The amphibians and reptiles of the Ambatovy-Analamay region

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Abstract

Nine different habitat types identified within Ambatovy-Analamay region were the subject of a herpetological survey between 6 January and 21 February 2009. Three complementary sampling methods were used during the field survey. These include: 1) direct observations and general collecting along trails, 2) systematic refuge examination, and 3) pit-fall traps with drift fence. In total, 112 species were recorded (68 amphibians and 44 reptiles), making the Ambatovy-Analamay region one of the herpetologically richest zones in terms of diversity within the central-eastern portions of Madagascar. All of the species recorded in the zone, with the exception of the frog *Ptychadena mascareniensis*, are endemic to Madagascar. Several species have restricted distribution range within the central and central-eastern portions of Madagascar. Not one of the nine surveyed habitats showed a clear pattern of species dominance and all species demonstrate similar abundance index measures. Despite the current habitat and ecosystem disturbance in the Ambatovy-Analamay region, it is still viable for the local herpetofauna communities. Five species are listed on the IUCN Red List, including as *Mantella aurantiaca* as "Critically Endangered", *M*. *crocea* as "Endangered", and *Rhombophryne coronata*, *Scaphiophryne marmorata*, and *Sanzinia madagascariensis* as "Vulnerable". Several taxa (e.g. *Mantella* aff. *milotympanum*) may represent a new species to science.

Keywords: Amphibians, reptiles, habitat types, diversity, abundance index, population stability, Ambatovy-Analamay, central-east, Madagascar.

Résume détaillé

Les neuf habitats types principaux identifiés dans la région d'Ambatovy-Analamay ont fait l'objet d'un diagnostique biologique de leur herpétofaune entre le 6 janvier et 21 février 2009. Trois principales méthodes complémentaires ont été déployées. Il s'agit des observations directes sur itinéraires échantillons, de la fouille systématique des refuges et de la capture aux trous-pièges. Un total de 112 espèces a été recensé dont 68 amphibiens et 44 reptiles. La forêt d'Ambatovy-Analamay représente en effet un écosystème important pour la diversité de l'herpétofaune malgache en particulier pour le centre-est de Madagascar. Outre l'espèce *Ptychadena mascareniensis*, toutes les autres espèces d'herpétofaune recensées dans cette forêt d'Ambatovy-Analamay sont endémiques de Madagascar. La plupart de ces espèces présentent une aire de répartition restreinte dans la région du centre-est ou du centre. Les résultats des analyses ont révélé que la majorité des espèces présentent une valeur d'abondance relative sensiblement identique, signifiant ainsi l'absence d'une dominance spécifique particulière au sein de chaque habitat type. Par ailleurs, les données quantitatives à travers ces neuf habitats principaux suggèrent qu'à l'état actuel des choses, les milieux naturels d'Ambatovy-Analamay sont encore relativement stables pour permettre la viabilité de populations herpétofauniques saines malgré les perturbations constatées. Cinq parmi les 112 espèces recensées sont figurées dans la liste rouge de l'IUCN. Il s'agit de *Mantella aurantiaca* classée «Gravement menacée», *M*. *crocea* classée «En danger» et *Rhombophryne coronata*, *Scaphiophryne marmorata* et *Sanzinia madagascariensis* sont classées «Vulnérables ». De nombreuses formes présentant une affinité morphologique à des espèces connues, mais formant des populations homogènes (exemple le cas de *Mantella* aff. *milotympanum*) dans l'ensemble de la communauté pourraient être nouvelles pour la science. L'habitat «Azonal Impacted Degraded» représente un paysage écologique homogène très pauvre en espèces, mais il constitue un milieu unique constituant un biotope spécial pour la communauté herpétofaunique composée essentiellement par *Trachylepis boettgeri* et *Blommersia domerguei*.

Mots clés : Amphibiens, reptiles, types d'habitats, diversité, indice d'abondance, stabilité des populations, Ambatovy-Analamay, centre-est, Madagascar

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Introduction

In recent published tabulations, 244 species of amphibians (Vieites *et al*., 2009) and 363 species of reptiles (Glaw & Vences, 2007a) are recognized for Madagascar. The island represents one of the most extraordinary herpetological faunas in the world; new taxa continue to be described at an astounding frequency. For example, amphibian species diversity on the island is estimated to be a minimum of 373 and perhaps reaching 465 taxa (Vieites *et al*., 2009). Much still remains to be discovered with respect to the herpetological fauna in the natural landscapes of eastern Madagascar, which is well known for its rich and variable humid forest habitats. Unfortunately, the humid forests of the island have experienced devastating destruction due to anthropogenic activities (Sussman *et al*., 1994; Agarwal *et al*., 2005), which, in some cases, pushed the native biota towards local extirpation or to the brink of extinction. The effects of forest destruction and fragmentation on the fauna, as well as selective resource extraction, are well documented on Madagascar (e.g., Vallan, 2002, 2003; Brown & Gurevitch, 2004; Ramanamanjato, 2007). Slash-and-burn agriculture practices and other types of forest habitat degradation are considered as the principal sources of natural habitat loss on Madagascar (Green & Sussman, 1990; Sussman *et al*., 1994; Agarwal *et al*., 2005).

Over the course of the last few decades, the non-regulated exploitation of terrestrial mineral resources on Madagascar has contributed considerably to the degradation of natural landscapes. In several cases, the zones with some of the richest and notably endemic forest-dwelling biota also contain or contained areas of plentiful natural forest resources with relatively rich soils suitable for agricultural activities and sites with rich mineral resources. We can cite, for example, the littoral forests of the extreme southeast (Ganzhorn *et al*., 2007) and the Mikea forest and the region of Ranobe in the extreme southwest (Raselimanana & Goodman, 2004; Thomas *et al*., 2006). The conception and promotion of a management and conservation mechanism, taking into account these aspects, are important to preserve the integrity of representative ecological landscapes and the remaining biological diversity of Madagascar. In many cases, it is rather ambitious and complex to address these objectives when confronted with the urgent human socio-economic needs of the Malagasy and associated development activities.

According to their fields of interest, scientists need to help with the proper evaluation of different aspects that are associated with biological diversity and provide the qualitative and quantitative information needed to guide development projects in order to achieve the proper balance between exploitation and conservation. One paramount aspect of this knowledge is that it should be based on field studies and biological inventories, which use standardized methodologies shown to be practical and provide the needed insights into measures of species richness and local ecological communities. These data provide fundamental information on the uniqueness of certain biotic elements of a given area and are the basis for conservation prioritization.

With the intent of advancing a viable long-term conservation program associated with the development of a mineral exploitation program at Ambatovy, field scientists from the Association Vahatra were engaged to conduct intensive and fine-scale biological inventories of the terrestrial vertebrate fauna of nine different habitat types with variable levels of degradation (see Goodman & Raselimanana, pp. 36-37). The principal objectives of these field inventories were to provide qualitative and quantitative information of the terrestrial vertebrates occurring in these different habitats and to explain different biotic and abiotic factors associated with their distributions. Herein, we present the herpetological results of the fieldwork conducted between 6 January and 21 February 2009 in the Ambatovy-Analamay region and provide insight into the relative abundance and biogeography of reptiles and amphibians with respect to local variation within this immediate zone and in the central portion of the eastern humid forests of Madagascar.

Methods

Sampling techniques and methods

Three complementary field techniques were used in this study: 1) direct observations and general collecting during the day and night, 2) systematic sampling of potential refuges, and 3) pit-fall traps with drift fences. These methods have been regularly used for herpetological inventories across Madagascar since 1989 (e.g., Raxworthy & Nussbaum, 1994). The standardization of inventory techniques across sites is critical to allow for comparative analysis on species richness and other ecological and natural history parameters. Further, it is important to underline that in order to have the best approximation of local species richness levels at a given site or within a given habitat type, survey efforts need to be directly proportional to local habitat heterogeneity.

The first objective of our field inventories was to obtain information concerning the biological and ecological aspects of the local herpetological fauna in the Ambatovy-Analamay region. In addition, the tabulation of species accumulation curves for a given habitat is informative to determine if the sampling effort was largely effective with regard to the estimation of species richness of the local fauna. An analysis of the spatial distribution of these communities provides a window into the ecological preferences of each taxon. The second aspect of the field research was to provide specimen material for morphological and molecular genetic studies on the phylogeny, systematics, and phylogeography of Malagasy reptiles and amphibians. The resulting information from these integrated studies provides critical insight into faunistics and biogeography, which in turn, is closely linked with informed decisions associated with management and conservation of a specific site or in a broader regional context.

The inventory period of a given site or habitat type is usually seven days. However, in the case of our early 2009 research in the Ambatovy-Analamay region, the period was extended an extra day to provide sufficient time for local reconnaissance of each habitat, survey activities, and to compensate for the considerable amount of time lost each day due to logistics.

Direct observations and general collecting

This method consists of observation and capture of reptiles and amphibians within a study area along a pre-established trail system. It is important that within a given habitat or site, the paths cross a variety of local environment types, specifically different vegetational communities and microhabitats. At sites with considerable habitat heterogeneity, the trail system is more complex. In the case of multidisciplinary surveys, as during the early 2009 Vahatra surveys, members of the research group employ the same transects for the different study organisms (e.g., birds, small mammals, and lemurs). Existing and a few newly created trails or paths were used and were marked every 10 m with colored flagging.

As reptiles and amphibians are poikilotherms, their body temperature is roughly the same as the ambient temperature. Hence, the latter portion of the morning and the first portion of the afternoon are the periods of maximum activity for diurnal species. For nocturnal species, transects were visited from nightfall to around midnight. As most nocturnal species have distinct eye shine associated with light reflection, the use of a relatively strong 6-volt headlamp provided an excellent means to locate them. Further, certain diurnal species rest during the night on exposed branches and branchlets and either retain their bright day coloration or become a whitish-beige, and are therefore, easily spotted with this same type of headlamp. Calls were often used to locate and identify frogs particularly cryptic species or those above eye-level in trees or in refuges, such as water-filled cavities.

Systematic sampling of potential refuges or refuge examination

This technique is generally conducted in parallel to the preceding one and is only practiced during the day (Raselimanana *et al*., 2000). It consists of careful examination of different biotopes or microhabitats that might be potential refugia for reptiles and amphibians with special life history traits. These biotopes consist of rotten wood (fallen tree trunks), under dead tree bark, small crevices and fissures in exposed rock, tree trunk cavities, holes within bamboo stalks, termite mounds, dense leaf litter at the base of large trees, and water-filled leaf axils or phytotelms (palms [Family Arecaceae], *Pandanus* [Family Pandanaceae], and *Ravenala* [Family Strelitziaceae]). Further, water sources and riverbanks, particularly in marshy habitats, are excellent sites for frog and snake prospection. Other particularly important microhabitats are the rocky zones of river rapids or vertical rock surfaces of cascades, where rupicolous species occur. This type of refuge sampling provides precise information on the very specific microhabitats occupied by certain taxa, particularly active diurnal and resting nocturnal animals. Finally, this approach allows the capture of species with particular life-history traits (e.g., fossorial habits) that would be difficult to locate with the general collecting technique mentioned above.

Pit-fall traps with drift fence

The trapping technique referred to as pit-fall traps is composed of a series of 11 buckets (15 l each) sunk into the ground with the rim flush with the soil level and spaced 10 m apart from one another on an approximately 0.5 m wide precut 100 m trail. Along the pit-fall line, about 0.60 m of the 0.85 m high plastic sheeting was stapled to vertical stakes that bisected the center of each bucket. The base of the fence, about 0.25 m, was covered with soil litter to provide a barrier to animals moving on the ground and that subsequently fell into the buckets. The bottom of each bucket was pierced with small holes to allow rainwater drainage. Pit-fall lines were installed and left operational for at least six nights, although for certain lines, an extra night was added for logistical reasons or to augment the trapping effort for a given habitat type. The term “pit-fall night” is defined as one bucket in operation for 24 hours (dawn to dawn the following day). The pit-fall lines were visited a minimum of twice per day, once in the early morning around 5h 30 and again in the late afternoon before 16h 30. The placement, description, and characteristics of each pit-fall line are presented in Table 1.

Table 1. Details on the pit-fall traps employed during the biological surveys of the Ambatovy-Analamay forest, including installation date, geographic coordinates, and ecological descriptions. ABE = Azonal Benchmark, AIG = Azonal Impacted Good Quality, AID = Azonal Impacted Degraded, TBE = Transitional Benchmark, TIG = Transitional Impacted Good Quality, TID = Transitional Impacted Degraded, ZBE = Zonal Benchmark, ZIG = Zonal Impacted Good Quality, and ZID = Zonal Impacted Degraded (see Goodman & Raselimanana, pp. 36-37, for a definition of these vegetational types).

Type of vegetational formation	Line	Period in use	Geographical coordinates latitude S, longitude E, elevation		Ecological description
			Start	End	
ABE	8	26 Jan.- 1 Feb. 2009	48°12’4.86”E 8°28’56.1”S 1048 m	48°12’4.39”E 18°28’58.65”S 1048 m	Open canopy humid thicket forest with vine-like bamboo and dense understory plants. Disturbed forest and canopy at 7 m in the Sakalava River valley. Little leaf litter and scarce understory grasses and rotten logs.
	9	26 Jan.- 1 Feb. 2009	48°12’7.17”E 18°28’58.66”S 1073 m	48°12’7.77”E 18°28’59.48”S 1082 m	Closed canopy thicket forest on slope. Dense and low vegetation associated with *Pandanus* trees. Canopy less than 10 m. Thin leaf litter and rotten logs notably rare. Forest floor with hard packed ferruginous soils.
	10	26 Jan.- 1 Feb. 2009	48°12’10.26”E 18°29’1.25”S 1096 m	48°12’10.87”E 18°29’0.99”S 1099 m	Almost closed canopy thicket forest on extensive hillcrest and close to a seasonally inundated marsh. Canopy at about 10 m. Thin leaf litter, rotten logs notably rare, forest floor with hard packed ferruginous soils.
AIG	18	16-21 Feb. 2009	48°12’1.11”E 18°29’33.18”S 1054 m	48°12’1.44”E 18°29’33.29”S 1053 m	Open canopy degraded humid forest. Dense scrub especially along the edges of streams. Canopy at 12 m. Forest floor dominated by grasses and dense leaf litter; rotten logs present.
	19	16-21 Feb. 2009	48°12’2.63”E 18°29’31.41”S 1070 m	48°12’2.19”E 18°29’30.59”S 1079 m	Semi-open canopy and partially degraded humid forest on slope with tracks of selectively removed trees. Canopy at 10-12 m. Dense leaf litter, abundant moss and lichen, and not particularly dense understory.
AID	11	26 Jan.- 1 Feb. 2009	48°11’44.22”E 18°28’58.84”S 1098 m	48°11’43.4”E 18°28’58.94”S 1096 m	Open degraded ericoid forest. Exposed rock area of hard packed ferruginous soils. Seasonal swamp.
TBE	4	18-24 Jan. 2009	48°12’5.54”E 18°28’25.15”S 1040 m	48°12’6.27”E 18°28’25.58”S 1037 m	Largely closed canopy and undisturbed humid forest in valley. Emergent trees reaching 15-20 m. Dense leaf litter with grasses, ferns, and rotten logs, as well as dense herbaceous understory.
	5	18-24 Jan. 2009	48°12’3.21”E 18°28’24.96”S 1076 m	48°12’3.79”E 18°28’25.65”S 1070 m	Open canopy humid forest on slope. Canopy at 15 m with a few taller emergent trees. Forest floor covered by relatively dense leaf litter, understory, and ferns; rotten logs present.
	6	18-24 Jan. 2009	48°11’45.49”E 18°28’25.22”S 1114 m	48°11’44.88”E 18°28’26.07”S 1110 m	Open canopy humid forest on slope, dominated by *Uapaca* reaching 7-10 m. Very thin leaf litter and understory trees scarce.
	7	18-24 Jan. 2009	48°11’44.23”E 18°28’27.81”S 129 m	48°11’43.94”E 18°28’28.74”S 1141 m	Almost closed canopy and partially disturbed humid forest in slope and valley formation. Canopy at 15-20 m with some larger emergent trees. Dense leaf litter and herbaceous understory plants; rotten logs present.

Table 1. (cont.)

Type of vegetational formation	Line	Period in use	Geographical coordinates latitude S, longitude E, elevation		Ecological description
			Start	End	
TIG	1	9-15 Jan. 2009	48°11'35.05"E 18°28'32.27"S 1095 m	48°11'35.37"E 18°28'31.44"S 1100 m	Partially intact open canopy humid forest on slope. Canopy at about 15 m. Dense leaf litter associated with some grass cover in the understory; rotten logs not present.
	2	9-15 Jan. 2009	48°11'31.38"E 18°28'31.94"S 1080 m	48°11'30.63"E 18°28'31.62"S 1069 m	Relatively degraded open canopy humid forest in valley; cut tree trunks present. Canopy at 15-20 m. Thin leaf litter with some grasses and ferns.
	3	9-15 Jan. 2009	48°11'27.35"E 18°28'31.27"S 1059 m	48°11'26.98"E 18°28'30.36"S 1052 m	Closed canopy degraded humid forest. Canopy at 10-15 m with emergent trees reaching 15-20 m. Dense understory with spiny vines. Forest floor with sparse covering of grasses and leaf litter.
TID	20	16-21 Feb. 2009	48°12'3.64"E 18°29'29.65"S 1108 m	48°12'4.25"E 18°29'29.07"S 1105 m	Semi-open canopy and partially degraded humid forest on ridge with tracks of old selectively removed trees. Canopy at 12-15 m. Dense leaf litter, less dense understory with *Dracaena*, *Cyathea*, and *Pandanus*. Epiphytes notably abundant.
ZBE	15	6-11 Feb. 2009	48°12'48.60"E 18°11'5.37"S 998 m	48°12'49.18"E 18°28'57.40"S 1009 m	Semi-open canopy humid forest in valley along small stream. Canopy at 15-20 m. Forest floor covered by dense leaf litter, grasses, and a few rotten logs. Ferns and herbaceous vegetation notably common.
	16	6-11 Feb. 2009	48°12'48.43"E 18°28'57.47"S 1005 m	48°12'49.99"E 18°28'58.30"S 1011 m	Almost closed canopy humid forest on slope, in close proximity to narrow valley with temporary stream. Canopy at 15-20 m. Dense leaf litter and rotten logs covered by moss and lichens. *Pandanus* and *Cyathea* notably common, and understory not particularly dense.
	17	6-11 Feb. 2009	48°12'49.97"E 18°28'55.49"S 1006 m	48°12'50.26"E 18°28'56.42"S 1015 m	Semi-open canopy and partially degraded humid forest on ridge with tracks of old selectively removed trees. Understory relatively sparse, dense leaf litter, rotten logs, and *Pandanus*.
ZIG	21	16-21 Feb. 2009	48°11'7.58"E 18°29'34.91"S 1159 m	48°11'6.61"E 18°29'34.84"S 1145 m	Degraded humid forest on slope and crest formation. Semi-closed canopy with abundant bamboo and vines (some spiny). Canopy at 15 m. Notably open understory, thin leaf litter, and no rotten logs.
	22	16-21 Feb. 2009	48°11'8.70"E 18°29'31.99"S 1125 m	48°11'7.94"E 18°29'31.52"S 1115 m	Semi-open canopy and partially degraded humid forest in valley along stream with tracks of old selectively removed trees. Canopy at 15 m. Understory with little vegetation, few rotten logs, and sparse leaf litter.
	23	16-21 Feb. 2009	48°11'9.24"E 18°29'30.44"S 1110 m	48°11'8.70"E 18°29'30.23"S 1099 m	Degraded and semi-open humid forest in valley and in close proximity to marsh habitat, with rotten cut tree trunks. Canopy at 15 m. Understory with little vegetation, no rotten logs, and sparse leaf litter.
ZID	12	6-11 Feb. 2009	48°12'46.98"E 18°28'57.39"S 982 m	48°12'46.58"E 18°28'58.11"S 987 m	Open degraded humid forest in valley along a small stream. Canopy at 20-25 m. Ferns and herbaceous vegetation common in relatively open understory, as well as numerous large fallen trees, epiphytes, and bamboo. Sparse leaf litter.
	13	6-11 Feb. 2009	48°12'45.46" 18°28'57.50" 1027 m	48°12'44.79"E 18°28'58.33"S 1023 m	Semi-degraded humid forest on ridge, with semi-open canopy and evidence of former timber exploitation. Canopy at 15-20 m. Understory largely open, dense leaf litter, and with rotten logs.
	14	6-11 Feb. 2009	48°12'44.35" 18°28'58.48" 1030 m	48°12'43.31"E 18°28'58.66"S 1028 m	Open canopy and degraded humid forest on slope and ridge formation, with clear evidence of former timber exploitation. Canopy at 15-20 m. Understory quite dense, and forest floor dominated by grass, with notable leaf letter, and rotten logs.

The placement of the different pit-fall lines and the number of lines installed in a given habitat is a function of the level of heterogeneity of a zone (= habitat type). In cases, when a given habitat showed considerable ecological variation, three lines were installed; one in a valley bottom, another on a slope, and the third on a hillcrest. In the case of the Transitional Benchmark habitat, a fourth line was established to sample a distinct homogenous vegetational community dominated by *Uapaca* trees (Family Euphorbiaceae). However, in the Azonal Impacted Degraded habitat, which is largely a homogeneous formation of *Erica* (Family Ericaceae) scrub growing on a hard-packed and heavily oxidized ferrous lateritic soil that is extremely difficult to dig in, only a single line was installed.

Measures of relative abundance

In order to provide a quantitative measure of individual species within each habitat type, specifically relative abundance, a calculated index was used. The level of sampling effort and the level of ecological heterogeneity within each habitat type were considered when calculating this index. The relative abundance of the majority of reptile and amphibian species was estimated using the following formula:

$$Ar = ni / N \times 100$$

where ni is the number of individuals of a given species censused within a given habitat type based on a defined sampling effort and N is the total number individuals of all species censused in the same habitat type.

These relative abundance measures are expressed as a percentage. Sampling effort is defined as 10 human-working hours per transect line (based on five hours during the day and five hours during the night). The census process was only conducted in one direction along the transect line to avoid double-counting of individuals. The total of the maximum numbers of individuals for each species found during the 10 human-working hour searches within each transect line represents the number of individuals of this species (ni) within the surveyed habitat type. This maximum number was used for the calculation of the total number individuals (N) of all species as well as for the estimation of relative abundance within a given habitat type.

In several cases, for common diurnal species, the sampling effort system was modified, for which the mean number of individuals encountered along 100 m of survey trail was estimated. This change was associated with time constraints as counting the actual number of common species along complete transects would have been too time consuming. However, the balance of the other taxa 10 human-working hour search for the transect line was respected. In some cases, associated with the counts along the sampling itinerary, the estimation might be conservative. In the case of refuge dwelling species, particularly those occupying the phytotelms of *Pandanus*, the estimation of relative abundance is more complicated. For this habitat, the average number per species per *Pandanus* tree was evaluated by deriving the average number per 3-4 different *Pandanus* trees. Further, the number censused (ni) corresponds to average number of individuals found in all *Pandanus* trees occurring along the transect trail.

Analysis of specific diversity in the different habitat types

In order to evaluate aspects of species diversity in the herpetological fauna within the study area, the Shannon-Weaver H' index was employed, using the following formula (Magurran, 1988):

$$H' = -\Sigma(ni/N)\log(ni/N)$$

where ni = number of a given species; N = total number of individuals captured.

Further, the Shannon-Weaver index takes into account the distribution of the number of individuals by species or their evenness (E) based on the following formula:

$$E = H'/\log S$$

where S is the total species richness. Evenness measures the abundance/rarity of the different taxa.

When constituent species have similar proportions, the E value is near 1, and in cases where they are dissimilar, composed of rare or abundant species, the value decreases.

Analysis of faunal similarity between sites

In order to understand the faunal and biogeographic relationships of the herpetofauna within the different habitat types, the Jaccard Index was used, based on the following formula:

$$I = C / N1 + N2 – C$$

where N_1 = specific richness in habitat type 1, N_2 = specific richness in habitat type 2, and C = number of species occurring in both habitats.

The associated coefficients were entered into the “Cluster Analysis” program of SYSTAT (Linkage

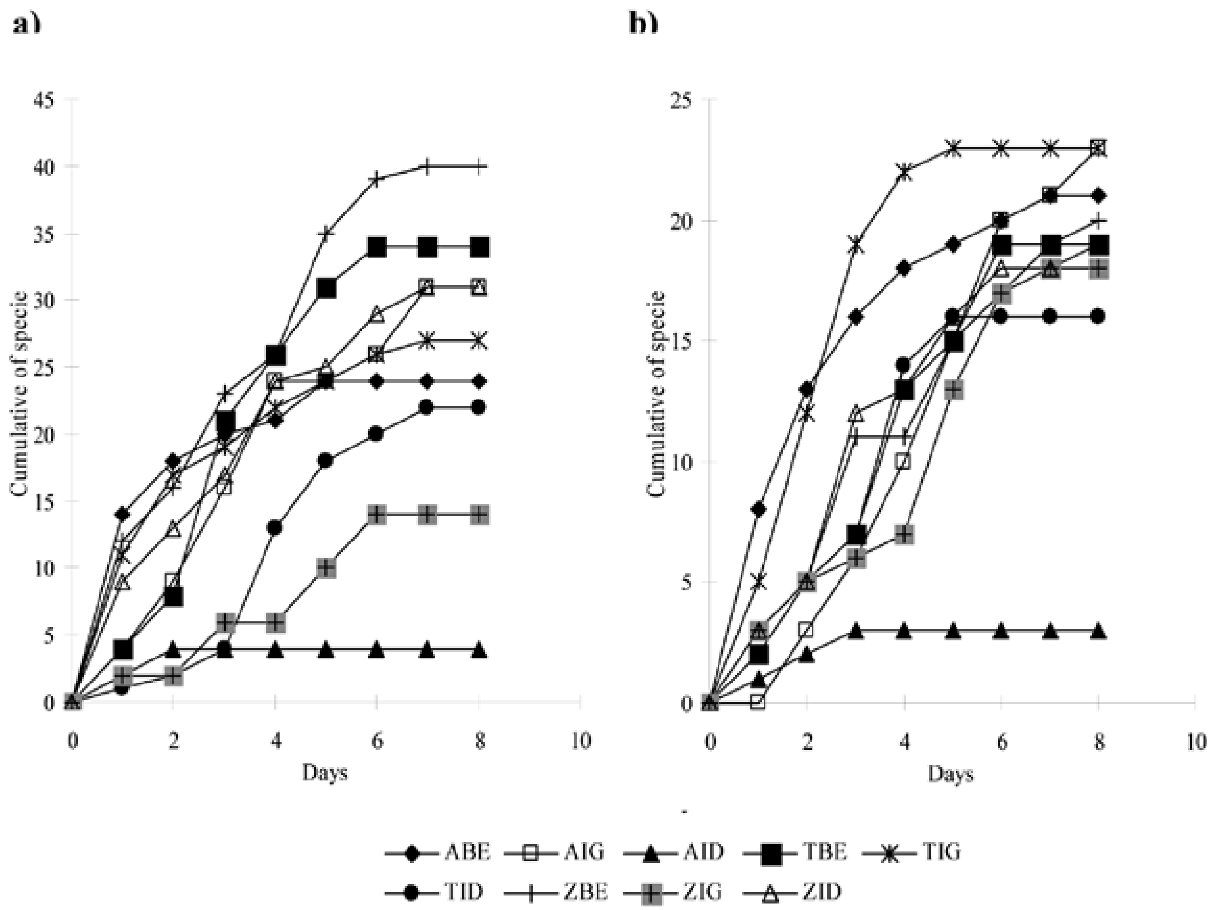

Figure 1. Species accumulation curves (a: amphibians, b: reptiles) for the surveyed species in the nine habitat types in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

= Complete, Distance = Euclidean) to produce a branching diagram illustrating the biogeographic affinities of animals in the different habitat types.

Taxonomy

Herein, higher level and species taxonomy follow Glaw & Vences (2007a). However, identification keys and descriptions from the original sources were often used for species determination. These include for amphibians Glaw *et al*. (2001), Vallan *et al*. (2003), Vences & Glaw (2004) and for reptiles Andreone & Greer (2002) and Vences *et al*. (2004a). Specific scientific names presented in parentheses, and not in italics, indicate an undescribed species mentioned by Glaw & Vences (2007a). Species names preceded by "aff." indicate undetermined taxa that share some morphological characters with the species indicated but their taxonomic identification remains to be determined. The use of the term "n. sp." indicates an undescribed species and "sp." an unidentified species.

Specimen collection, deposition, and other details

A maximum of five individuals per species were collected during the course of this study to serve as reference and voucher specimens of each encountered taxon. These collections follow the research permit N° 328/08/MEFT/SG/DGEF/DSAP/SSE issued by the Direction Générale des Eaux et Forêt. Further, at least one individual per species was photographed in its biotope to document natural coloration.

Collected individuals were anesthetized in a solution of chloro-butanol (chlorotone) and then injected and soaked in 12.5% formaldehyde for at least 10 days. Subsequently, the specimens were rinsed during two to three days in water to remove the formaldehyde and then stored in jars containing 65% ETOH (for amphibians) and 75% ETOH (for reptiles). Further, tissue samples were preserved in small cryogenic tubes containing a solution of EDTA for on-going and future molecular genetic studies.

Individual specimens received a unique field number, all associated tissue samples and other preserved parts, have the same number. Information associated with the ecology and biology of each collected animal was noted in a field catalog, including the type and condition of the habitat where it was found, time, GPS coordinates, elevation (based on both GPS and altimeter readings), and aspects of its behavior, including interspecific interactions. The voucher material is housed in the collection of the Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo. A list of reference specimens used in the specific determinations is provided in Appendix 1.

Results

Species accumulation curves

The species accumulation curves of the inventoried herpetological species for each habitat type are presented for amphibians (Figure 1a) and reptiles (Figure 1b) over the course of the eight-day inventory. In most cases, the accumulation curves did not reach their respective plateaus for most habitats until the sixth survey day, and thereafter, the chance of encountering a previously unrecorded species for the site diminish considerably. In other words, after the sixth day of inventory work in a given habitat the vast majority of locally occurring taxa had been sampled. The exception is the Azonal Impacted Degraded habitat, where the curve reached an asymptote after the second day for amphibians and the third day for reptiles, even though further intensive survey work was conducted within this zone. Obtaining such a plateau after a short period of investigation is best interpreted as depicting a zone of notably low ecological and biological diversity within this homogeneous habitat. Hence, this zone was easy to rapidly inventory with a certain degree of completeness.

Species richness

During the fieldwork conducted in early 2009 in the Ambatovy-Analamay region, a total of 112 species (68 amphibians and 44 reptiles) were inventoried. Amongst these species, 51 (45.5%) have strictly arboreal life styles, and the balance occur in arboreal/terrestrial or aquatic/terrestrial settings. A non-negligible proportion of the local herpetofauna (17/112 species or 15%) are strictly fossorial (living in the ground) and an additional three taxa are at least partially fossorial. Most of these 112 taxa live in forest settings, which, in certain cases, also include the forest edge. In other words, the vast majority of these species inhabit vegetated zones, particularly natural forest.

A few caveats need to be mentioned to place this current study in its proper context. With ongoing herpetological studies on Madagascar, numerous cryptic species have been discovered in recent years, often with the aid of molecular genetic studies (Glaw & Vences, 2007a). It is highly probable that amongst the Ambatovy-Analamay material, undescribed taxa exist. In the upcoming years, laboratory investigations will help to resolve this question for a number of genera. Further, it needs to be emphasized that no single field inventory in forests such as those of Ambatovy-Analamay, no matter how in depth, can capture all of the species richness for a specific group of terrestrial vertebrates. The synthesis of different studies and ongoing investigations, combined with follow-up studies, is the only means to obtain measures of species richness approaching 100%. A detailed list of all reptile and amphibian taxa found during the early 2009 survey, as well as information on their distribution in the nine habitat types, conservation status, distribution, and other life-history traits are presented in Table 2.

The distributional data presented in Table 2, clearly shows that the various taxa are not evenly distributed amongst the nine habitat types. In some cases, there are species with broad distributions and others that are only known from one or two habitats (Figure 2). Further, the species richness in these different habitat types is notably variable.

In general, for each habitat type, the number of amphibian species is greater than reptile species, which is typical of the eastern humid forests of Madagascar. Amongst the three habitat categories (azonal, transitional, and zonal), measures of species richness did not differ considerably within each of the habitat types (benchmark, impacted good quality, and impacted degraded), with the exception of the azonal category. The differentiation of these habitat types is a function of their vegetational structure and composition, and most importantly, state of degradation. However, this classification was not in all cases directly correlated with the composition and species richness of the herpetological community. The Azonal Impacted Degraded habitat has notably the lowest species richness of any of the nine habitat types.

Spatial distribution in the nine habitat types

Even though the early 2009 inventories cannot be considered exhaustive with regards to measures of species richness, they are certainly useful to

Table 2. List of the species of amphibians and reptiles collected during the inventories of nine different habitat types in the Ambatovy-Analamay region. Key to different entries **--** biotope & life history: V (valley), VE (valley in immediate vicinity of water course), VS (valley & slope); SC (slope & crest), VSC (valley, slope & crest); IUCN Status: LC (Least Concern), CR (Critically Endangered), EN (Endangered), VU (Vulnerable), DD (Data Deficient), NE (Not Evaluated); Distribution: CE (central east), NE (northeast), SE (southeast); Habitat types: ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

	Characteristics				**Habitat Types**								
	Habitat	**Biotope & life history**	**IUCN status**	**Distribution & endemicity**	**ABE**	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Class AMPHIBIA													
Family HYPEROLIIDAE													
Heterixalus betsileo	Bush, marsh,	SC, arboreal	LC	Center			*	*					
Family MANTELLIDAE													
Subfamily BOOPHINAE													
Boophis albilabris	Forest	VS, arboreal	LC	Madagascar				*					
Boophis boehmei	Forest	VE, arboreal	LC	CE				*	*		*		
Boophis erythrodactylus	Forest	VE, arboreal	LC	Center	*								
Boophis feonnyala	Forest	VE, arboreal	DD	CE		*							
Boophis goudoti	Forest	VE, arboreal	LC	Center	*						*		*
Boophis guibei	Forest	VS, arboreal	LC	CE				*			*		*
Boophis idae	Bush, marsh	SC, terrestrial, arboreal	LC	CE-SE			*						
Boophis luteus	Forest	VE, arboreal	LC	Madagascar	*	*		*		*	*		*
Boophis madagascariensis	Forest	VSC, arboreal	LC	Madagascar	*			*	*		*	*	*
Boophis picturatus	Forest	VE, arboreal	LC	CE, SE		*					*		*
Boophis pyrrhus	Forest	VE, arboreal	LC	East coast	*	*		*		*	*		*
Boophis reticulatus	Forest	VE, arboreal	LC	Center, CE	*	*		*			*		*
Boophis sibilans	Forest	VE, arboreal	LC	CE-NE					*				
Boophis tephraeomystax	Forest	SC, arboreal	LC	Madagascar					*				
Boophis sp.	Forest	SC, arboreal	NE	Madagascar								*	
Subfamily LALIOSTOMINAE													
Aglyptodactylus madagascariensis	Forest	VSC, terrestrial	LC	East coast	*	*		*	*	*	*	*	*
Subfamily MANTELLINAE													
Blommersia blommersae	Forest, marsh	V, semi-aquatic	LC	East coast				*		*	*	*	
Blommersia domerguei	Open marsh	Semi-aquatic	LC	Center			*						
Blommersia grandisonae	Forest	VS, terrestrial, herbaceous vegetation	LC	East coast	*						*	*	*
Blommersia sarotra	Forest, marsh	V, terrestrial	DD	CE									*
Gephyromantis asper	Forest	VS, terrestrial, arboreal	LC	CE, NE				*	*	*	*		*
Gephyromantis boulengeri	Forest	VSC, terrestrial, arboreal	LC	East coast	*	*		*	*	*	*	*	*
Gephyromantis cornutus	Forest	VE, arboreal	DD	CE						*			
Gephyromantis sculpturatus	Forest	VS, terrestrial, arboreal	LC	CE, Center				*					

Table 2. (cont.)

	Characteristics				Habitat Types								
	Habitat	**Biotope & life history**	**IUCN status**	**Distribution & endemicity**	**ABE**	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Gephyromantis thelenae	Forest	SC, terrestrial, arboreal	DD	CE							*		
Gephyromantis aff. *malagasius*	Forest	VS, arboreal	NE	"CE"					*	*	*		
Guibemantis depressiceps	Forest	VS, arboreal	LC	CE					*				
Guibemantis liber	Forest	VS, *Pandanus* phytotelms	LC	Madagascar	*	*		*		*		*	*
Guibemantis pulcher	Forest	VSC, *Pandanus* phytotelms	LC	East coast		*		*	*		*		
Guibemantis timidus	Forest	VS, arboreal	NE	East coast		*							
Guibemantis tornieri	Forest	VE, arboreal	LC	CE, SE		*							
Guibemantis aff. *albolineatus*	Forest	VS, *Pandanus* phytotelms	NE	CE	*			*	*	*	*		
Guibemantis aff. *bicalcaratus*	Forest	VS, *Pandanus* phytotelms	NE	"CE"		*				*			
Guibemantis aff. *punctatus*	Forest	VS, *Pandanus* phytotelms	NE	"CE"	*	*			*				
Mantella aurantiaca	Forest	VS, terrestrial	CR	CE	*	*					*		
Mantella baroni	Forest	VS, terrestrial	LC	CE, SE	*	*		*	*		*		*
Mantella crocea	Forest	VE, terrestrial	EN	CE, Center	*								
Mantella aff. *milotympanum*	Forest	SC, terrestrial		CE		*							
Mantidactylus aerumnalis	Forest	VE, terrestrial	LC	CE, SE				*			*		
Mantidactylus argenteus	Forest	VE, arboreal	LC	East coast	*	*		*			*		*
Mantidactylus betsileanus	Forest	VE, semi-aquatic	LC	CE	*	*		*	*	*	*	*	*
Mantidactylus aff. *betsileanus*	Forest	VS, semi-aquatic	NE	"CE, SE"		*							
Mantidactylus biporus	Forest	VE, semi-aquatic	LC	CE				*		*	*		*
Mantidactylus cowani	Forest	VE, semi-aquatic	NE	CE		*							
Mantidactylus grandidieri	Forest	VE, aquatic	LC	East coast		*		*	*		*		*
Mantidactylus femoralis	Forest	VE, river banks (ground, roots, branches)	LC	Madagascar	*	*		*	*		*		*
Mantidactylus lugubris	Forest	VE, rock-dwelling, aquatic	LC	CE	*			*					
Mantidactylus melanopleura	Forest	VE, terrestrial	LC	East coast	*			*	*	*	*	*	*
Mantidactylus opiparis	Forest	VE, terrestrial	LC	Madagascar	*			*		*	*		*
Mantidactylus zipperi	Forest	VE, terrestrial	LC	CE		*							
Spinomantis aglavei	Forest	VE, arboreal	LC	East coast		*		*	*	*	*		*
Family MICROHYLIDAE													
Subfamily COPHYLINAE													
Anodonthyla boulengeri	Forest	SC, arboreal	LC	East coast					*			*	
Platypelis barbouri	Forest	VS, arboreal	LC	CE, NE				*		*	*		*
Platypelis pollicaris	Forest	VS, arboreal	DD	CE							*		*
Platypelis tuberifera	Forest	VSC, arboreal	LC	East coast		*		*	*	*	*		*
Platypelis n. sp.	Forest	VS, arboreal	NE	Madagascar						*			

Table 2. (cont.)

	Characteristics				Habitat Types								
	Habitat	**Biotope & life history**	**IUCN status**	**Distribution & endemicity**	**ABE**	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Plethodontohyla guentheri	Forest	VS, terrestrial	DD	NE		*					*		
Plethodontohyla mihanika	Forest	SC, terrestrial, arboreal	LC	CE		*		*	*	*	*	*	*
Plethodontohyla notosticta	Forest	VS, terrestrial	LC	East coast		*			*		*	*	*
Plethodontohyla ocellata	Forest	VS, terrestrial, fossorial	LC	East coast							*		*
Rhombophryne alluaudi	Forest	VSC, terrestrial, fossorial	LC	Center, East coast		*		*	*		*		*
Rhombophryne coronata	Forest	VS, terrestrial, fossorial	VU	CE		*		*	*	*	*		
Stumpffia "kibomena"	Forest	VS, terrestrial, fossorial	NE	"CE"	*	*		*	*	*	*		
Subfamily SCAPHIOPHRYNINAE													
Paradoxophyla palmata	Forest	VE, terrestrial	LC	East coast									*
Scaphiophryne marmorata	Forest	SC, terrestrial	VU	CE	*				*		*	*	*
Scaphiophryne spinosa	Forest	SC, terrestrial	LC	East coast	*			*	*		*	*	*
Family PTYCHADENIDAE													
Ptychadena mascareniensis	Open bush, marsh	SC, terrestrial, aquatic	LC	Not endemic			*						
Total: 68					**24**	**31**	**4**	**34**	**27**	**22**	**40**	**14**	**31**
Class REPTILIA													
Family GEKKONIDAE													
Ebenavia inunguis	Forest	VS, arboreal	NE	Madagascar	*								
Lygodactylus guibei	Forest	VSC, arboreal	NE	CE	*	*		*	*		*		*
Microscalabotes bivittis	Forest	VS, arboreal	NE	CE, NE		*			*				
Paroedura gracilis	Forest	SC, arboreal	NE	CE, NE		*				*		*	*
Phelsuma lineata	Forest	VSC, arboreal	NE	Madagascar	*	*		*	*	*	*	*	*
Phelsuma quadriocellata	Forest	VSC, arboreal	NE	Madagascar	*	*		*	*	*	*	*	*
Uroplatus phantasticus	Forest	VSC, arboreal	NE	Center, CE	*	*		*	*	*	*	*	*
Uroplatus pietschmanni	Forest	SC, arboreal	NE	CE				*	*			*	
Uroplatus sikorae	Forest	VSC, arboreal	NE	Madagascar	*	*		*	*	*	*	*	*
Family SCINCIDAE													
Amphiglossus astrolabi	Forest	VE, aquatic	NE	East coast		*							
Amphiglossus frontoparietalis	Forest	VE, terrestrial, fossorial	NE	East coast							*		*
Amphiglossus macrocercus	Forest	VSC, terrestrial, fossorial	NE	Center					*		*	*	*
Amphiglossus mandady	Forest	VS, terrestrial, fossorial	NE	NE	*								
Amphiglossus ornaticeps	Forest	VS, terrestrial, fossorial	NE	Madagascar							*		
Amphiglossus "phaeurus"	Forest	VS, terrestrial, fossorial	NE	Madagascar		*						*	
Madascincus ankodabensis	Forest	VS, terrestrial, fossorial	NE	Center, SE	*								
Madascincus melanopleura	Forest	VSC, terrestrial	NE	Madagascar	*	*		*	*	*	*	*	*
Madascincus mouroundavae	Forest	VS, terrestrial, fossorial	NE	Madagascar	*	*		*	*	*	*	*	*
Madascincus "baeus"	Forest	SC, terrestrial, fossorial	NE	CE				*	*		*		*

Table 2. (cont.)

	Characteristics				Habitat Types								
	Habitat	Biotope & life history	IUCN status	Distribution & endemicity	ABE	AIG	AID	TBE	TIG	TID	ZBE	ZIG	ZID
Madascincus sp.	Forest	SC, terrestrial, fossorial	NE	Madagascar	*	*							
Trachylepis boettgeri	Open, marsh	SC, terrestrial	NE	Center			*						
Trachylepis gravenhorstii	Forest edge	SC, terrestrial	NE	Madagascar	*	*	*	*	*	*		*	
Family CHAMAELEONIDAE													
Brookesia superciliaris	Forest	VSC, terrestrial, arboreal	NE	East coast				*	*	*	*	*	*
Brookesia thieli	Forest	VSC, terrestrial, arboreal	NE	CE, NE	*	*		*	*	*	*	*	*
Calumma gastrotaenia	Forest	VS, arboreal	NE	Madagascar								*	
Calumma nasutum	Forest	VSC, arboreal	NE	Madagascar	*	*		*	*	*	*	*	*
Furcifer willsii	Forest	SC, arboreal	NE	Madagascar					*				
Family GERRHOSAURIDAE													
Zonosaurus aeneus	Forest	VSC, terrestrial	NE	Madagascar	*	*		*	*	*	*	*	*
Zonosaurus madagascariensis	Forest	VE, terrestrial	LC	Madagascar		*					*		
Family COLUBRIDAE													
Thamnosophis epistibes	Forest	VSC, terrestrial	NE	East coast	*	*		*	*		*		
Thamnosophis infrasignatus	Forest	VS, terrestrial	NE	East coast NW	*			*					
Compsophis infralineatus	Forest	VE, arboreal	NE	Center, SE						*			
Compsophis laphystius	Forest	VE, arboreal	NE	East coast					*				
Ithycyphus perineti	Forest	VSC, arboreal	NE	East coast, N	*	*			*				
Leioheterodon madagascariensis	Forest, edge	SC, terrestrial	NE	Madagascar	*	*			*	*			
Leioheterodon modestus	Bush	SC, terrestrial	NE	Madagascar			*						
Liophidium rhodogaster	Forest	VS, terrestrial, fossorial	NE	East coast				*	*		*		*
Liophidium torquatum	Forest	SC, terrestrial	NE	Madagascar		*							
Pseudoxyrhopus heterurus	Forest	VE, terrestrial, fossorial	NE	East coast									*
Pseudoxyrhopus oblectator	Forest	VS, terrestrial, fossorial	NE	Center				*					
Pseudoxyrhopus tritaeniatus	Forest	VE, terrestrial, fossorial	NE	East coast							*		*
Stenophis arctifasciatus	Forest	SC, arboreal	NE	East coast, N								*	
Stenophis betsileanus	Forest	VSC, arboreal	NE	East coast, N	*	*				*		*	
Family BOIDAE													
Sanzinia madagascariensis	Forest	VSC, arboreal	VU	East coast	*	*		*	*	*	*		*
Total: 44					**21**	**23**	**3**	**19**	**23**	**16**	**20**	**18**	**19**
Amphibians & Reptiles: 112					**45**	**54**	**7**	**53**	**50**	**38**	**60**	**32**	**50**

Table 3. Species distribution with respect to the nine different habitat types in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

	Habitat Types (HT)								
	ABE	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Species restricted to specific habitat	5 (11.1%)	9 (16.4%)	5 (71.4%)	3 (5.7%)	5 (10.0%)	3 (7.9%)	2 (3.3%)	3 (9.4%)	3 (6.1%)
Species shared with 1 other habitat	3 (6.7%)	7 (12.7%)	1 (14.3%)	4 (7.5%)	2 (4.0%)	1 (2.6%)	6 (10.0%)	2 (6.3%)	3 (6.1%)
Species shared with 2 other habitats	4 (8.9%)	4 (7.3%)	0 (0.0%)	3 (5.7%)	5 (10.0%)	1 (2.6%)	6 (10.0%)	1 (3.1%)	3 (6.1%)
Species shared with more than 2 habitats	33 (73.3%)	35 (64.6%)	1 (14.3%)	43 (81.1%)	38 (76.0%)	33 (86.8%)	46 (76.7%)	26 (81.3%)	40 (81.6%)
Total	**45**	**55**	**7**	**53**	**50**	**38**	**60**	**32**	**49**

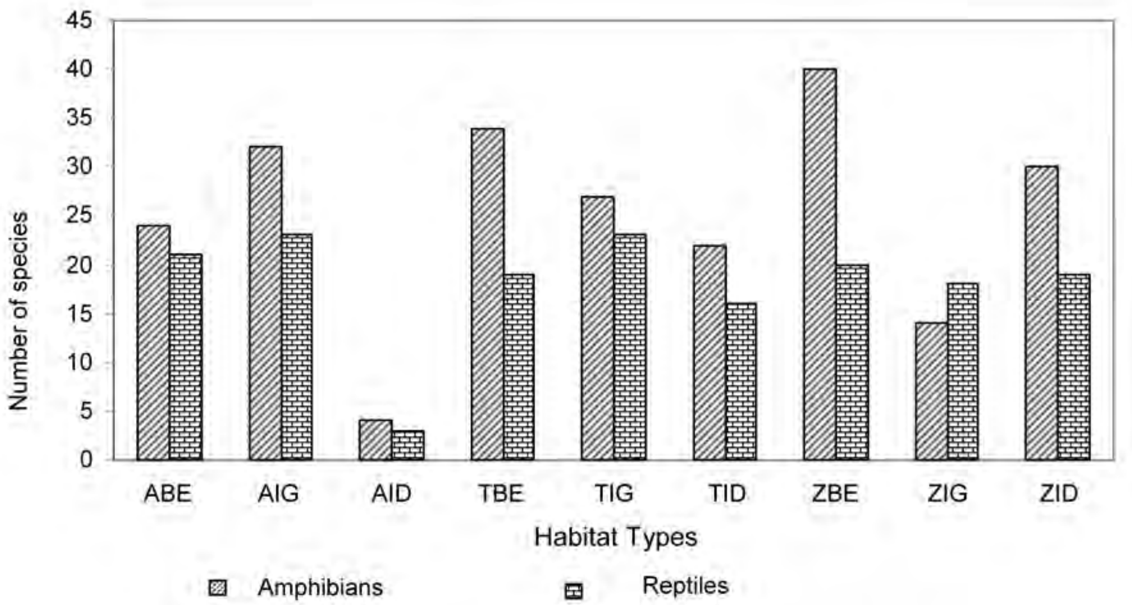

Figure 2. Species richness of reptiles and amphibians in each of the nine habitat types in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

characterize the distribution of the various taxa within the nine habitat types. Numerous species have very limited distributions within the different habitat types. Summaries on the number of species unique to a given habitat and aspects of those occurring in different habitats are presented in Table 3.

With the exception of the Azonal Impacted Degraded habitat, more than 60% of the identified species occur in at least four of the habitat types. On the other hand, a non-negligible percentage (3.3% to 16.4%) of the species only occur in a single habitat. In the case of the Azonal Impacted Degraded habitat, this figure is 71.4%. Figure 3 illustrates a series of diagrams, by habitat, of the levels of uniqueness and shared species between the nine different habitats. Hence, even given the close proximity of these nine different habitats in a geographic sense, each possesses its own faunal particularities.

Endemism and distribution

With the exception of the frog *Ptychadena mascareniensis*, all of the herpetofauna identified from the Ambatovy-Analamay region consists of endemic species to Madagascar, most of them confined to the eastern humid forests. Of these taxa, more than 30% are endemic to the central or central eastern portion of the island. There are also numerous species with broad distributions, encompassing much of the eastern portion of the island, from the northern to southern extremes. It is important to note that there are several species that are presently being described as new to science that are only known from the forested areas of Moramanga and Andasibe, several of which have been mentioned as morphospecies by Glaw & Vences (2007a). These species with provisional names in non-italics and in quotation marks are presented in Table 2.

Relative abundance

The results of the quantitative evaluation of abundance measures for the inventoried taxa are presented in Table 4. The reported values represent measures of relative abundance for each species by habitat type with respect to all of the species encountered in the same habitat, and are hence given as a percentage. In general, there are few cases of dominant species in a given habitat, the exception being in the Azonal Impacted Degraded habitat, where a couple of taxa are dominant.

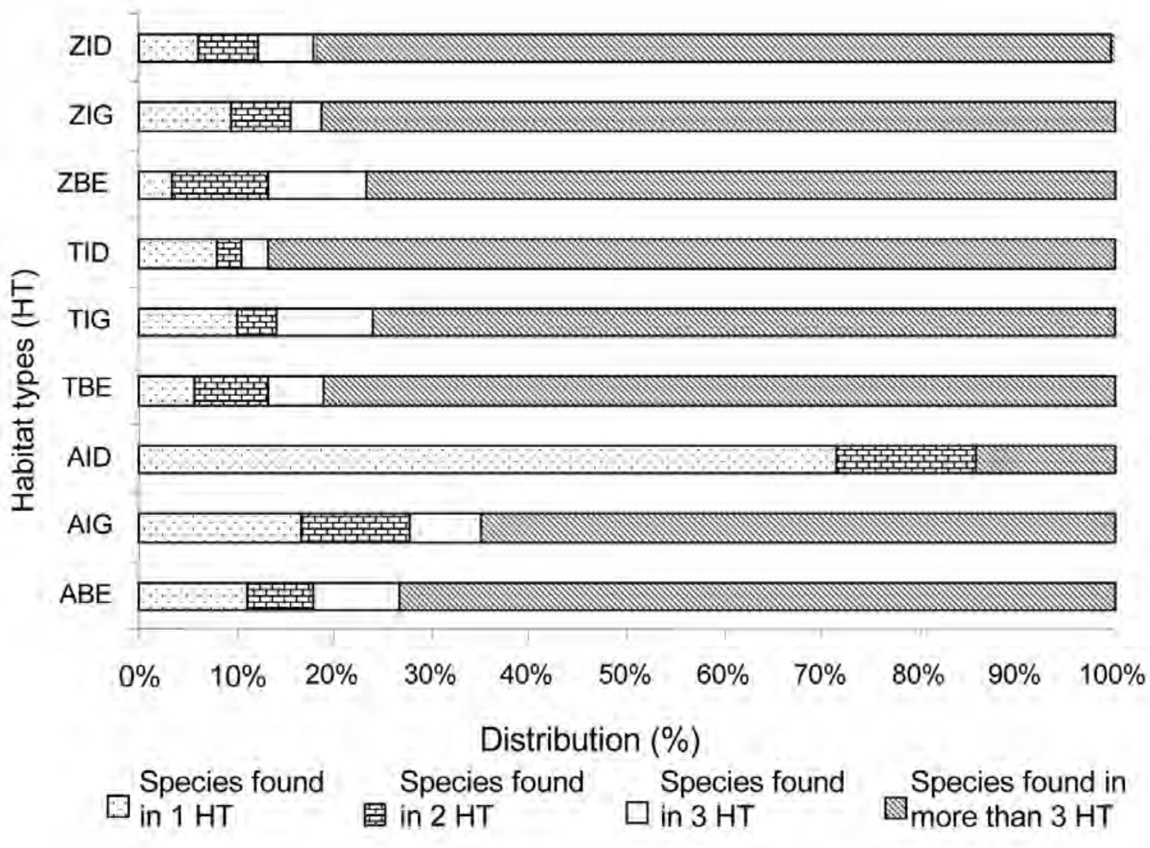

Figure 3. Distribution (by percent occurrence) of the herpetofauna community amongst the nine different habitat types (HT) in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

Table 4. Relative abundance (in %) of the herpetofauna in the nine different habitat types in the Ambatovy-Analamay region. See the Methods section (p. 104) for an explanation of how the data were quantified. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

	Azonal			Transitional			Zonal		
	ABE	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Amphibians									
Heterixalus betsileo			2.41	0.23					
Boophis albilabris				0.46					
Boophis boehmei				2.28	3.13		2.03		
Boophis erythrodactylus	4.55								
Boophis feonnyala		0.66							
Boophis goudoti	3.03						1.01		0.88
Boophis guibei				0.68			0.61		0.88
Boophis idae			4.82						
Boophis luteus	3.03	1.65		3.42		1.94	2.03		1.47
Boophis madagascariensis	2.42			2.28	1.56		2.03	2.56	
Boophis picturatus		0.33					0.41		0.59
Boophis pyrrhus	6.06	3.30		2.28		1.94	4.06		4.41
Boophis reticulatus	4.55	4.95		1.14			3.04		2.94
Boophis sibilans					1.56				
Boophis tephraeomystax					0.31				
Boophis sp.								0.51	
Aglyptodactylus madagascariensis	7.58	8.25		6.85	8.75	7.75	6.09	12.82	8.82
Blommersia blommersae	3.03			3.42		1.94	3.04	5.13	
Blommersia domerguei			24.10						
Blommersia grandisonae							2.03	5.13	2.94
Blommersia sarotra									1.47
Gephyromantis asper				0.91	0.63	1.16	1.01		0.88
Gephyromantis boulengeri	7.58	6.60		7.99	10.94	11.63	7.10	10.26	8.82
Gephyromantis cornutus						1.55			
Gephyromantis sculpuratus				0.23					
Gephyromantis thelenae							1.01		
Gephyromantis aff. *malagasius*					1.25	1.16	1.01		
Guibemantis depressiceps					0.31				
Guibemantis liber	1.52	1.65		1.83		3.88		2.56	1.18
Guibemantis pulcher		2.31		2.28	3.13		3.04		
Guibemantis timidus		0.33							
Guibemantis tornieri		0.33							
Guibemantis aff. *albolineatus*	1.52			2.28	3.13	3.88	3.04		
Guibemantis aff. *bicalcaratus*		1.65				3.88			
Guibemantis aff. *punctatus*	0.91	1.65			3.13				
Mantella aurantiaca	0.30	0.99					2.03		
Mantella baroni	4.55	4.95		1.14	1.25		3.04		2.94
Mantella crocea	0.91								
Mantella aff. *milotympanum*		0.99							
Mantidactylus aerumnalis				0.91			1.01		
Mantidactylus argenteus	1.52	1.98		0.46			0.81		1.18
Mantidactylus betsileanus	1.82	2.31		2.28	1.25	1.94	2.03	1.54	2.94
Mantidactylus aff. *betsileanus*		1.65							
Mantidactylus biporus				2.28		1.94	1.01		1.47
Mantidactylus cowani		0.33							
Mantidactylus grandidieri		1.65		0.68	0.94		0.61		0.88
Mantidactylus femoralis	1.52	2.64		1.37	1.25		2.03		1.47
Mantidactylus lugubris	0.91	0.66		0.68					
Mantidactylus melanopleura	2.42			1.37	1.56	1.55	2.03	2.56	1.47
Mantidactylus opiparis	1.52			1.14		1.16	1.01		1.18
Mantidactylus zipperi		1.32							
Spinomantis aglavei		1.65		3.42	0.94	1.94	2.03		1.76
Anodonthyla boulengeri					1.56			1.54	
Platypelis barbouri				0.23		0.78	0.61		1.18
Platypelis pollicaris							0.20		0.29
Platypelis tuberifera		2.64		3.42	3.13	1.94	2.03		2.94

Table 4. (cont.)

	Azonal			Transitional			Zonal		
	ABE	**AIG**	**AID**	**TBE**	**TIG**	**TID**	**ZBE**	**ZIG**	**ZID**
Platypelis n. sp.						0.78			
Plethodontohyla guentheri		0.66					0.20		
Plethodontohyla mihanika		1.65		1.60	1.25	1.94	0.41	1.03	1.18
Plethodontohyla notosticta		0.99			0.94		0.41		0.29
Plethodontohyla ocellata							0.41		0.29
Rhombophryne alluaudi		2.31		2.51	0.63		2.23		2.94
Rhombophryne coronata		0.33		1.14	0.63	1.16	0.41		
Stumpffia “kibomena”	1.52	0.66		2.97	1.88	3.10	0.61		
Paradoxophyla palmata									0.29
Scaphiophryne marmorata	0.91				0.31		0.41	2.05	1.18
Scaphiophryne spinosa	1.21			1.14	0.63		0.81	0.51	1.18
Ptychadena mascareniensis			18.07						
Reptiles									
Ebenavia inunguis	0.30								
Lygodactylus guibei	1.52	1.65		0.68	0.94		0.61		0.88
Microscalbotes bivittis		0.66			0.94				
Paroedura gracilis		0.99				1.16		1.54	0.29
Phelsuma lineata	2.42	1.65		2.28	3.13	3.88	3.04	5.13	2.94
Phelsuma quadriocellata	2.12	1.65		2.28	3.13	3.88	3.04	5.13	2.94
Uroplatus phantasticus	0.91	0.99		0.68	0.94	3.10	2.03	2.56	2.94
Uroplatus pietschmanni				0.46	0.31			1.54	
Uroplatus sikorae	0.61	1.32		0.68	0.94	3.10	1.01	5.13	1.47
Amphiglossus astrolabi		0.33							
Amphiglossus frontoparietalis							0.20		0.29
Amphiglossus macrocercus					0.31		0.41	1.03	0.59
Amphiglossus mandady	0.30								
Amphiglossus ornaticeps							0.41		
Amphiglossus “phaeurus”		0.33						0.51	
Madascincus ankodabensis	0.61								
Madascincus melanopleura	4.55	3.30		3.42	3.13	3.88	4.06	2.56	5.88
Madascincus mouroundavae	1.52	0.99		0.46	0.31	1.16	0.81	0.51	0.88
Madascincus “baeus”				1.14	1.56		0.61		0.88
Madascincus sp.	2.42	3.30							
Trachylepis boettgeri			12.05						
Trachylepis gravenhorstii	4.55	3.30	36.14	2.28	1.56	1.94		2.56	
Brookesia superciliaris				2.28	4.69	1.94	3.04	2.56	2.94
Brookesia thieli	3.03	2.64		3.42	4.69	3.88	3.04	5.13	4.41
Calumma gastrotaenia								1.03	
Calumma nasutum	1.52	1.32		2.28	2.50	1.94	1.01	5.13	1.47
Furcifer willsii					0.31				
Zonosaurus aeneus	6.06	6.60		6.85	10.94	9.69	5.07	7.69	7.35
Zonosaurus madagascariensis		0.99					0.20		
Thamnosophis epistibes	0.91	1.65		1.14	1.56		1.01		
Thamnosophis infrasignatus	0.61			0.68					
Compsophis infralineatus						0.39			
Compsophis laphystius					0.31				
Ithycyphus perineti	0.30	0.66			0.31				
Leioheterodon madagascariensis	0.30	0.33			0.31	0.39			
Leioheterodon modestus			2.41						
Liophidium rhodogaster				0.68	0.63		0.61		0.59
Liophidium torquatum		0.33							
Pseudoxyrhopus heterurus									0.29
Pseudoxyrhopus oblectator				0.23					
Pseudoxyrhopus tritaeniatus							0.41		0.29
Stenophis arctifasciatus								1.03	
Stenophis betsileanus	0.30	0.33				0.39		1.03	
Sanzinia madagascariensis	0.30	0.66		0.68	0.63	0.39	0.41		0.29

Conservation status

Amongst the 112 species identified in the Ambatovy-Analamay region during the course of this inventory, one species (*Mantella aurantiaca*) is considered by the IUCN (2008) as Critically Endangered, one species (*M. crocea*) as Endangered, and three (*Rhombophryne coronata*, *Scaphiophryne marmorata*, and *Sanzinia madagascariensis*) as Vulnerable. Four of the six species occur in more than two or three habitats, while *M. crocea* is restricted to the Azonal Benchmark habitat.

Diversity

An evaluation of herpetofauna species diversity in each habitat using the Shannon-Weaver H' and Evenness (E) indices is presented in Table 5. Other than the Azonal Impacted Degraded, Transitional Impacted Degraded, and Zonal Impacted Good Quality habitats, the diversity index is close to 1.5. This shows that these communities are not saturated and the local populations are largely in ecological equilibrium. In general, the Evenness (E) measures for most habitat types are relatively elevated, indicating that there are no notably rare or common taxa making up the local herpetofauna communities. Thus, these communities tend to have a more-or-less uniform species composition. The exception is the low Evenness value for the Azonal Impacted Degraded habitat, in which there are a few very common species.

Table 5. Calculated Shannon-Weaver H' and Evenness measures for the reptiles and amphibians occurring in nine habitat types in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

Characteristics	Habitat types								
	ABE	AIG	AID	TBE	TIG	TID	ZBE	ZIG	ZID
Shannon-Weaver index (H`)	1.51	1.59	0.70	1.59	1.49	1.41	1.63	1.35	1.52
Evenness (E)	0.74	0.78	0.34	0.77	0.73	0.69	0.80	0.66	0.74

Faunal similarity

The herpetofauna data matrix of calculated Jaccard Index coefficients of the nine habitat types derived from the presence-absence data (Table 2) are presented in Table 6. These values show the degree of faunal similarity between the sites. Several of the habitat types share a considerable portion of their herpetofauna, for example, the degree of similarity between the Zonal Benchmark and Zonal Impacted Degraded habitats is 0.719; Transitional Benchmark and Zonal Benchmark habitats is 0.632; and Transitional Benchmark and Zonal Impacted Degraded habitats is 0.561. Given that a similarity value of 1.0 between two habitats would be 100% faunal resemblance, the three comparisons presented above, which are the highest values in the data matrix, show a moderate level of faunal similarity. The majority of the other values in the matrix are below 0.5. Hence, several of the habitat types show appreciable faunal differences between them, with largely unique combinations of species.

Table 6. Data matrix of the degree of similarity, based on the Jaccard Index, for the reptiles and amphibians occurring in nine habitat types in the Ambatovy-Analamay region. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

Habitat	ABE	AIG	AID	TBE	TIG	TID	ZBE	ZIG	ZID
ABE	1								
AIG	0.456	1							
AID	0.020	0.016	1						
TBE	0.455	0.427	0.035	1					
TIG	0.388	0.425	0.018	0.530	1				
TID	0.373	0.394	0.023	0.483	0.387	1			
ZBE	0.411	0.425	0	0.632	0.521	0.412	1		
ZIG	0.364	0.265	0.027	0.339	0.379	0.417	0.304	1	
ZID	0.418	0.377	0	0.561	0.449	0.419	0.719	0.367	1

In Figure 4, a dendrogram is presented, derived from the Jaccard Index coefficients, for the nine habitat types presented in Table 6. The outlying habitat is the Azonal Impacted Degraded, which holds a notably different herpetofauna community than the other eight habitats. Two distinct groups can be recognized. The first composed of six different habitat types (Azonal Benchmark, Azonal Impacted Good Quality, Transitional Benchmark, Transitional Impacted Good Quality, Zonal Benchmark, and Zonal Impacted Degraded) and the second of two different habitat types (Transitional Impacted Degraded and Zonal Impacted Good Quality). Within the first group, there are two distinct subgroups, indicating closer faunal similarity to one another than any other habitat types, the first comprised of azonal habitats (Azonal Benchmark and Azonal Impacted Good Quality) and the second subgroup of zonal habitats (Zonal Benchmark and Zonal Impacted Degraded). In summary, the faunal relationships between the eight forest habitats, excluding the Azonal Impacted Degraded, to a large extent follow the habitat categories (azonal, zonal, and transitional), but not in all cases as exemplified by the close faunal similarity between the Transitional Impacted Degraded and Zonal Impacted Good Quality habitats. However, based on the distances between the nodes of the two major groups, as well as the Jaccard Index coefficients, there is a notable level of heterogeneity in the Ambatovy-Analamay herpetofauna.

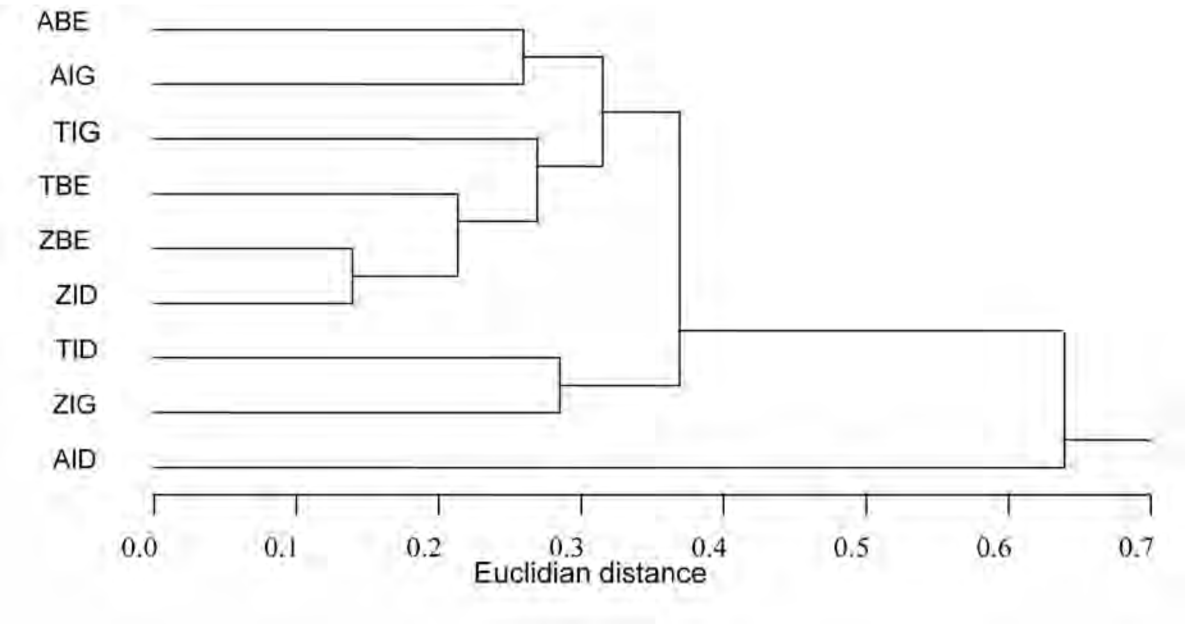

Figure 4. Dendrogram of the faunal affinities of the herpetofauna in the nine different habitat types in the Ambatovy-Analamay region based on the Jaccard Index coefficients presented in Table 6. ABE: Azonal Benchmark, AIG: Azonal Impacted Good Quality, AID: Azonal Impacted Degraded, TBE: Transitional Benchmark, TIG: Transitional Impacted Good Quality, TID: Transitional Impacted Degraded, ZBE: Zonal Benchmark, ZIG: Zonal Impacted Good Quality, and ZID: Zonal Impacted Degraded.

Discussion

Species accumulation curves

The timing of these inventories, during the months of January and February 2009, falls during the warm and rainy season in the central eastern portion of Madagascar, which corresponds to the period of maximum activity for the majority of the regional reptiles and amphibians. Accordingly, many frog species were reproductively active with vocalizing males, copulating pairs, and gravid-laying females being common. For reptiles, no case of mating was observed. However, numerous gravid females were handled and a number of recently laid eggs were found. Hence, reptiles were also actively breeding during the inventory period, but in a less conspicuous manner than frogs.

Implicit in these seasonal aspects, with respect to the regional herpetofauna, is that this period of maximum annual activity (seeking food, establishing and defending territories, seeking mates, etc.) for many species, is the ideal time to conduct inventory work. Hence, it is not surprising that for the majority of habitats, the species accumulation curves reached near asymptotes on the fifth or sixth day of eight days of intensive investigation per habitat type (Figure 1). During long-term monitoring work of the herpetofauna of the littoral forests in southeastern Madagascar, Ramanamanjato (2007) also found that eight days of inventory work at a given site was sufficient to have a good estimation of the local fauna. The most difficult portion of the herpetofauna to document during inventories includes taxa with particular life-history traits, such as those with a very brief reproductive period, canopy dwelling, fossorial, etc.

The low species diversity of certain habitats, such as the Azonal Impacted Degraded, is a direct result of the homogeneity of this habitat, specifically due to no microhabitat variation. The vegetation type was largely monoculture *Erica* sp. (Family Ericaceae) bush with hard packed ferruginous soil. Hence, in this habitat type, the species accumulation curve quickly reached a plateau and the completion of the inventory was relatively simple. The temporary marsh area within the Azonal Impacted Degraded habitat, with herbaceous plant ground cover and hard packed soils, is seasonally important for certain species of frogs, as well as water birds.

Species richness

With 112 species of reptiles and amphibians, the Ambatovy-Analamay region represents an important area with respect to diversity for the Malagasy herpetofauna. To place these levels of species richness into a wider context, the Ambatovy-Analamay fauna is similar to other relatively intensively studied sites such as the Parc National de Marojejy (113 species; 51 amphibians and 62 reptiles) (Raselimanana *et al*., 2000), and is notably richer than the Anjozorobe-Angavo forest corridor (74 species; 38 amphibians and 36 reptiles) (Raselimanana & Andriamampionona, 2007), the Parc National d'Andringitra (92 species; 57 amphibians and 35 reptiles) (Raxworthy & Nussbaum, 1996), and the Ranomafana-Andringitra forested corridor (108 species; 78 amphibians and 30 reptiles) (Rakotomalala *et al*., 2001). On the basis of less extensive inventory work in the nearby Parc National de Mantadia, as compared to our research in the Ambatovy-Analamay region, the former has 43 species (29 amphibians and 14 reptiles) (Rabibisoa *et al*., 2005).

In virtually all of the above-mentioned comparisons, the inventoried zones span a considerable elevational range, certainly more than our sites at Ambatovy-Analamay (990-1120 m), and a greater range of habitats and microhabitats. Hence, this underlines the notable biological richness of the herpetofauna in the Ambatovy-Analamay region and its considerable ecological complexity. The different habitat types in this zone represent a mosaic of vegetational communities, providing many different microhabitats, which directly correlates to its rich herpetofauna.

The Ambatovy-Analamay forests are situated in the central east portion of Madagascar, a zone that has been noted as a biodiversity hotspot for humid forest-dwelling animal groups (Lees, 1996). This has been explained by the regional overlapping of altitudinal distributions of taxa, vegetational types, and existing forest cover, which give rise to exceptional levels of species diversity. These patterns have been labeled as the "Périnet effect" or "mid-domain effect" (Colwell & Lees, 2000) and the local herpetofauna seems to follow the same levels of high species richness (however, see Goodman, p. 26).

Spatial distribution in the nine habitat types

In general, reptiles and amphibians represent two groups of vertebrates that show considerable subtle adaptation to local ecological conditions. This results in the spatial distribution of many taxa being directly linked to certain ecological characteristics of a given zone, particularly with respect to biotopes and microhabitats. Accordingly, the herpetological fauna of a given habitat is closely associated with the vegetational community. Water sources (flowing or stagnant) and other features of the aquatic landscape (streams with or without rocks, waterfalls, etc.), comprise specific habitats for aquatic forms. In five of the inventoried habitats (Azonal Benchmark, Azonal Impacted Good, Transitional Benchmark, Zonal Benchmark, and Zonal Impacted Degraded), there were marshes and permanent water sources. Moreover, the different microhabitats (valleys, slopes, and hillcrests) within the forests of these five habitat types had varying vegetation and structure, which constitute a variety of different ecological settings for reptiles and amphibians, particularly when not too degraded by human activities.

Endemism and distribution

Other than *Ptychadena mascareniensis*, all of the reptile and amphibian species documented in the Ambatovy-Analamay region are endemic to Madagascar (Table 2). A recent phylogeographic study of *P. mascareniensis*, a species that has a wide distribution on portions of the African continent and islands in the western Indian Ocean, found that this species colonized Madagascar naturally and before human colonization of the island (Vences *et al*., 2004b) some 2,400 years ago (Burney *et al*., 2004). Hence, even though this species is not endemic to Madagascar, it should not be considered as introduced.

An analysis of the biogeographic distribution of the species documented in the Ambatovy-Analamay forest found that a considerable proportion have restricted distributions in the central eastern portion of the humid forests, hence they can be considered regional endemics. This is the case for *Mantella aurantiaca*, *M. crocea*, and *M.* aff. *milotympanum*.

In other cases, several taxa have broad distributions across the eastern humid forests, for example from the region of Maroantsetra south to near Tolagnaro. This is, for example, the case of the aquatic skink, *Amphiglossus astrolabi*. Some species are only known from a few localities. *Amphiglossus mandady*, a burrowing skink, was previously only known from the Masoala region (Andreone & Greer, 2002). Its presence in Ambatovy-Analamay extends the distribution range of the species by about 400 km to the south. It was caught in a pit-fall trap placed within closed canopy humid forest at 1000 m altitude in a zone with relatively thick leaf litter and rotten wood covering the soil.

Another uncommon species is the nocturnal burrowing snake, *Pseudoxyrhopus oblectator*. This species was only previously known from the Ranomafana (Ifanadiana) region (Cadle, 1999). With the new locality of Ambatovy-Analamay, its distribution range extends about 300 km to the north. The animal was found in a pit-fall placed on slope in humid forest at about 1060 m and surrounded by thick leaf litter, rotten logs, and organically rich topsoil.

Another important aspect of the Ambatovy-Analamay amphibian community is the presence of four species of *Mantella* (*M. aurantiaca*, *M. baroni*, *M. crocea*, and *M.* aff. *milotympanum*). *Mantella aurantiaca* and *M. baroni* are quite common and frequent valley forest along the stream, slope, as well as up-slope humid forest far from water sources. They are often found together on the forest floor along the streamside. In the valley forest along the Sakalava River, they are in syntopy with *M. crocea*. In contrast, *M.* aff. *milotympanum* forms an apparent isolated population on slopes in humid forest, often in the same area as *M. aurantiaca*, but not in syntopy.

Relative abundance

Even though the techniques used to calculate estimates of the relative abundance of the different taxa comprising the Ambatovy-Analamay herpetofauna are approximate, they provide important insight into the local communities (Table 4). Two different patterns emerge from these surveys with respect to relative abundance. The first aspect is that in virtually all cases, with the exception of the Azonal Benchmark habitat, within a given habitat type, the majority of species have similar measures of relative abundance and dominant taxa are largely unknown. Further, certain species have relatively low abundances and are rarely encountered. In certain cases, these rarely observed species may be uncommon at the site or difficult to capture, such as fossorial animals, or more common in the upper forest strata, which was not accessible during our inventories. Examples of animals falling into this latter class are certain chameleons, such as *Furcifer willsii*, or arboreal snakes. In other cases, the nature of the substrate makes observation and capture of animals difficult. For example, in relatively thick peaty soils with densely tangled or superficial tree roots, animals can quickly disappear into crevices and hiding places.

The second pattern of note is that the analysis of relative abundance of species across the different habitat types, suggests that, in general, there are no notable differences. In the inventoried portions of each habitat type, we found that the vegetation classification (Good Quality or Degraded) used to differentiate them was not reflected in measures of species richness within the herpetological data, with the exceptions of the secondary and heavily degraded homogenous Azonal Impacted Degraded and the Zonal Impacted Good habitats. Even given a certain sensitivity of the regional herpetofauna to the effects of habitat fragmentation and degradation, the local communities in partially disturbed and larger blocks of natural forest seem to be stable with regards to relative abundance. The minimum area of forest cover in each of these habitats seems sufficient to maintain viable populations, at least in the short or medium term. However, it is known in Madagascar that certain reptiles and amphibians react negatively to subtle changes in forest structure associated with anthropogenic activities (Andreone, 1994), and that these impacts are progressive over time (Vallan *et al.*, 2004).

Another important aspect is that the Ambatovy-Analamay region has been the subject of different types of exploitation. The remaining forested areas contain numerous old access trails, mineral extraction holes and excavations, as well as the stumps of cut trees. The relatively few differences noted for a given taxon in their relative densities, may be explained by past levels of human disturbance of a given habitat or site. Given the degree of sensitivity of a species to different degrees of perturbation, across different levels and perhaps time scales, and their capacity to recover to seemingly normal population levels, this might explain differences in relative abundance between habitat types. Clearly the size of a given forest parcel and the extent of the disturbance within it are important parameters for the ability of species to recover from disturbance. Remnant populations are very important for the re-colonization of a disturbed area.

Within the Parc National de Mantadia, chameleon densities are seemingly low. This may be at least partially associated with habitat disturbance derived from graphite exploitation or directly linked to the collection of animals for trade (Rabibisoa *et al*., 2005). According to local villagers living in the immediate vicinity of the Ambatovy-Analamay forest, this zone has not been exploited for reptiles and amphibians that are gathered for the pet trade. Hence, the rarity of some taxa, especially the arboreal species, is probably associated with previous disturbance, for example wood extraction, affecting this forest block.

Conservation status

Amongst the five species found in the Ambatovy-Analamay region that are classified by IUCN as of conservation concern, three (*Mantella aurantiaca*, *M. crocea*, and *Rhombophryne coronata*) have limited distributional ranges (Bora *et al*., 2008). Further, these three taxa are not well represented within the current protected areas system of Madagascar. The presence of these animals in the Ambatovy-Analamay region has several important aspects from both biological and conservation perspectives. Firstly, this is the only known area where three *Mantella* species (including *M*. aff. *milotympanum*) occur in sympatry and underline several interesting aspects associated with their habitat use. Further, members of the genus *Mantella* have been widely collected for commercial purposes in the Andasibe area (Andreone *et al*., 2005) and, based on current information, the Ambatovy-Analamay region has not yet been subjected to such exploitation. Hence, ecological research on the local populations of these frogs is presumed to occur in a largely natural setting notwithstanding the question of habitat degradation. As a side note, the local populations of *M. crocea* are phenotypically different from those in Ambohitantely and Zahamena, as they have a yellowish central dorsum and dorsal flanks and moderately dark anterior and central flanks, whereas those from the last two sites are green on the central dorsum with black anterior and central flanks and a light frenal stripe (A. Raselimanana, unpublished data).

Diversity

The species diversity measures, based on the Shannon-Weaver H' index, for many of the habitat types is approximately 1.5 (Table 5), indicating an important level of faunal heterogeneity in the azonal, zonal, and transitional habitat categories. A considerable number of microhabitats occur in these different habitats, providing the ecological settings for a diverse herpetofauna. Hence, it is not surprising that each habitat type has a certain percentage of fauna not shared with other habitats or only with a few other habitats (Table 3, Figure 3). For animals such as reptiles and amphibians, particularly small species, an area of several tens of hectares can accommodate viable populations. To illustrate this aspect, in the Transitional Benchmark habitat there was a small marsh vegetated with aquatic plants near a small stream; a diverse fauna occurred at the site, with most species having considerable populations.

Faunal similarity

The Azonal Impacted Degraded habitat holds only seven species of reptiles and amphibians, of which two species were encountered in the other habitat types. Based on the dendrogram produced from the Jaccard Index coefficients (Figure 4), this habitat is faunistically different from the eight forested habitats. This open bush, without permanent water, is unsuitable habitat for most reptiles and amphibians, which in turn gives rise to its low species diversity and taxa adapted to harsh conditions. Two habitat types, Azonal Benchmark and Azonal Impacted Good Quality, form a separate group, and in many ways, these two areas are ecologically similar and form more-or-less continuous forested blocks within the study sites separated by 2-3 km direct distance.

The case of the group formed by the Transitional Impacted Degraded and Zonal Impacted Good Quality habitats is particular. These two habitats are ecologically different, with considerable levels of habitat degradation and disturbance that show parallels. Hence, both habitats have a considerable number of ubiquitous species, adapted to poor quality habitats. This being said, sufficient microhabitats occur in these two habitats, which permit a certain number of forest-dwelling taxa to occur, which are not identical between the sites. A comparison of the species occurring in these two habitats (Table 2), clearly illustrates this point. Two other habitat types, Zonal Benchmark and Zonal Impacted Degraded, form a separate group. Actually, these two areas are ecologically very similar and are physically continuous. Only a few species of frogs and reptiles are not shared between these two habitats.

Conclusion

The Ambatovy-Analamay mid-elevation forests hold an important herpetofauna that is biogeographically associated with the central and central east portions of the Malagasy humid forests. With 112 species of reptiles and amphibians, this forested zone figures amongst the richest known forested regions on the island. With a considerable variety of biotopes and microhabitats, the Ambatovy-Analamay area possesses considerable faunal overlap with different portions of the eastern humid forest, associated with the vegetational types and the elevational distribution of herpetofauna. These aspects confer a particular importance to the zone, not only in terms of its ecological diversity, but also for maintaining exchange and genetic variability between different populations.

The Ambatovy-Analamay forests hold at least five herpetofauna species considered threatened with extinction by the IUCN. These commercially exploited taxa, at least in other portions of their range, are poorly represented within the current protected areas system of Madagascar. Hence, the Ambatovy-Analamay forests are important for these taxa, and necessary conservations steps need to be taken to ensure their long-term existence. Most importantly, these forests are not currently figured amongst the sites for commercial collection of these animals, and the zone needs to be closed to such exploitation.

An important percentage of the local herpetofauna shows broad geographical distribution across the eastern humid forests and some taxa have more limited ranges in the central portion of this zone. Certain species are poorly known from one or two other localities, and their occurrence in the Ambatovy-Analamay region provided important range extensions. Examples include the snake *Pseudoxyrhopus oblectator*, which was previously only known from the Ranomafana area (Cadle, 1999). It is also the case for the microhylid frog *Plethodontohyla guentheri*, which was formerly only recorded from the Parc National de Marojejy (Glaw & Vences, 2007b).

The Azonal Impacted Degraded habitat is notably poor concerning biotopes and herpetological species richness. The associated seasonal marshes provide breeding sites for certain amphibians and the hard packed earth is occupied by the frog *Blommersia domerguei* and the skink *Trachylepis boettgeri*, both typical of open high montane zones of the Central Highlands.

Reptiles and amphibians are amongst the vertebrate groups that are sensitive to habitat fragmentation and degradation effects (Vallan, 2002, 2003; Vallan *et al*., 2004). However, all of the recorded taxa within the natural and partially disturbed and large forested habitats of the Ambatovy-Analamay region show no perceivable evidence of stress associated with habitat degradation. In other words, the minimum area of forest cover in each of these habitats seems sufficient to maintain viable populations, at least in the short or medium term.

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Appendix 1. List of reference specimens associated with the specific identifications of the Ambatovy-Analamay material deposited in the collections of the Département de Biologie Animale, Université d'Antananarivo. APR is the field number acronym of Achille P. Raselimanana.

Species	Field number	Species	Field number
Amphibians		**Amphibians** (cont.)	
Heterixalus betsileo	APR 8735	*Plethodontohyla guentheri*	APR 9162
Boophis albilabris	APR 8923	*Plethodontohyla mihanika*	APR 8695
Boophis boehmei	APR 8651	*Plethodontohyla notosticta*	APR 8724
Boophis erythrodactylus	APR 8996	*Plethodontohyla ocellata*	APR 9192
Boophis feonnyala	APR 9391	*Rhombophryne alluaudi*	APR 8667
Boophis goudoti	APR 8992	*Rhombophryne coronata*	APR 8666
Boophis guibei	APR 8944	*Stumpffia* "kibomena"	APR 8740
Boophis idae	APR 8665	*Paradoxophyla palmata*	APR 9109
Boophis madagascariensis	APR 8654	*Scaphiophryne marmorata*	APR 8647
Boophis picturatus	APR 9222	*Scaphiophryne spinosa*	APR 8744
Boophis pyrrhus	APR 8924	*Ptychadena mascareniensis*	APR 8734
Boophis reticulatus	APR 8842		
Boophis sibilans	APR 8655	**Reptiles**	
Boophis tephraeomystax	APR 8789	*Ebenavia inunguis*	APR 8982
Boophis sp.	APR 9569	*Lygodactylus guibei*	APR 8716
Aglyptodactylus madagascariensis	APR 8652	*Microscalbotes bivittis*	APR 8664
Blommersia blommersae	APR 8833	*Paroedura gracilis*	APR 9262
Blommersia domerguei	APR 8737	*Phelsuma lineata*	APR 8674
Blommersia grandisonae	APR 9318	*Phelsuma quadriocellata*	APR 8730
Blommersia sarotra	APR 9206	*Uroplatus phantasticus*	APR 8663
Gephyromantis asper	APR 8710	*Uroplatus pietschmanni*	APR 8714
Gephyromantis boulengeri	APR 8672	*Uroplatus sikorae*	APR 8692
Gephyromantis cornutus	APR 9464	*Amphiglossus astrolabi*	APR 9466
Gephyromantis sculpuratus	APR 8921	*Amphiglossus frontoparietalis*	APR 9342
Gephyromantis thelenae	APR 9150	*Amphiglossus macrocercus*	APR 8767
Gephyromantis aff. *malagasius*	APR 8659	*Amphiglossus mandady*	APR 9017
Guibemantis depressiceps	APR 8662	*Amphiglossus ornaticeps*	APR 9140
Guibemantis liber	APR 8829	*Amphiglossus* "phaeurus"	APR 9439
Guibemantis pulcher	APR 8688	*Madascincus ankodabensis*	APR 8983
Guibemantis timidus	APR 9424	*Madascincus melanopleura*	APR 8670
Guibemantis tornieri	APR 9389	*Madascincus mouroundavae*	APR 8972
Guibemantis aff. *albolineatus*	APR 8684	*Madascincus* "baeus"	APR 8669
Guibemantis aff. *bicalcaratus*	APR 9548	*Madascincus* sp.	APR 8978
Guibemantis aff. *punctatus*	APR 8777	*Trachylepis boettgeri*	APR 8793
Mantella aurantiaca	APR 8807	*Trachylepis gravenhorstii*	APR 8736
Mantella baroni	APR 8727	*Brookesia superciliaris*	APR 8689
Mantella crocea	APR 9041	*Brookesia thieli*	APR 8691
Mantella aff. *milotympanum*	APR09347	*Calumma gastrotaenia*	APR09469
Mantidactylus aerumnalis	APR08918	*Calumma nasutum*	APR08713
Mantidactylus argenteus	APR08930	*Furcifer willsii*	APR08712
Mantidactylus betsileanus	APR08750	*Zonosaurus aeneus*	APR08673
Mantidactylus aff. *betsileanus*	APR09351	*Zonosaurus madagascariensis*	APR09249
Mantidactylus biporus	APR08749	*Thamnosophis epistibes*	APR08700
Mantidactylus cowani	APR09486	*Thamnosophis infrasignatus*	APR08877
Mantidactylus grandidieri	APR08653	*Compsophis infralineatus*	APR09438
Mantidactylus femoralis	APR08649	*Compsophis laphystius*	APR08726
Mantidactylus lugubris	APR08994	*Ithycyphus perineti*	APR08732
Mantidactylus melanopleura	APR08650	*Liophidium rhodogaster*	APR08696
Mantidactylus opiparis	APR08759	*Liophidium torquatum*	APR09365
Mantidactylus zipperi	APR09425	*Pseudoxyrhopus heterurus*	APR09164
Spinomantis aglavei	APR08660	*Pseudoxyrhopus oblectator*	APR08927
Anodonthyla boulengeri	APR08648	*Pseudoxyrhopus tritaeniatus*	APR09135
Platypelis barbouri	APR08940	*Stenophis arctifasciatus*	APR09559
Platypelis pollicaris	APR09108	*Stenophis betsileanus*	APR09026
Platypelis tuberifera	APR08678	*Sanzinia madagascariensis*	APR08734
Platypelis n. sp.	APR09455		