors dissimilar plant communities, perhaps associated with some differences in soil types, these characteristics presumably have had important influences on herpetofauna composition. This influence could be in the form of maintaining viable populations after their separation from mainland Madagascar in recent geological time, or supporting species after their over water dispersal from the mainland. An example of specialized ecological preferences can be found in *Paracontias* aff. *hildebrandti*, which was very abundant in a portion on Nosy Manampao, but not found despite considerable systematic searching on Nosy Ankao and Nosy Ratsy. More specifically, it was found in a section of Nosy Manampao designated as the *Mimusops coriacea* and *Ficus tiliifolia* formation (see botanical section above), which is characterized by closed canopy woody vegetation and humid soils resting on non-consolidated sand dunes. This same biotope is where another burrowing species, *Xenotyphlops* aff. *grandidieri* (Figure 38), was also found.

A few rare and threatened species were found on islands in the Nosy Ankao group. For example, the nocturnal gecko *Paroedura lohatsara* (Figure 37A), which is considered by the IUCN as Critically Endangered, and which was previously only known from Montagne des Français (Glaw *et al*., 2001) and Orangea (Raselimanana, unpublished data). Another example is a new form that is currently being described (Frank Glaw, personnel communication) and assigned here the name *Liophidium* aff. *torquatum*. This new species is apparently restricted to the northern portion of Madagascar and some offshore islands and is closely related to the widespread *L. torquatum* species complex (Glaw & Vences, 2007).

Elsewhere in the world, invasive *Rattus* spp. are known to have negative impacts on native reptile and amphibian populations and after rat eradication many species have recovered (Jones *et al*. 2016). Rat eradication on Nosy Manampao and rat control on Nosy Ankao would likely provide similar benefits to the reptiles on these islands.

Seasonality of reproduction

The patterns already outlined concerning the breeding periods of various reptile species on islands in the Nosy Ankao group provide an indication of seasonal differences at the insular community level. In certain cases, local populations were found to be represented solely by adults (*Zonosaurus madagascariensis*), while others were dominated by juveniles or recent hatchlings (*Furcifer petteri*), or gravid females (*Paracontias* aff. *hildebrandti*). It is very probable that during our March 2016 visit to the archipelago, the young of certain reptile species had not yet hatched, a circumstance presumably associated with the breeding strategies of different sympatric taxa and resource partitioning. Further work should be conducted in the archipelago during other seasons to better examine and test this hypothesis.

Birds

Faunistic, biogeographic, and conservation considerations

In general, the landbird fauna of the islands of the Nosy Ankao group are depauperate with regards to species diversity. Nosy Ankao has the greatest number of species of any of the island group, with 24 taxa being recorded during our inventory work, as compared to 57 species known in the Réserve Spéciale d'Analamera and 77 in Daraina (Figure 1; ZICOMA, 1999), the latter is now known as Parc National de Loky-Manambato. This clearly indicates that a number of bird species were either unable to cross the relatively narrow water gap between the Madagascar mainland and the Nosy Ankao Archipelago, or if they made it cross, successful colonization did not take place.

Two aspects are of particular interest concerning the birds of the Nosy Ankao island group. The first is the large tern colony on Nosy Manampao, which has been estimated at over 22,000 breeding pairs and is composed of five different species (Le Corre & Bemanaja, 2009). Nosy Manampao is one of the most important seabird breeding sites in Malagasy waters (Figure 40). During the breeding season, terns, particularly nestlings, have been observed to be heavily infested with ticks (Figure 41), presumably reducing rate of young birds reaching fledgling stage. Studies are needed to identify these ticks and possible zoonotic diseases they might be transmitting, as well as to measure their impact on breeding success of nesting pairs. Further, it is presumed that introduced *Rattus* populations on this island have a negative impact on the nesting tern colony as these rodents feed on eggs and perhaps nestlings, and it is recommended that this mammal be eradicated (see small mammals below).

Another interesting aspect of the landbird fauna of the Nosy Ankao island group, particularly Nosy Ankao, is that it provides a window into the capacity of certain Malagasy bird species to disperse over water and colonize offshore and distant islands. A comparison of the list of bird species known from the Aldabra Atoll, a remote island in the western Seychelles and slightly more than 400 km NW of the northern tip of Madagascar, to that of the Nosy Ankao archipelago, certain patterns with respect to the species capable of overwater dispersal becomes evident. On the basis of molecular or classical museum specimen studies of birds of the western Indian Ocean islands, the following species occurring on Aldabra are closely related to a Malagasy form or are part of regional species complexes: *Dryolimnas cuvieri aldabranus*, *Centropus toulou insularis*, *Hypsipetes madagascariensis rostratus*, *Nectarinia souimanga aldabrensis*, *Zosterops maderaspatana aldabrensis*, *Dicrurus aldabranus*, and *Foudia* (*eminentissima*) *aldabrana* (Warren *et al*., 2003, 2005, 2006, 2012; Pasquet *et al*., 2007). In all cases, the ancestral or closely related forms of these different Aldabra bird species occur on mainland Madagascar and Nosy Ankao, providing a clear context for the capacity of a limited number of Malagasy species to disperse over water.

A number of vertebrate species introduced to the Nosy Ankao island group are probably having negative impacts on the local bird fauna (see Conservation recommendations and priorities, below). Feral cats occur on Nosy Ankao and are presumed to prey on native and endemic songbirds, including forest-dwelling species. This might account for the notably low densities of birds in the Nosy Ankao forest, where cats were documented during our inventory of the island.

The Indian Mynah, *Acridotheres tristis*, is introduced to Madagascar, and its occurrence on the islands of the Nosy Ankao island group is not natural. This notably aggressive species may be displacing other bird species from nesting holes in trees, such as *Upupa marginata*, as well as out competing local endemic birds for what is presumed at the seasonally limited food resources. Eradication of this species in the island group would be a worthwhile program (see Conservation priorities and recommendations, below).

Small mammals

Faunistics

Our small mammal surveys of three islands in the Nosy Ankao group found no evidence of locally occurring native species typically associated with natural forest formations on the mainland, which include a considerable diversity of endemic tenrecs of the Family Tenrecidae and rodents of the Subfamily Nesomyinae (Soarimalala & Goodman,

Figure 40. During the southern winter, Nosy Manampao is an important site for several species of breeding terns. Most of the flying adults and nestlings on the ground are Sooty Terns, *Sterna fuscata*, which is the dominant tern species nesting on the island. (Photograph by Greg Wepener.)

Figure 41. During the breeding season of terns on Nosy Manampao, outbreaks of tick infestations have been observed on nestling birds. Tick loads can be so great that some chicks have difficulty walking. (Photograph by Greg Wepener.)

2011). Instead, within the natural ecosystems of these islands, including a relatively large forest block on Nosy Ankao and different open vegetational types on Nosy Manampao, all species of documented small mammals are members of the genus *Rattus* (Family Muridae) and introduced. In short, no naturally occurring small mammals were found on any of these islands in the standard live traps or pitfall traps (Tables 18-20, 23).

The neighboring portion of mainland Madagascar, specifically the forested areas of the Parc National de Loky-Manambato (previously known as the Daraina Forest), which the Nosy Ankao island group is part of, a number of Tenrecidae and Nesomyinae have been documented (Raheriarisena & Goodman, 2006). These include seven species of Tenrecidae and several species of Nesomyinae, one of which was recently named as new to science (Goodman *et al*., 2009). At a littoral forest within the Parc National de Loky-Manambato known as the Sahaka Forest and not too far south of Nosy Ankao, three species of Tenrecidae were found (*Tenrec ecaudatus*, *Setifer setosus*, and *Microgale brevicaudata*); the local rodent fauna at this site consisted exclusively of introduced *R. rattus* (Raheriarisena & Goodman, 2006). On the basis of elevation and habitat, the Nosy Ankao forest has appropriate habitat for the three different tenrecs found in the Parc National de Loky-Manambato (Goodman *et al*., 2013). Members of the genera *Tenrec* and *Setifer* are large and conspicuous animals that often occur outside of forest formations and in some areas of Madagascar consumed as bush meat. On the basis of interviews conducted with more elderly residents of Nosy Ankao, they do not have in their recollection any memory of these two genera occurring on the island.

Rodent food resources on Nosy Ankao can be divided into two different forms: 1) natural sources associated with different types of vegetation, particularly fruits, occurring in forest formations, or animal matter such as beached remains, snails, invertebrates, and small vertebrates; and 2) those associated with human sources, such as stored foods or waste products. In contrast to Nosy Ankao, food resources of human origin are very limited to non-existent on Nosy Manampao and Nosy Ratsy, and any *Rattus* that might occur on these islands derives its nutrition from non-human related resources. During the breeding season of terns on Nosy Manampao, it is presumed that *Rattus* feed extensively on bird eggs and chicks. Dried bird cadavers might also be an important food resource for *Rattus* during a portion of the year.

During our inventories of Nosy Ratsy, we found no evidence of *Rattus* and several possible explanations can be presented. Perhaps with the island's vegetational cover of bush scrub, food resources are simply too limited and *Rattus* that land on the island cannot establish permanent populations. Crabs were particularly common on this island and regularly captured in our traps and pitfall devices. Crabs are presumed to be capable of predating on *Rattus*, particularly young animals. The combination of the island being round and small (6 ha), with dense bush and little ground vegetation, and having predatory foraging crabs across its entirety, might severely limit the ability of invasive mammals such as *Rattus* to establish local viable populations. Another possible predator of rats on Nosy Ratsy is the large predatory lizard *Zonosaurus madagascariensis*, which among the surveyed islands was only found on Nosy Ratsy. This is in contrast to Nosy Manampao, which is elongated and distinctly larger (29 ha). This island is more open and grassy vegetation presumably provides different food resources for *Rattus*, as well as seasonally available fruits, and has seemingly less dense foraging crab populations towards the central portions of the island. Nosy Manampao has a population of the boa *Acranthophis madagascariensis*, and *Rattus* likely forms an important prey base for these snakes when terns are not breeding on the island.

Conservation priorities and recommendations

Some important generalities associated with invasive invertebrates

High levels of micro-endemism and small population sizes among Malagasy arthropods in general mean that small forest patches may harbor important components of local biodiversity. This means that although larger vertebrates may be extirpated by different factors, ranging from natural and human-induced habitat changes or the presence of invasive species such as *Rattus*, arthropod communities may still be intact and, thus, these patches should be included in conservation planning.

The persistence of endemic lineages on small patches of habitat, such as islands in the Nosy Ankao group, is of particular interest as such sites are vulnerable to impacts from invasive species. Although colonization and species turnover are natural island processes, especially in the current case with 1) mainland Madagascar being so close to the Nosy Ankao Archipelago and 2) these islands being small and with limited biodiversity, they are inherently vulnerable to new species introductions (Underwood & Fisher, 2006; Hoffmann & Courchamp, 2016). Therefore, on islands, there are two factors to consider when designing conservation strategies: the habitat fragmentation caused by human development, together with species introductions accelerated by trade and construction that increases the vulnerability of remaining native species. Overall, pest ant species self-dispersing or dispersing through human assistance from the mainland pose biosecurity risks (see below) to different human interests and local native species on these islands.

Nosy Ankao

Introduced plants

The Nosy Ankao Development Company has engaged in a large-scale project to remove groves of *filao* trees, *Casuarina equisetifolia* (Casuarinaceae), presumed to be introduced (see Kull *et al*., 2012 for a discussion of this point) and replace them with vegetation that is definitely native. The name "ankao" is derived from the local Malagasy name for *C. equisetifolia* (Decary, 1963). Whether native to Nosy Ankao or not, the leaf litter of *C. equisetifolia* has been documented to reduce germination of native trees species on tropical islands, and, hence, impeding natural regeneration or human-associated reforestation processes (Hata *et al*., 2010). Conversely, leaf litter of this tree has been found at sites of the Kenyan coast with similar soil types to Nosy Ankao to advance succession stages of native plants in the presence of native millipedes that feed on the leaves and their feces provide critical humus (Haller & Baer, 1995).

The island also has a large population of the exotic invasive plant *Leucaena leucocephala* (Fabaceae) that needs to be closely monitored. This species is widely used around Madagascar in the context of agroforestry, construction, and firewood. In this context, existing areas of this plant should be exploited by local inhabitants and replaced by native trees that serve the same functions.

Introduced ants

On the mainland of northern Madagascar adjacent to Nosy Ankao, two of the most notorious invasive ant species, *Pheidole megacephala* and *Solenopsis geminata* are present. The former was found on all of the surveyed islands in the Nosy Anakao group, while the latter was not found (Table 11). *Pheidole megacephala* has been implicated in the blanket decimation of Hawaii's lowland arthropods; entomologists in the early 20th-century described in detail how the native beetle fauna was defenseless against the onslaught of this invader (Krushelnycky *et al*., 2005; Lach, 2005). On the smaller granitic islands of the Seychelles, invasive ants such as *P. megacephala* have already extirpated native ants and are now threatening nesting bird populations (Fisher, pers. obs.).

In addition to *P. megacephala*, an additional six species of introduced ants were found on Nosy Ankao: *Paratrechina longicornis*, *Plagiolepis alluaudi*, *Strumigenys maxillaris, S. emmae*, *Tetramorium sericeiventre*, and *T. delagoense* (Table 11). In addition, the introduced ant faunas of Nosy Ankao and Nosy Manampao are not exactly the same, which provides strong evidence of either differential forms of introduction or perhaps colonization capacity based on different ecologies of these two islands.

Monitoring invasive species is of particular importance on islands in the Nosy Ankao group where you have the juxtaposition of *P. megacephala* along with pockets of highly specialized endemic ants such the genera *Mystrium*, *Lioponera*, *Tanipone*, *Leptogenys*, and *Proceratium* on Nosy Ankao. The same situation occurs on other neighboring islands, such as Nosiborona, where *P. megacephala* occurs with the endemic genera *Xymmer* and *Malagidris*.

Control of invasive species will require preventive monitoring and possibly active land management measures to sustain habitat quality. Given the persistence of native ants, we recommend the monitoring and quantifying the extent of populations of *P. megacephala* on Nosy Ankao and other islands in the archipelago to avoid potential large-scale extirpation of native ants (Cooling & Hoffman, 2015). In addition, attention must be given to limiting habitat disturbance in areas that native ants persist. Programs of removal of invasive plant species in these areas should be considered in detail, since removing plant cover and disturbing the soil will provide opportunity for invasive ants to become established (Fisher, 2005).

Introduced rodents

Different natural and anthropogenic ecosystems on the island have been invaded by introduced rodents, most notably *Rattus rattus* and to a lesser extent *R. norvegicus*. These animals pose several problems. They create considerable difficulties for humans by feeding on food stocks and destroying clothes, portions of buildings, and other household items. They are potential reservoirs for a variety of different diseases that can be transmitted to humans; further work needs to be conducted to document these possible zoonotic exchanges. With respect to the natural ecosystems of the island, rats are presumably predating on a wide variety of native vertebrates and invertebrates, as well as feeding on fruits and other plant products that would normally be dispersed or consumed by native animals and helping to support regeneration of the floral community.

The situation on Nosy Ankao is very different from Nosy Manampao (see below); it is notably larger size (365 ha), has considerable human population spread across the island and in several different villages, and sees an extensive amount of boat traffic from the mainland and, hence, difficult to impose biosecurity measures upon (see below). These factors greatly reduce the chances that any rat eradication program might be successful on Nosy Ankao. In contrast, we can suggest some other aspects to help reduce or control introduced rodents on the island. The Nosy Ankao Development Company has implemented a program for the storage and removal of rubbish from buildings and structures associated with the hotel and employee housing. This program could be augmented, made island-wide, and combined with a regular system of rat removal via trapping in and around village settings and in forest habitats.

Other introduced mammals

Shrews – On the basis of interviews with local people living on the island, it was mentioned that an animal locally known as *voalavo arabo* (=*Suncus murinus*) occurs on the island as a commensal species. We did not find any evidence of this introduced shrew, although the number of accrued trap-nights in and around houses was limited. We suggest that further trapping be conducted in villages to confirm the presence of shrews on the island.

Cats – Domestic and semi-feral cats occur across the island. In the forest ecosystems of Nosy Ankao, specifically the large block between Andasibe and Andrangana, we found cat scats. While local cats almost certainly feed on introduced rodents, they are presumably also feeding on native birds and the contents of their nests, as well as other native vertebrates. The population density of songbirds on Nosy Ankao was remarkably low, which might be related to cat predation.

We recommend trapping feral cats across Nosy Ankao to keep their numbers low. Further, restrictions should be put in place on the transport and introduction of domestic cats to the island, specifically by individuals associated with the hotel operation. If deemed needed, a cat eradication campaign could be implemented.

Introduced birds

Indian mynahs – As of the first portion of 2016, Nosy Ankao had a small population of the introduced mynah, *Acridotheres tristis*. This aggressive bird is presumed to be in direct competition with native and endemic taxa, such as *Upupa marginata*, for nesting sites. Further, these introduced birds might be feeding upon a variety of small native vertebrates, as well as competing for different food resources with other native vertebrates on the island.

We recommend that an eradication program be put in place to remove this species from Nosy Ankao. Elsewhere on islands in the western Indian Ocean, mynah eradications have been successful (Canning, 2011; Feare *et al*., 2016). They have been described as very smart birds and any effort to eradicate them from an island requires lots of forethought to keep from training any remaining individuals how to avoid the employed removal methods. The removal of this species should be a priority before the local population increases to the point that their elimination becomes more difficult. Further, as it is capable of crossing open water, whether from neighboring islands or mainland Madagascar, a regular surveillance system would need to be put in place.

Nosy Manampao

Introduced ants

Six species of introduced ants were recorded in Nosy Manampao (*Paratrechina longicornis*, *Plagiolepis alluaudi*, *Pheidole megacephala*, *Strumigenys emmae*, *Tetramorium scytalum*, and *Leptogenys maxillosa*) (Table 11). At the same time, only 14 additional native species of ants were recorded, which is the lowest number of species compared to the other islands sampled. The types of monitoring programs proposed above for ants on Nosy Ankao should also be considered for Nosy Manampao.

Introduced snails

A species of introduced snail, *Lisachatina immaculata*, was found in very low density on Nosy Manampao. At least in the first portion of 2016, it does not appear to be invasive. It is recommended that potential population explosions of this species be followed in the context of ecological monitoring of the island.

Introduced rodents

During our small mammal inventory of Nosy Manampao, we found a population of *Rattus rattus*. These animals presumably feed upon small vertebrates that occur on the island, the eggs and young of breeding terns, and different grasses and fruits (e.g. *Ficus*). Given the uniqueness of Nosy Manampao with regards to its largely natural ecosystems and one of the largest tern colonies in the western Indian Ocean, we suggest that everything possible be done to maintain the island in an intact state.

Rat eradication on Nosy Manampao and surrounding islands would likely be the most significant management action available to help protect the biodiversity on these islands. The fact that this island and nearby islands are relatively small, uninhabited, and support no native small mammals makes rat removal a relatively straightforward process. Indeed, there have been over 700 successful rodent eradications from islands worldwide (DIISE 2016) and success rates for tropical islands are close to 90% (Keitt *et al*., 2015). We strongly suggest that the Nosy Ankao Development Company, the Parc National de Loky-Manambato, and the Malagasy authorities consider such a program.

If this program was implemented, the islands neighboring Nosy Manampao, particularly Nosy Lavahely, Nosy Tokana, Nosy Madinka, Nosy Bory, Nosy Bato, and Nosy Ratsy (Figure 2) should also be considered as a group. On most of these islands, seabirds, specifically terns, are present during the southern winter nesting season and are likely subjected to predation by rats. (However, on the basis of results presented herein, no *Rattus* were found on Nosy Ratsy.) Given, the capacity of *R. rattus* to swim across open water, which has been measured as up to 750 m (Innes, 2005) or the distance between Nosy Manampao and surrounding smaller islands, we suggest that if a rat eradication program is engaged for Nosy Manampao, these neighboring islands should also be treated during the same period. In the same context, putting into place a biological security system (biosecurity, see below) for Nosy Manampao and neighboring islands in advance of the eradication would be important, specifically controlling landings that could be the source of new *Rattus* colonization. This system would need to be maintained in perpetuity.

Introduced birds

Indian mynahs – Nosy Manampao has a small population of the introduced mynahs, *Acridotheres tristis*. These birds presumably fed upon a variety of small native vertebrates, such as reptiles, as well as predating on tern eggs during the latter's breeding season.

We recommend that an eradication program be put in place on the island to remove mynahs. This should be a priority before the local population of this species increases to the point that their elimination becomes more difficult. Further, as it is capable of flying across open water from neighboring islands or mainland Madagascar to Nosy Manampao, a regular surveillance system should be put in place.

Questions of biosecurity

Biosecurity refers to efforts to keep exotic species from being introduced to new locations or reintroduced to sites from which they have been eradicated. For Nosy Ankao and surrounding islands a biosecurity program should focus on two major aspects: 1) keeping new and damaging invasive species from being transported from the main island of Madagascar and 2) keeping invasive species present on some islands (mainly Nosy Ankao) from being spread to other islands in the archipelago.

We recommend that an analysis be conducted of the invasive species present in the northern and northeastern part of Madagascar and particularly those species that are abundant near the departure points for supplies to islands in the Nosy Ankao group. These species should be reviewed against potential impacts to native terrestrial biota of these islands, as well as from the perspective of human welfare and appropriate actions taken to prevent new damaging species from being introduced.

An effective biosecurity program preventing the spread of invasive species to and between the islands around Nosy Ankao is a critical aspect of any eradication campaign. If rats are to be removed from Nosy Manampao and other islands, it is only worthwhile if rats do not recolonize, including through natural recolonization such as by swimming or accidental introduction through the movement of supplies or other boat traffic to the island. Because rats are capable of swimming between the smaller islands surrounding Nosy Manampao and perhaps from Nosy Ankao to Nosy Ratsy (Innes, 2005), it is critical that the biosecurity program covers the entire Nosy Manampao island group. Vigilance for rats on the islands nearest to Nosy Ankao should be maintained so that incursions can be addressed before rat populations become established in the entire island group.

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