Amphibian Diversity in the Matrix of a Fragmented Landscape Around Ranomafana in Madagascar Depends on Matrix Quality

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Serge Herilala Ndriantsoa[1], Jana Carina Riemann[2], Noromalala Raminosoa[1], Mark-Oliver Rödel[3,4], and Julian Stefan Glos[2]

Abstract
Human-induced conversion of natural habitats into agricultural areas is one of the major drivers for biodiversity loss. In many tropical regions, the matrix habitat area (habitat between fragments of remaining natural habitat) considerably exceeds the area of the original habitat. Therefore, understanding the factors determining matrix quality for animals is a key step to guide conservation action in fragmented landscapes. Matrix habitat, although being often highly disturbed, might provide valuable habitat for some species, serves as buffer zone for remaining natural habitat or corridor between fragments, and hence could be an important component for biodiversity maintenance on a landscape scale. We evaluated the effects of matrix quality on frog diversity in a rainforest ecosystem in Eastern Madagascar. Although frog diversity was affected in all matrix habitats, we found that variation in matrix quality was an important factor. Matrix habitat could serve as valuable habitat and corridor (i.e., high frog diversity along streams in the matrix), as buffer zone (moderate diversity in banana plantations), or was unsuitable habitat for most frog species (very impoverished diversity in secondary vegetation and rice fields). The remaining natural vegetation in and outside protected areas in Madagascar and worldwide is decreasing and will not be sufficient to preserve its biodiversity on a long term. Therefore, we must understand responses of organisms to disturbance in order to create buffer zones and corridors combining both disturbed and natural habitats. Implementing corridors along matrix streams connecting forest habitats might be an important contribution to amphibian conservation in fragmented landscapes.

Introduction

The earth is currently experiencing an unprecedented, accelerated loss of biodiversity (Sodhi & Ehrlich, 2010), which results—among others—in changed interactions among species (Tylianakis, Didham, Bascompte, & Wardle, 2008) and a decline in ecosystem functioning (MEA, 2005). This loss and the respective results are mainly caused by human activities. Worldwide, and in particular in the tropics, one of the major thriving causes for biodiversity loss is human-induced conversion of natural habitats into agricultural areas. Natural habitats are thus also fragmented, that is, organism's preferred environments are no longer continuous. Most research on community properties in a fragmented landscape has primarily focused on the fragments itself as "habitat islands" (Wiser, Peet, & White, 1996). This is

not satisfactory for two reasons. First, the island analogy, and in particular, the restrictions of studies to the fragments themselves may limit our understanding of factors

[1]Mention Zoologie et Biodiversité Animale, Faculté des Sciences, Université d'Antananarivo, Antananarivo, Madagascar
[2]Zoological Institute, University of Hamburg, Martin-Luther-King Platz, Hamburg, Germany
[3]Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse, Berlin, Germany
[4]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Berlin, Germany

Corresponding Author:
Julian Stefan Glos, Zoological Institute, Martin-Luther-King Platz 3, Hamburg 20146, Germany.
Email: julian.glos@uni-hamburg.de

influencing community structure and biodiversity on a landscape scale because the nature of the matrix (=nonforest area) in which they occur may also be of key influence to the fragments (Prevedello & Vieira, 2010; Stouffer, Bierregaard, Strong, & Lovejoy, 2006; Umetsu & Pardini, 2007; Wiser & Buxton, 2008). Therefore, any dichotomous classification of the landscape into ''forest'' and ''nonforest'' as a homogeneous and static component of the landscape may miss essential information. Accordingly, when matrix variation was included in analyses of fragments, it has often helped to explain the outcome from fragmentation studies (Diekötter, Haynes, Mazeffa, & Crist, 2007; Lindenmayer, McIntyre, & Fischer, 2003; Richter-Boix, Llorente, & Montori, 2007; Stouffer et al., 2006). Second, in many regions, the matrix habitat area considerably exceeds the area of the original habitat, now remaining in fragments only (Harper, Steininger, Juhn, & Hawkins, 2007).

Matrix habitat, however, although it is often highly disturbed, might provide valuable habitat for some species and hence could be an important component for biodiversity maintenance on a landscape scale. Realistically, the remaining natural habitats and protected areas will be unable to preserve their biodiversity under the impact of increasing human pressure and climate change (Glos et al., 2008; Hannah et al., 2008; Kremen et al., 2008). Therefore, it is important to understand responses of native plants and animals to disturbance in order to assess the intrinsic value of matrix habitats for biodiversity and to create buffer zones and corridors combining secondary and natural habitats (Nopper, Lauströer, Rödel, & Ganzhorn, in press).

One major factor in this context is the suitability of the matrix for dispersal. Matrix habitat may facilitate movement among fragments by acting as a corridor of habitat that is at least suitable for travel (Antongiovanni & Metzger, 2005; Ricketts, 2001; Rosenberg, Noon, & Meslow, 1997; Selonen & Hanski, 2003; Watling, Nowakowski, Donnelly, & Orrock, 2011), or it may represent a true barrier for dispersal. Therefore, variation in matrix quality can affect matrix use by species (Norton, Hannon, & Schmiegelow, 2000; Sisk, Haddad, & Ehrlich, 1997; Tubelis, Lindenmayer, & Cowling, 2004), which can ultimately affect population persistence and assemblage composition in isolated fragments (Santos-Filho, Peres, da Silva, & Sanaiotti, 2012; Vandermeer & Carvajal, 2001; Watling et al., 2011). Furthermore, higher quality matrix reduces the isolation of patches by allowing species to expand their activities (e.g., feeding) outside of fragments, thus increasing effective fragment size (Tubelis et al., 2004). Beyond its direct effects, matrix structure can affect the degradation of fragments through its capacity to buffer fragments from deleterious edge effects (Gascon, Williamson, & da Fonseca, 2000).

The tropical forests of Madagascar are among the most biologically rich and unique in the world (Kremen et al., 2008; Myers, Mittermeier, da Fonseca, & Kent, 2000), and more than 90% of Madagascar's endemic animal species live exclusively in forest or woodland (Dufils, 2003). Habitat loss mainly due to slash-and-burn agriculture (''tavy'' in Malagasy), fragmentation, and degradation is a striking threat to this biodiversity (Andreone et al., 2008; Glos et al., 2008; Irwin et al., 2010). By the 1950s, 27% of Madagascar was forested and even a conservative estimate of prehuman forest cover suggests it had already lost half (or even more than two thirds) of its forest. Forest then decreased by almost 40% from the 1950s to 2000s and was heavily fragmented with a reduction in ''core forest'' ($>1\,km$ from a nonforest edge) of almost 80% (Harper et al., 2007). A human population growing by 2.7% annually (UNPF, 2009), and 61% of this population living outside urban areas, causes various types of disturbance in natural ecosystems. This process clearly continued from 2000 to today (personal observation).

The plant and animal species' reactions to disturbance are usually negative, but remain poorly known as studies in highly disturbed areas such as typical matrix areas are dramatically lacking (reviewed in Irwin et al., 2010). Forest fragments and, depending on their structural heterogeneity, even some agricultural sites can be valuable habitats to maintain species diversity in the human-used landscape (Nopper et al., in press; Riemann, Ndriantsoa, Raminosoa, Rödel, & Glos, 2015). However, disturbance in Madagascar typically reduces species diversity (especially of native or endemic species), but also causes species turnover, with forest species usually being replaced by grassland generalists and endemics replaced by nonendemics (Irwin et al., 2010). Related species often have divergent reactions to disturbance, even within lower taxonomic groupings (i.e., families or genera). As it is apparent that the structure and the level of disturbance of matrix areas can be important drivers of community structure in a fragmented landscape, a better understanding of the matrix is needed by explicitly including environmental differences of the matrix into studies on diversity in fragmented landscapes (Jules & Shahani, 2003; Lindenmayer & Frankling, 2002).

In this study, we focused on these environmental differences, that is, the matrix quality. Our study aims to contribute to a better understanding of the response of highly diverse Malagasy amphibian assemblages to habitat disturbance for the implementation of future conservation strategies with special emphasis on the conservation value of matrix habitats. We therefore examined species richness and species turnover of frog assemblages in four different matrix types (i.e., streams and gallery forests, banana plantations, secondary vegetation, rice fields) and compared them to a continuous

rainforest and nearby forest fragments. We hypothesized that (a) species richness decreases and (b) species turnover increases, with increasing disturbance between matrix types and compared sites in continuous forest and forest fragments.

Methods

Study System

Field work was conducted in the Ranomafana National Park (RNP, 21°02′−21°24′S, 47°20′−47°35′E), East Madagascar, in forest fragments located east of RNP, and in different matrix sites located between these forest fragments (Figure 1). More detailed information on the location of the sites in RNP and the fragments is provided in Riemann et al. (2015). Most of the remaining rainforest habitat in the Ranomafana region is located within RNP, a 43,500 ha mid-altitude montane rainforest (500–1,300 m a.s.l.) with an annual precipitation between 1,700 and 4,300 mm (Wright & Andriamihaja, 2003). As a result of traditional Malagasy slash and burn agriculture ("tavy"), the remaining forest fragments around RNP are embedded in a matrix of cultivated land (e.g., banana plantations and rice fields) and secondary vegetation (i.e., grasslands with bush and shrub vegetation).

We categorized the matrix habitat as (a) "matrix stream," that is, streams crossing nonforested areas with adjacent riparian vegetation consisting of trees and bushes (between 1 and 5 m on each stream bank), (b) "banana plantation," that is, plantations of bananas with some understory plants and nonpermanent rills or irrigation ditches, relatively structurally rich, (c) "secondary vegetation," that is, abandoned fields or paddy fields dominated by grasses, shrubs, and bushes (mainly guavas), at least 50 m distant to the next stream, and (d) "rice fields" characterized by stagnant water and irrigation ditches or small streams but little or no higher vegetation strata. We chose sites within RNP and nine different forest fragments that range in size between 2 and 16.5 ha (for details see Riemann et al., 2015) as forest control sites. Five of these forest fragments comprise streams, including one fragment with two streams. Aerial photographs show that all but two fragments were separated from continuous forest already in 1950, and interviews with local people revealed that all studied fragments were at least 50 years separated from RNP. The Ranomafana region is globally exceptional by its amphibian diversity with almost 120 taxa known (Glaw & Vences, 2007; Vieites et al., 2009; own unpublished data).

Sampling Design

We determined species richness, relative abundance, and species composition on transects distributed along all four matrix categories, and compared these with data collected along streams and in terrestrial habitats inside RNP and forest fragments using the identical methods

Figure 1. Map of the study plots within Ranomafana National Park (RNP) in South-Eastern Madagascar (dark grey area represents the official RNP boundaries), in forest fragments (light grey areas) outside RNP, and in the matrix (white area). Each symbol represents one transect in the matrix (matrix stream: circles, secondary vegetation: triangles, banana plantation: diamonds, rice field: squares) or study site in continuous forest (stream and terrestrial transect: crosses). Upper inset represents the location of RNP within Madagascar, lower inset the location of the study area related to RNP.

(22 transects inside RNP or continuous forest and 16 transects in 9 different forest fragments; from Riemann et al., 2015). We established a total of 18 independent line transects (50 × 2 m) (Marsh & Haywood, 2010): five transects were matrix streams, four were banana plantations, four were secondary vegetation, and five were in rice fields. In RNP and fragmented forests transects, we differentiated between stream and terrestrial habitats to equally account for stream depending species (either semiaquatic or stream breeding) and for species that reproduce independent from streams (i.e., phytotelmata, pond or terrestrial breeders; Riemann et al., 2015). Accordingly, in this study, we followed the sampling scheme of terrestrial transects (searching a band of 2 m width) and included in matrix stream transects 1 m riparian vegetation on each stream bank in addition to the water body.

Each transect was sampled nine times using standardized visual and acoustic transect sampling methods (Rödel & Ernst, 2004). A combination of acoustic and visual methods is recommended to detect all major ecological guilds of frogs (Rödel & Ernst, 2004; Vences et al., 2008). Visual sampling was most suitable for terrestrial leaf litter species, and acoustic sampling was particularly useful to detect arboreal species and species calling from hidden places, such as tree holes, phytotelmata or dense leaf litter. Transects were sampled during day and night as in the study area nocturnal as well as diurnal species occur (Glaw & Vences, 2007). Each transect was surveyed twice (once by day, once by night) between May and June 2010, and seven times (three times by day, four times by night) between January (beginning of the heavy rainy season) and June (drier season) 2011.

Visual sampling covered all visible individuals on the ground and in arboreal structures and in addition the aquatic habitat on stream transects. Logs and rocks were not displaced, neither was vegetation pulled apart (e.g., *Pandanus* leafs) to keep disturbances of the study system as low as possible and to ensure equal sampling effort in all sites. All visually detected individuals were captured, measured, sexed, marked via toe clipping (no functionally important toes, following the recommendations by Grafe, Stewart, Lampert, & Rödel, 2011), and identified by morphology in the field (according to Glaw & Vences, 2007). After data sampling, all individuals were immediately released at point of capture, except some vouchers that were collected to ascertain species affiliation (see Appendix 1). Visual transect sampling was performed at constant speed (approx. 2.5 m/min), but interrupted during handling time and for acoustic sampling at four fixed points (start, 12.5 m, 25 m, 37.5 m). At each point, we registered all calling individuals in a 12.5 m distance (Rödel & Ernst, 2004) straight, left, and right for 5 min and identified them to species level. Two species (one found in secondary vegetation: *Plethodontohyla notosticta*;

one from continuous forest: *Gephyromantis depressiceps*) were singletons for the complete data set and were therefore excluded from all analyses.

Voucher specimens were euthanized, preserved in 75% ethanol, and deposited at the Mention Zoologie et Biodiversité Animale, Faculté des Sciences, University of Antananarivo, Madagascar (UADBA) and the Museum für Naturkunde Berlin, Germany (ZMB). All toe clips were collected as tissue samples and stored in pure ethanol for DNA barcoding (or dried and stored for further analyses). We used barcoding to confirm identification to species level based on a fragment of the mitochondrial 16S rRNA gene (Vences, Thomas, van der Meijden, Chiari, & Vieites, 2005; Vences et al., 2008), following the molecular protocol described in Ndriantsoa et al. (2013). We determined sequences at least once for species that where assumed to be identifiable by a distinct morphology. Barcoding was repeated for each transect sampling for highly cryptic species (e.g., taxa of the subgenera *Chonomantis* and *Ochthomantis*) and supposed undescribed taxa. Obtained sequences were compared with published data on GenBank or own reference sequences (Appendix 1).

Data Analyses

We compared local species richness (absolute number of species detected) and relative abundance (number of frog individuals of all species) per transect between the four matrix categories and to the continuous forest and forest fragments for all habitats using Kruskal–Wallis ANOVA tests. *p* values of post hoc pairwise comparisons using Wilcoxon rank sum test were adjusted according to Benjamini and Hochberg (1995). For illustrating total species richness in relation to sampling effort (i.e., number of transects), sample-based rarefaction curves were calculated. We further compared patterns of species composition between matrix, continuous forest, and forest fragment sites. We used nonmetric multidimensional scaling (NMDS) to visualize and evaluate patterns of dissimilarity among transects based on their species composition. The ordination was constructed from a Bray-Curtis dissimilarity matrix using species presence or absence data. We then performed permutational multivariate analyses of variance (perMANOVA; Anderson, 2001; McArdle & Anderson, 2001) to test the hypothesis of differences in species composition between the four matrix categories, and continuous forest and forest fragments for terrestrial and stream habitats. This nonparametric permutation-based variant of MANOVA partitions sums of squares of multivariate data equivalent to univariate ANOVA and the pseudo F statistic can be calculated directly from any distance measure (Anderson, 2001). We performed perMANOVA based on Bray-Curtis dissimilarities using species presence or absence

data. p values were obtained from 9,999 permutations. p values for post hoc pairwise comparisons were Bonferroni corrected, that is, multiplied by the number of pairwise tests. All statistical analyses, except calculation of species accumulation curves (PAST 3.13 statistics; Hammer, Harper, & Ryan, 2001), were performed in R version 3.2.2 (R Core Team, 2015).

Results

General Results

With a combination of visual and acoustic encounter sampling (and DNA barcoding for species identification), we detected a total of 43 species over all matrix habitats (on 18 transects; Appendix 1). This is comparable to total species richness detected in continuous forest (42 species, on 22 transects, terrestrial and stream) and forest fragments (40 species, on 16 transects, terrestrial and stream) by Riemann et al. (2015). Combined, we found 62 frog species on all 56 transects in RNP and the adjacent forest fragments and matrix sites. Total species richness within the matrix was highest along streams (35), followed by banana plantations (18), and lowest in secondary vegetation (7) and rice fields (8). Between stream habitats, when visually comparing estimated species numbers in relation to standardized sampling effort (Figure 2), there was no obvious difference in total species richness (SR; i.e., matrix vs. forest fragment streams vs. continuous forest streams). However, in nonstream habitats, the total SR was reduced in highly disturbed matrix habitats (secondary vegetation, rice fields) compared with less-disturbed (continuous forest, forest fragments) habitats or disturbed but structurally rich (banana plantations) matrix habitats (Figure 2).
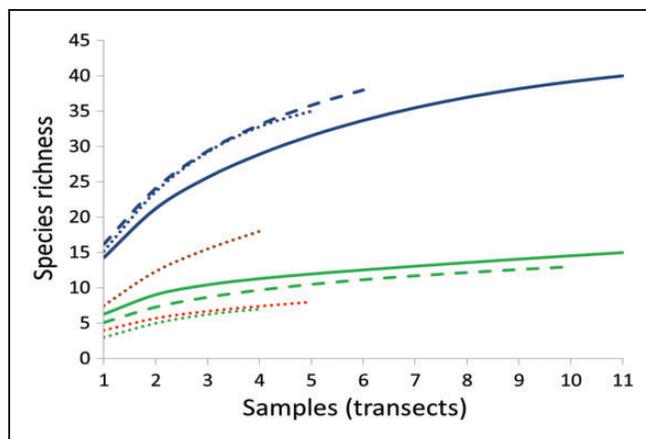

Figure 2. Sample-based rarefaction of mean estimated species numbers. Continuous forest (continuous lines), fragmented forest (dashed lines), and matrix sites (dotted lines). Stream transects (blue), terrestrial transects and secondary vegetation (green), banana plantation (brown), and rice field (red).

Local Species Richness

Local species richness, that is, the number of species encountered on a transect during the 2-year study period, differed significantly between matrix sites, continuous forest, and forest fragments (Kruskal-Wallis, $\chi^2 = 45.1$, DF = 7, N = 56, $p < 0.001$; Figure 3). Species richness was significantly higher in stream habitats compared with all other habitats; however, species richness did not differ between streams in the matrix, in forest fragments, or continuous forest (see Appendix 2 for post hoc comparisons). In nonstream habitats, local SR was significantly different between the habitat types, being lower in highly disturbed matrix habitats (i.e., secondary vegetation, rice fields) than in forest habitats (i.e., continuous forest, forest fragments) and banana plantations (Figure 3).

Local Relative Abundance

Due to possible double counts in acoustic records, we analyzed the number of frog individuals per transect (i.e., local relative abundance) separately for individuals detected by visual encounter surveys (VES) and acoustic encounter surveys (AES). Local relative abundance, that is, the number of frog individuals on a transect during the 2-year study period divided by the number of surveys per transect (i.e., nine surveys), differed significantly between matrix sites, continuous forest, and forest fragments when including only VES data (Kruskal-Wallis, $\chi^2 = 44.1$, DF = 7, N = 56, $p < 0.001$; Figure 4) and also AES data (Kruskal-Wallis, $\chi^2 = 20.7$, DF = 7, N = 56, $p = 0.004$), although post hoc comparisons did not reveal any differences for AES data between habitats (Appendix 3). In stream habitats, local relative abundance did not differ between streams in the matrix, in forest fragments, or continuous forest, neither when including only visually detected frogs (i.e., applying VES; Figure 4; see Appendix 4 for post hoc comparisons) nor when including only acoustically detected frogs (i.e., applying AES; see Appendix 3 for post hoc comparisons). In nonstream habitats, there was a significant difference between the habitat types when including visually detected frogs (i.e., VES), with relative local abundance being lower in highly disturbed matrix habitats (i.e., secondary vegetation) than in forest habitats (i.e., continuous forest, forest fragments), however, being not lower in banana plantations and rice fields (Figure 4; see Appendix 4 for post hoc comparisons). We detected the same pattern but no statistical significance when including only acoustically detected frogs (Appendix 3).

Species Composition

The species composition differed generally between the habitat types (perMANOVA, Bray-Curtis dissimilarity
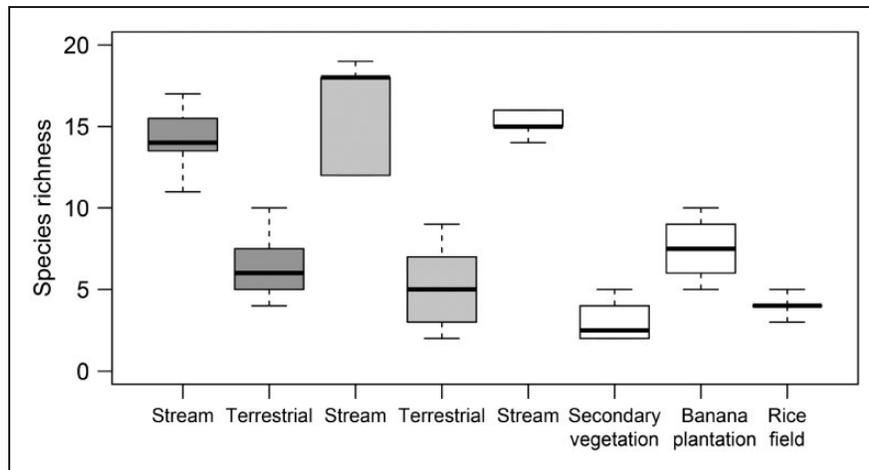
Figure 3. Local species richness (number of species per transect) in each habitat type (dark grey = continuous forest, light grey = forest fragments, white = matrix habitats). Shown are median, 25% and 75% percentiles (box), and minimum and maximum values (whiskers). Data on continuous forest and forest fragments are taken from Riemann et al. (2015).
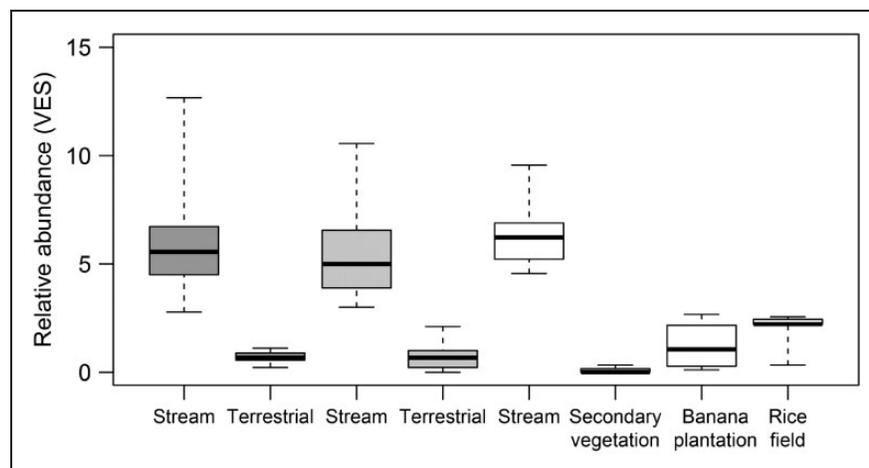

Figure 4. Local relative abundance (number of frog individuals per transect/number transect surveys) in each habitat type, data for visual encounter surveys (dark grey = continuous forest, light grey = forest fragments, white = matrix habitats). Shown are median, 25% and 75% percentiles (box), and minimum and maximum values (whiskers).

using presence or absence data, 9999 permutations, $F_{7,48} = 9.2$, $p < 0.0001$). Matrix streams, banana plantations, and rice fields showed clear clusters in the NMDS that were not overlapping (Figure 5). Variation in species composition between transects in secondary vegetation habitat was highest, and some of these transects overlapped with banana plantation transects. Multiple post hoc comparisons between all matrix and forest types showed significant differences in assemblage composition between most matrix types and of matrix types to most forest and fragment habitat types (Appendix 5).

Discussion

Worldwide, and particularly in Madagascar, highly disturbed areas such as small forest fragments and nonforested matrix areas represent the largest part of remaining habitat for animals including amphibians (Irwin et al., 2010). Areas of natural vegetation and protected areas (e.g., ~6 million ha in 2008 in Madagascar) will probably be unable to preserve their full biodiversity under the severe and even increasing anthropogenic pressure (Hannah et al., 2008; Kremen et al., 2008). Therefore,
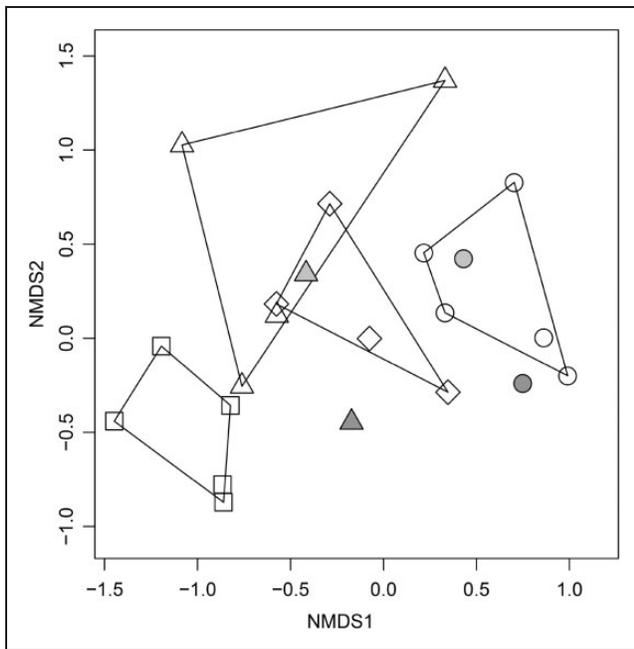
Figure 5. Dissimilarity of species composition in different matrix types. Nonmetric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity for binary (i.e., presence-absence) data. Each white symbol represents one transect in the matrix (matrix stream: circles, secondary vegetation: triangles, banana plantation: diamonds, rice field: squares). Distances between transects in the two-dimensional NMDS plot represent dissimilarities in species composition (stress = 0.187). Data for continuous forest (dark grey symbols) and forest fragments (light grey symbols; terrestrial habitats: triangles, stream habitats: circles) are from Riemann et al. (2015) and are summarized as centroids calculated from 6 to 11 transects.

it is essential to understand responses of native fauna and flora to disturbance in order to assess the intrinsic value of disturbed areas for biodiversity and to create buffer zones and corridors combining secondary and natural habitats. We assessed the amphibian species diversity and species turnover in matrix sites in eastern Madagascar that differed in their structure and their degree of disturbance, with a combination of visual and acoustic methods for detection and a combination of morphological, bioacoustic, and molecular methods for species identification. Two factors were mainly associated with both species richness and species composition of frog assemblages, namely the presence of lotic water systems (i.e., one to five meter wide streams) and the level of disturbance and associated habitat structures.

The Innate Value of Matrix Habitats for Amphibian Diversity

Matrix habitats vary greatly in terms of their capacity to support forest species (Lawton, Naeem, Thompson, Hector, & Crawley, 1998), with sites with higher disturbance having usually lower species richness (Gascon et al.,

1999; Tocher, Gascon, & Zimmerman, 1997; Vasconcelos, Sorenson, Watanabe, Foguel, & Palacios, 2015). In our study, this was only true for highly disturbed habitats with highly degraded vertical structuring, namely in secondary vegetation (i.e., dominated by bushes and small guava trees) and rice fields. However, in stream habitats, we surprisingly detected that both species richness and relative abundance of frogs were independent of where the streams were located (in continuous forest, forest fragments or matrix), that is, in a small area around streams with only a few meters of gallery forest at each side embedded in a matrix of rice fields and highly disturbed secondary vegetation, occurred as many frog species as around streams surrounded by either small and partly disturbed (fragments) or large and undisturbed (RNP) forest patches.

The most important factor for reproduction of amphibians in many systems is the availability of lentic or lotic habitats (Hillers, Veith, & Rödel, 2008; Hofer, Bersier, & Borcard, 2000; Pineda & Halffter, 2004). We could show that streams are important habitats to support high species richness not only in forest fragments and continuous forest (Riemann et al., 2015) but also in the matrix and further supported comparable relative abundances of frogs. The regional frog assemblage in eastern Madagascar includes a high proportion of species that depend on lotic systems for reproduction (i.e., many species of Mantellidae). Stream-independent breeding species included a wide variety of reproductive modes (e.g., phytotelmata breeder, terrestrial breeder, pond breeder) and were also found in stream habitats. However, corresponding to the availability of their respective breeding habitat, species living in open lentic systems (i.e., *Heterixalus alboguttatus, Ptychadena mascareniensis*) were predominantly found in rice fields (Figure 6).

Disturbance had yet an effect on the species composition of frog assemblages, that is, a set of different species was found around streams in matrix, fragmented and continuous forest with stream assemblages of matrix and forest fragments being more similar, and assemblages in the continuous forest having the most distinct species composition. Accordingly, several species did not occur in highly disturbed matrix stream habitats, in particular, microhylid frogs usually breeding in phytotelmata (mainly tree holes, e.g., *Platypelis grandis, Plethodontohyla inguinalis, Plethodontohyla brevipes*), while there was a set of generalistic species that did occur in large abundances at all levels of disturbance along streams (e.g., *Gephyromantis tschenki, Boophis madagascariensis*).

In the matrix, in particular, streams with some surrounding riparian vegetation and banana plantations represent an important component of amphibian diversity in this fragmented landscape and might be themselves valuable habitats. Accordingly, these sites should be included into local conservation planning, in particular, in a landscape where not many alternatives of low-disturbed
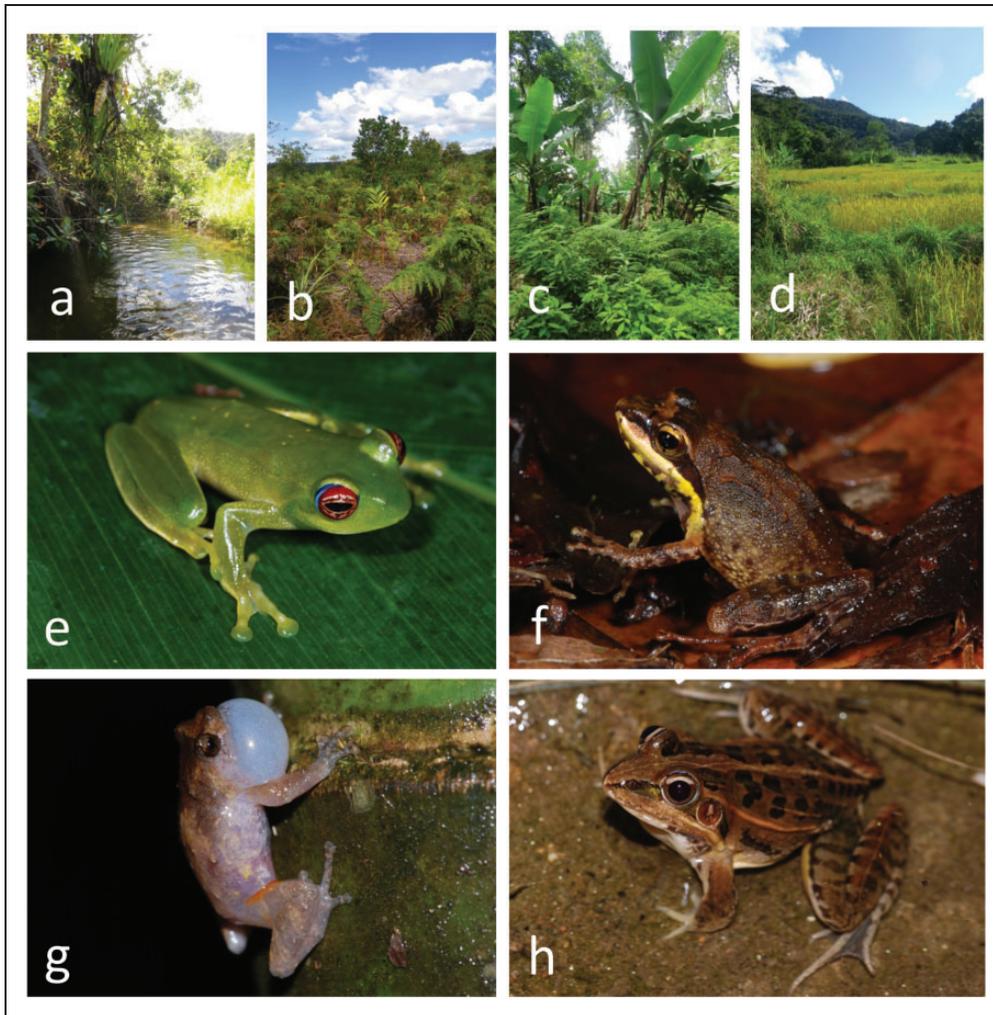
Figure 6. Matrix types and frequently encountered frog species in each matrix type in the Ranomafana region, South-Eastern Madagascar: matrix streams (a) and *Boophis luteus* (e), secondary vegetation (b) and *Gephyromantis enki* (f), banana plantation (c) and *Anodonthyla boulengeri* (g), and rice fields (d), and *Ptychadena mascareniensis* (h).

habitat are available (see also Nopper et al., in press, for an example of hedges as longitudinal structures that might be valuable as corridors for reptiles between dry forest habitats in Madagascar). However, it is yet unclear whether the amphibian populations in matrix habitat represent viable populations on a long term. There is no data available if the amphibian populations of the matrix streams are sustained only by recurring immigrations (i.e., source-sink dynamics) by either migrating frogs or tadpoles that are flushed downstream after heavy rains from forested parts on higher altitude.

Matrix as Corridor Between Natural Habitats

Matrix can act as a selective filter for migration through the landscape. It may facilitate animal movements among fragments of natural habitat by acting as a corridor of habitat that is at least suitable for travel (Antongiovanni & Metzger, 2005; Ricketts, 2001; Rosenberg, Noon, & Meslow, 1997; Selonen & Hanski, 2003), and might therefore connect two patches of natural habitat and subsequently decreasing presumably negative effects on small and isolated populations (e.g., decrease in genetic diversity, sensitivity to stochastic events). Alternatively, it may represent a true barrier for dispersal. The critical factor thereby is the suitability of the matrix for dispersal. Therefore, variation in matrix quality can affect matrix use by species living in isolated fragments (Norton et al., 2000; Sisk et al., 1997; Tubelis et al., 2004), which can ultimately affect assemblage composition (Richter-Boix et al., 2007) and population size and persistence in these fragments (Joly, Miaud, Lehmann, & Grolet, 2001; Vandermeer & Carvajal, 2001). In Brazil, Gascon et al. (1999) showed for various taxa (birds, frogs, mammals, ants) that a high proportion of nominally primary-forest species use matrix habitats for movements (and/or reproduction), as did

Laurance (1991) for tropical rainforest mammals in Australia. In this study, the high frog diversity and abundance in and along matrix streams and adjacent narrow gallery forests indicate that this type of matrix habitat might be important as corridor between forest patches in the highly fragmented landscape of Madagascar. Migration in streams, or inadvertent flushing downstream after heavy rains, might happen in either the tadpole or the frog stage, and from fragment to fragment in or along these streams, or between the remaining rainforest (RNP) and adjacent forest fragments. In addition, terrestrial migrations might be facilitated along stream banks by relatively higher air humidity as compared with those matrix sites where open water is missing. Examples from western Africa show that typical rainforest frogs do indeed occur outside natural rainforest as long there is a considerable wide and dense riverine forest (Barej et al., 2015; Rödel, 2000).

Banana plantations in Madagascar are usually not homogeneous monocultural plantations but are a structurally rich habitat including a distinct understorey and scattered canopy trees. This habitat is used by a rather high diversity of frogs, indicating the general suitability as corridor for frog migration. However, these plantations are usually located only in the perimeter of forest fragments and are not connecting forest patches and are therefore not serving as corridors at present. Other types of matrix habitat are obviously not suitable corridors due to their low quality for most amphibian species (i.e., rice fields, secondary vegetation) and thus are likely to be barriers for migrating individuals of forest specialists.

The establishment of corridors to increase the connectivity between habitat fragments is an often recommended idea in conservation management (Prevedello & Vieire, 2010; Rosenberg et al., 1997). In Madagascar, where the natural rainforest is highly fragmented and where realistic and pragmatic options for biodiversity conservation are urgently needed, the protection of streams including small stripes of gallery forest in matrix habitat, or replanting at streams where this riparian vegetation is missing, might be a suitable and achievable target for conservation outside officially protected areas.

Matrix Habitat as Buffer Zone

High-quality matrix reduces the isolation of patches by allowing species to expand their activities (e.g., feeding) outside of fragments, thus increasing effective fragment size (Tubelis et al., 2004). Beyond its direct effects, matrix structure can affect the degradation of fragments through its capacity to buffer fragments from deleterious edge effects (Gascon et al., 2000).

In Malagasy rainforest, banana plantations are often situated in the periphery of natural forest, mainly adjacent to forest fragments. They might be suitable buffer zones as they are structurally rich (i.e., comprising understorey vegetation, mid-storey banana plants and scattered canopy trees) and therefore buffer the microclimate (e.g., humidity, temperature) toward the center of the forest patch. Consequently, frog diversity is comparatively high, in particular, when the plantations are associated with lotic waters. If plantations are structurally rich (e.g., if they include shade trees) and if they contain suitable breeding habitats (e.g., streams for amphibians), they might be suitable habitat and buffer zone, for at least a set of the local assemblage. This was shown, for example, in amphibians in shaded coffee plantations in Mexico (Pineda & Halffter, 2004; Pineda, Moreno, Escobar, & Halffter, 2005) and for lizards and frogs in pine plantations in Uganda (Vonesh, 2001).

Implications for Conservation

Worldwide the size of the area of matrix habitat often exceeds the area of the original habitat or of fragments (Hannah et al., 2008). It is apparent that matrix quality can be an important driver of animal community structure in a fragmented landscape (Watling et al., 2011). Therefore, a better understanding of the matrix is needed by explicitly including environmental differences of the matrix, spatial context, and dispersal processes into studies on disturbed landscapes (Jules & Shahani, 2003; Leibold et al., 2004; Lindenmayer & Franklin, 2002; Watling et al., 2011). It is still ambiguous whether populations in matrix habitats, such as matrix streams and banana plantations in Madagascan rainforest, represent viable populations in the long term and whether matrix quality and structure allow for migration and genetic exchange between populations in different fragments or fragments and continuous forests. However, our study indicates that particular matrix types might serve indeed as suitable habitat (i.e., matrix streams, banana plantations), corridors between forest fragments (i.e., matrix streams), or buffer zones for natural forest patches (i.e., banana plantations), while other matrix types are not suitable habitat for most forest frog species or are dispersal barriers (i.e., secondary vegetation, rice fields; Figure 6). Since frogs have relatively short generation times and our study landscape was disturbed and fragmented at least 50 years ago (and probably much longer), it can be assumed that the observed patterns of frog diversity represent reliable patterns for fragmented rainforest landscapes in Madagascar.

Understanding the factors determining matrix quality for animals is a key step to guide conservation action in fragmented landscapes. As one important action, it was suggested to increase the structural similarity between matrix and natural habitat as a recommendation for management of the matrix in fragmented landscapes (Barnes, Emberson, Chapman, Krell, & Didham, 2014; Prevedello & Vieira, 2010). According to our data, we suggest to guide conservation actions in this system, in

particular, to streams in the matrix and their adjacent gallery forests.

The remaining natural vegetation in and outside protected areas in Madagascar is decreasing and will be unable to preserve its biodiversity on a long term (Andreone et al., 2008). Therefore, we must understand responses of organisms to disturbance (Gardner et al., 2007) in order to create buffer zones and corridors combining both disturbed and natural habitats. In particular, more studies are needed that finely differentiate between different matrix types, and analyze which human-modified landscapes (e.g., disturbed primary habitat, secondary habitats, plantations, agricultural systems) have the most conservation potential, as well as studies identifying the proximate mechanisms of disturbance sensitivity.

Appendices

Appendix 1. Amphibian Species Detected per Habitat Type.

Species	MS	SV	BP	RF	TS	Collection numbers	GenBank accession
Hyperoliidae							
Heterixalus alboguttatus	0	0	1	1	LC	ZMB 81830, UADBA A 62096	
Heterixalus betsileo	1	1	1	0	LC	ZMB 81832 – ZMB 81833, UADBA A 43144, UADBA A 62097	
Mantellidae							
Blommersia blommersae	0	0	1	0	LC	ZMB 81837 – ZMB 81838, UADBA A 62066 – UADBA A 62067	KT240389 - KT240392, KT240624
Boophis albilabris	1	0	0	0	LC	ZMB 81842, UADBA A 43117	KT240636
Boophis elenae	1	0	0	0	NT	ZMB 81845, UADBA A 64015	KT240991 – KT240992
Boophis luciae	1	0	0	0	LC	ZMB 81847 – ZMB 81850, UADBA A 43119 - UADBA A 43120, UADBA A 62068, UADBA A 62070, UADBA A 62075	KT240638 - KT240639
Boophis luteus	1	0	0	0	LC	ZMB 81851 – ZMB 81853, UADBA A 62071, UADBA A 64017	KT240993 - KT240994
Boophis madagascariensis	1	1	1	0	LC	UADBA A 43122, UADBA A 62069	KT240642
Boophis marojezensis	1	0	0	0	LC	ZMB 81863	KT240643, KT240995
Boophis narinsi	1	0	0	0	EN	ZMB 81857 – ZMB 81862, UADBA A 43128 – UADBA A 43130, UADBA A 62072, UADBA A 62076 – UADBA A 62077	KT240393 - KT240395, KT240625

(continued)

Appendix 1. Continued

Species	MS	SV	BP	RF	TS	Collection numbers	GenBank accession
Boophis obscurus	0	0	0	1	NT	ZMB 81864, UADBA A 62073	
Boophis pyrrhus	1	0	0	0	LC	ZMB 81868, UADBA A 62074	KT240407 - KT240409
Boophis quasiboehmei	1	0	1	0	NT	ZMB 81869 – ZMB 81870, UADBA A 43125 - UADBA A 43127	
Boophis reticulatus	1	0	0	0	LC	ZMB 81871 – ZMB 81873, UADBA A 43123 - UADBA A 43124, UADBA A 64019	KT240997 - KT240998
Boophis tasymena	1	0	0	0	LC	ZMB 81875, UADBA A 62078 – UADBA A 62079	KT240396
Boophis tephraeomystax	0	0	1	1	LC	ZMB 81876, UADBA A 62080	KT240626 - KT240627,
Gephyromantis boulengeri	1	1	1	1	LC	ZMB 81879 – ZMB 81883, UADBA A 62082 - UADBA A 62084	KT240415 - KT240423, KT240648 - KT240659, KT240999
Gephyromantis decaryi	0	1	1	1	NT	ZMB 81884	KT240660
Gephyromantis enki	1	1	1	1	VU	ZMB 81885 – ZMB 81889, UADBA A 43134 - UADBA A 43136, UADBA A 62085 - UADBA A 62086	KT240424, KT240661 - KT240665
Gephyromantis sculpturatus	1	0	1	0	LC	ZMB 81892, UADBA A 43137 - UADBA A 43139, UADBA A 62087	KT240429 - KT240434, KT240672 - KT240687
Gephyromantis tschenki	1	0	1	0	LC	ZMB 81895 – ZMB 81896, UADBA A 43140, UADBA A 62088, UADBA A 64024	
Gephyromantis ventrimaculatus	1	0	0	0	LC	ZMB 81897, UADBA A 62089 - UADBA A 62090	KT240688 - KT240689
Guibemantis tornieri	1	0	0	0	LC	ZMB 81912, UADBA A 43143, UADBA A 62095	KT240437 - KT240440, KT240695 - KT240699
Mantidactylus betsileanus	1	0	1	1	LC	ZMB 81914, ZMB 81916, UADBA A 43147	KT240441 - KT240446, KT240710 - KT240712, KT240714
Mantidactylus femoralis	1	0	0	0	LC	ZMB 81937 - ZMB81938, UADBA A 43163, UADBA A 62099 - UADBA A 62100, UADBA A 62114	KT240447 - KT240455, KT240715 - T240728
Mantidactylus grandidieri	1	0	0	0	LC	UADBA A 43156, UADBA A 43161	KT240456 - KT240466
Mantidactylus majori	1	0	0	0	LC	ZMB 81940 – ZMB 81941, UADBA A 43157 - UADBA A 43158, UADBA A 64029 - UADBA A 64031	
Mantidactylus melanopleura	1	0	0	0	LC	ZMB 81942 – ZMB 81944	KT240467 - KT240471, KT240729 - KT240734
Mantidactylus paidroa	1	0	1	0	EN	ZMB 81956 – ZMB 81957, UADBA A 62103, UADBA A 62111 - UADBA A 62112	KT240472 - KT240485, KT240736 - KT240771
Mantidactylus sp. 9	1	0	0	0	NA	ZMB 81927 – ZMB 81930, UADBA A 43145 - UADBA A 43146, UADBA A 43154, UADBA A 62110	KT240602 - KT240613, KT240913 - KT240936
Mantidactylus sp. 13	1	0	0	0	NA	ZMB 81931 – ZMB 81932, UADBA A 43153, UADBA A 62098, UADBA A 62108 - UADBA A 62109	KT240486 - KT240494, KT240773 - KT240787
Mantidactylus sp. 24	1	0	0	0	NA	ZMB 81925, UADBA A 43160	KT240495 - KT240496, KT240788 - KT240792

(continued)

Appendix 1. Continued

Species	MS	SV	BP	RF	TS	Collection numbers	GenBank accession
Mantidactylus sp. 28	**1**	**0**	**0**	**0**	NA	ZMB 81918 – ZMB 81920, ZMB 81922, UADBA A 43149, UADBA A 62104 - UADBA A 62106	KT240497 - KT240530, KT240700 - KT240701, KT240793 - KT240844
Mantidactylus sp. 44	**1**	**0**	**0**	**0**	NA	ZMB 81947 – ZMB 81948	KT240531 - KT240538, KT240845 - KT240857
Mantidactylus sp. 47	**1**	**0**	**0**	**0**	NA	ZMB 81949 – ZMB 81951, ZMB 81953 – ZMB 81954, UADBA A 64040 - UADBA A 64041	KT240539 - KT240570, KT240858 - KT240896
Mantidactylus sp. 48	**1**	**0**	**0**	**0**	NA	ZMB 81933, ZMB 81935 – ZMB 81936, UADBA A 43162, UADBA A 62113, UADBA A 64037 - UADBA A 64039	KT240571 - KT240583, KT241005 - KT241009
Mantidactylus sp. 58	**0**	**0**	**1**	**0**	NA	ZMB 81955, UADBA A 62116	KT240584 - KT240599, KT240897 - KT240908
Mantidactylus sp. 64	**1**	**0**	**0**	**0**	NA	ZMB 81952, UADBA A 62115	KT240600 - KT240601, KT240909 - KT240912
Spinomantis sp. 2	**0**	**0**	**1**	**0**	NA	ZMB 81968, UADBA A 43168 - UADBA A 43169, UADBA A 62119	KT240619 - KT240622, KT240948 - KT240951
Microhylidae							
Anodonthyla boulengeri	**1**	**1**	**1**	**0**	NT	ZMB 81970 – ZMB 81973, UADBA A 43112 - UADBA A 43116, UADBA A 62063 - UADBA A 62064	KT240404, KT240635
Plethodontohyla notosticta*	**0**	**1**	**0**	**0**	LC	ZMB 81990	KT240628
Stumpffia miery	**0**	**0**	**1**	**0**	EN	ZMB 77453 – ZMB 77456, UADBA A 62120 – UADBA A 62124	KC351191 – KC351193
Stumpffia sp. 9	**1**	**1**	**1**	**0**	NA	ZMB 81994 – ZMB 81997, ZMB 81999, UADBA A 43170, UADBA A 62125 - UADBA A 62127, UADBA A 64052	KT240623, KT240952
Ptychadenidae							
Ptychadena mascareniensis	**1**	**0**	**0**	**1**	LC	ZMB 81829, UADBA A 43166 - UADBA A 43167	

Note. MS: matrix stream, SV: secondary vegetation, BP: banana plantation, RF: Rice fields; 1: present, 0: absent and actual threat status (TS) according to IUCN red list criteria (NA: not assessed, LC: least concern, NT: near threatened, VU: vulnerable, EN: endangered; IUCN, 2016). Nomenclature for so far undescribed candidate species refers to Vieites et al. (2009). Collection numbers are given for voucher specimens deposited at the Mention Zoologie et Biodiversité Animale, Faculté des Sciences, University of Antananarivo, Madagascar (UADBA), and voucher specimens deposited at the Museum für Naturkunde Berlin, Germany (ZMB). GenBank accession numbers are provided for sequence data.
*singleton not included in the analyses.

Appendix 2. Post Hoc Pairwise Comparisons Using Wilcoxon Rank-Sum Test for Species Richness Data.

	CFs	CFt	FFs	FFt	MS	SV	BP
CFt	0.0016	–	–	–	–	–	–
FFs	0.2486	0.0089	–	–	–	–	–
FFt	0.0016	0.2333	0.0089	–	–	–	–
MS	0.2855	0.0093	0.4158	0.0101	–	–	–

(continued)

Appendix 2. Continued

	CFs	CFt	FFs	FFt	MS	SV	BP
SV	0.0141	0.0255	0.0255	0.1526	0.0312	–	–
BP	0.0141	0.3398	0.0255	0.1526	0.0312	0.0602	–
RF	0.0093	0.0230	0.0192	0.4158	0.0249	0.2867	0.0378

Note. MS: matrix stream; SV: secondary vegetation; BP: banana plantation; RF: Rice fields; CF: continuous forest (RNP); FF: forest fragments; s: stream; t: terrestrial.

Appendix 3. Post Hoc Pairwise Comparisons Using Wilcoxon Rank Sum Test for AES Relative Abundance Data.

	CFs	CFt	FFs	FFt	MS	SV	BP
CFt	0.29	–	–	–	–	–	–
FFs	0.89	0.10	–	–	–	–	–
FFt	0.10	0.64	0.08	–	–	–	–
MS	1.00	0.06	0.74	0.06	–	–	–
SV	0.06	0.06	0.06	0.29	0.06	–	–
BP	0.44	1.00	0.25	1.00	0.06	0.08	–
RF	0.44	1.00	0.20	0.67	0.12	0.06	1.00

Appendix 4. Post Hoc Pairwise Comparisons Using Wilcoxon Rank Sum Test for VES Relative Abundance Data.

	CFs	CFt	FFs	FFt	MS	SV	BP
CFt	0.0017	–	–	–	–	–	–
FFs	0.7229	0.0096	–	–	–	–	–
FFt	0.0017	0.7229	0.0096	–	–	–	–
MS	0.6938	0.0102	0.5455	0.0107	–	–	–
SV	0.0154	0.0192	0.0261	0.0468	0.0314	–	–
BP	0.0154	0.8954	0.0222	0.6938	0.0296	0.0727	–
RF	0.0102	0.0727	0.0203	0.0468	0.0257	0.0391	0.6557

MS: matrix stream; SV: secondary vegetation; BP: banana plantation; RF: Rice fields; CF: continuous forest (RNP); FF: forest fragments; s: stream; t: terrestrial.

Appendix 5. Multiple Post Hoc Comparisons Between All Habitat Types.

	CFt	FFs	FFt	MS	SV	BP	RF
P-values:							
CFs	0.0028	0.0028	0.0028	0.0224	0.0280	0.0168	0.0112
CFt	–	0.0056	0.0028	0.0056	0.0112	0.0336	0.0112
FFs	–	–	0.0028	1	0.1372	0.1064	0.0616
FFt	–	–	–	0.0056	0.0756	1	0.0140
MS	–	–	–	–	0.2548	0.2212	0.2548
SV	–	–	–	–	–	1	0.6468
BP	–	–	–	–	–	–	0.2072

(continued)

Appendix 5. Continued

	CFt	FFs	FFt	MS	SV	BP	RF
F-values:							
CFs	16.77	6.42	23.20	4.45	8.86	6.63	18.19
CFt	–	14.41	11.65	12.12	6.75	5.24	16.95
FFs	–	–	9.42	2.14	5.24	3.40	14.54
FFt	–	–	–	11.03	4.00	2.46	17.47
MS	–	–	–	–	4.18	3.01	10.33
SV	–	–	–	–	–	0.58	4.75
BP	–	–	–	–	–	–	5.50

Note. Pairwise per MANOVAs, 9,999 permutations; MS: matrix stream; SV: secondary vegetation; BP: banana plantation; RF: Rice fields; CF: continuous forest (RNP); FF: forest fragments; s: stream; t: terrestrial. P values were Bonferroni corrected, that is, multiplied by the number of pairwise tests.

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