Diversity erosion beyond the species level: Dramatic loss of functional diversity after selective logging in two tropical amphibian communities

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A B S T R A C T

Assessing the effects of logging on different aspects of biodiversity and general ecosystem properties is of prime importance if the few remaining areas of intact tropical forest are to be efficiently protected. Commonly used measures of biodiversity may only inadequately reflect actual disturbance after logging and studies restricted to only one specific eco-region do not allow for generalizations of results. We hence measured the impact of selective logging on different levels of diversity of two tropical anuran communities in two geographically distinct eco-regions. Species-diversity patterns were incoherent both, within and between studies. In West Africa, species richness did not differ between primary and exploited forest sites, whereas South American anuran communities exhibited higher species richness in primary sites. Yet, in both eco-regions, functional diversity (FD) was higher in primary forest communities. Absolute values of FD were higher in South American anuran communities, despite higher species richness in West African communities. FD was higher in older recovery, as compared to younger recovery states, even though species-diversity did not differ significantly. Three major conclusions can be drawn from our results. 1. Scale matters: it is important to monitor different levels of biodiversity in order to reveal its actual loss after anthropogenic disturbance. 2. Time matters: the disturbance history of a site is important in order to detect patterns that otherwise remain unnoticed. 3. Geographic history matters at the local scale: whereas general patterns at higher diversity levels were identical in both eco-regions, species richness, species diversity and turnover patterns differed.

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1. Introduction

Timber harvesting is currently the most common and lucrative utilisation of tropical forest resources (Johns, 1996), and logging has been identified as one of the major threats to global vertebrate diversity in a number of studies (e.g. Thiollay, 1992; Lauck, 2005). Despite this fact, there is still little consensus on the actual impacts of human habitat alteration on different aspects of biodiversity. The same dissension persists with regard to appropriate diversity assessment methods and the importance of particular factors to be monitored (e.g. Hamer and Hill, 2000; Dumbrell and Hill, 2005). Yet, assessing the effects of logging activities on biodiversity and general ecosystem functions is of prime importance to

conservation, especially since remaining areas of intact tropical forest are coming under increasing pressure (Fimbel et al., 2001; Curran et al., 2004).

It is well established that the dynamics of tropical forests are strongly influenced by natural tree falls (Whitmore, 1991). However, gaps created by selective logging are typically larger and their frequency is being increased through ongoing logging operations (Vieira, 1995). This change in disturbance regime can induce changes in biodiversity and species composition (Clark, 1990; Denslow, 1995). It is also known to affect relative abundances in arboreal ants (Floren et al., 2001), insect herbivores (Basset et al., 2001), termites (Lima et al., 2000), lizards (Goldingay et al., 1996), birds (Thiollay, 1992; Sekercioglu, 2002; Laiolo et al., 2003), and mammals (Laurance and Laurance, 1996; Clarke et al., 2005). The direction of the effects of logging on forest communities is not consistent among different forests and different species groups. Both, increased and decreased diversity after selective logging have been reported (insect herbivores: Basset et al., 2001; birds: Craig and Roberts, 2005; butterflies: Dumbrell and Hill, 2005; bats, frogs, dung beetles: Pineda et al., 2005; for comparison of amphibian studies see Demaynadier and Hunter, 1998).

The measurement of diversity as it relates to disturbance poses a challenge due to the universal nature of rank abundance curves (Hubbell, 2001). The majority of species is usually very rare and only a few species are very common. Much of our knowledge of species responses is thus based on the study of only a few species. Additionally, diversity is usually compressed in a single number, which could be species richness per se or any form of information index, such as the Shannon or Fisher's α. We do not have adequate information on the sensitivity of these measures in systems that are subject to disturbance. Recent studies (e.g. Nummelin and Kaitala, 2004) however, indicate that commonly used indices may be unsuitable indicators of forest disturbance. One major concern involves the problem of distinguishing effects of species diversity from those of species composition. At the species diversity level, two communities, one consisting of 10 different, equally abundant species belonging to a single genus, the second consisting of 10 different, equally abundant species belonging to five different genera exhibit identical species richness, diversity and evenness, however, their composition is clearly distinct. Yet, these differences bear the potential of answering the question of why disturbances such as logging not only affect system descriptors, such as species richness, abundance, and diversity, but also drastically alter the system's dynamics (e.g. structure, composition, resilience, and compositional predictability). The latter has recently been shown to be the case in a West African amphibian community (Ernst and Rödel, 2005). The occurrence of functional redundancy amongst species suggests that functional diversity is the key determinant of these pattern changes. Composition and number of species is determined by biogeographical, i.e., regional filters, local dispersal filters, and site filters. The diversity that passes these filters does not necessarily represent a random sample with respect to functional traits. A reduction of species numbers is hence not an unbiased reduction of functional trait diversity. As evidence of links between functional diversity and ecosystem processes is constantly growing (Chapin

et al., 2000; Díaz and Cabido, 2001; Loreau et al., 2001; Kinzig et al., 2001), it appears to be of utmost importance to be able to quantify the loss of functional diversity after human disturbances, such as logging. This is especially true in the light of a growing awareness of the urgent need for an internationalization and standardization of environmental impact assessments, aimed at effectively protecting entire ecosystems. Species richness has been the most common measure of diversity in biodiversity-ecosystem functioning experiments. This approach assumes that species' delineations embody functionally significant information and are distinct. However, functional traits are more directly related to ecosystem processes, whereas organisms with very different phylogenies may be very similar functionally (Hooper et al., 2004).

Recently, the identification of functional groups and measures of functional diversity have attracted considerable interest. Mere functional group number has the advantage of simplicity, whereas more detailed indices have the disadvantage of being more difficult to estimate but the advantage of being more complete measures of diversity (Tilman and Lehman, 2001). Both aspects, simplicity of usage and completeness of information are important in the light of applied conservation biology. A simple measure of functional diversity (FD) that suites both requirements has been established by Petchey and Gaston (2002a) and is used in the following analyses. FD is a quantitative measure based on the distribution of species in trait space defined by a set of functionally important specific characteristics. Using only phylogenetic information, such as the number of different orders or families, etc., as a proxy for functional diversity may be too crude a measure to reveal the patterns of interest as has recently been pointed out by Blackburn et al. (2005). FD measures diversity at hierarchical scales simultaneously by avoiding any decision about the ecological significance of differences among species (Petchey and Gaston, 2002a). Previously developed measures of functional-group diversity require arbitrary decisions about the scale at which differences between species are functionally insignificant (Fonseca and Ganade, 2001; Root, 2001; Tilman et al., 2001). As a continuous measure, FD does not require grouping and therefore includes the large functional differences that delineate functional groups, as well as smaller differences that are commonly ignored by assigning species to functional groups (Petchey and Gaston, 2002b).

In the present study, we assay the impact of selective logging on the diversity of two tropical anuran communities in two geographically distinct eco-regions. Anuran communities have previously proven to be an appropriate model system for studies on the impacts of human-induced environmental changes on the dynamics of complex biological systems (Ernst and Rödel, 2005). They readily reflect landscape differences and exhibit a high sensitivity to habitat modification (Pineda et al., 2005). In our comparison we address three particular aspects of diversity changes after anthropogenic disturbance that highlight our results.

1. Effects attributable to the level of diversity being investigated (species richness and species-diversity vs. functional diversity). These analyses are performed in order to shed light on two commonly hypothesized mechanisms driving

the loss of species in communities. Trait random loss on one hand and functional trait-based loss on the other hand (e.g. Fonseca and Ganade, 2001; Díaz et al., 2003; Elmqvist et al., 2003). Both mechanisms are not necessarily mutually exclusive. However, in the first case changes at the species diversity level may be observed while functional diversity remains unchanged, whereas in the second case significant changes in functional diversity should be observed.

2. Effects attributable to disturbance history of sites. This addresses the temporal scale (time since disturbance), as temporal environmental variability may affect likelihood of functional redundancy or maintenance of coexistence (sensu Loreau, 2004).

3. Effects attributable to geographic history of sites (Neotropic realm vs. Afrotropic realm). This addresses the spatial scale, as investigations of species responses in one system cannot distinguish between dynamics that depend on local parameters and those that are general across systems. The two eco-regions are being compared in order to test for general patterns and hence potentially facilitate broad scale applicability of results across various tropical regions of international importance for conservation.

First we look at species richness and species diversity changes by comparing commonly used parametric and non-parametric indices and testing underlying species distributions for their suitability as indicators for disturbance. We then quantify the changes in FD between forest patches of different disturbance levels and history and discuss how these changes relate to ecosystem processes and predictability patterns in natural communities specifically addressing implications for conservation management.

2. Methods

2.1. Study areas and disturbance history

Taï National Park (TNP), in south-western Ivory Coast, is the largest remaining protected area of rain forest in West Africa. Our study sites (5°50′ N, 7°20′ W) comprised about 30 km^2 of primary and exploited rain forest. In TNP anthropogenic disturbance (selective logging, coffee and cacao plantations) ceased approximately 25 years ago. Past human influence was still visible in this area, e.g. absence of a closed canopy. For a detailed description of TNP see Riezebos et al. (1994). The Mabura Hill Forest Reserve (MHFR) is situated approximately 20 km south-east of the township Mabura Hill, Central Guyana (5°13′ N, 58°48′ W). It comprises an area of approximately 20 km^2 of primary rain forest and is part of the Wappu compartment located within a 500 km^2 Timber Sales Agreement concession. Disturbed sites were located outside the reserve's core area, within the main logging concession. Disturbed sites included in the analyses have been logged at different times (1988 and 1992) but with equal intensities (i.e. 19.5 trees or approximately 57 m^3 ha^{-1}). For a detailed description of MHFR and particular study sites see ter Steege et al. (1996) and Ernst et al. (2005).

2.2. Data acquisition

The field data were acquired between February 1999 and September 2002 (TNP) and November 2002 and September 2004 (MHFR). We established 10 transects, six in primary forest, four in exploited forest (TNP) and 11 transects, six in primary forest and five in exploited forest (MHFR), respectively. Two of the exploited forest transects in MHFR were located in an area that had been logged in 1992, the three remaining transects were located in an area in which logging occurred in 1988. As comparable data did not exist for TNP, we could not make a distinction within disturbed sites with reference to recovery time since logging. This comparison is hence restricted to the MHFR study. In both cases, sites included in the analyses are to be considered as classical chronosequences (sensu Plumptre, 1996).

Generally, transects covered all major forest types present in both habitat complexes thus circumventing a possible bias due to general habitat differences between primary and exploited forest sites.

Each rectangular transect had a total length of 600 m. Transects were subdivided in 25 m subunits (SUs; 24 SUs/transect). We registered a total of 15,007 individuals of 37 different anuran species belonging to eight families during 382.5 h of visual and acoustic transect sampling in TNP, and 7799 individuals of 30 different anuran species belonging to six families during 393.5 h of visual and acoustic transect sampling in MHFR, respectively. Additionally we performed visual and acoustic encounter surveys (VES and AES) in all available macrohabitats. These methods were supplemented by the installation of drift fences and bucket traps. Additional species (11 including two additional families in MHFR and 18 including one additional family in TNP) were recorded during AES, VES, and through the use of drift fences and bucket traps. The sampling was designed to ideally cover the entire anuran community including terrestrial and arboreal, as well as aquatic and fossorial species. In a comparative analysis of amphibian monitoring programs using transects in East Africa, West Africa (including the data presented herein), Madagascar and Borneo, we recently have shown that ⩾20 independent transect walks seem to be necessary to achieve a species saturation (Veith et al., 2004). During this study, every transect was walked independently at least 41 times and additional searching techniques were regularly applied. It is thus justified to assume that the local communities have been almost completely recorded.

Detailed descriptions and discussion of the transect design, data acquisition routine, tests for spatial autocorrelation, and an evaluation of various methods have been published earlier (Rödel and Ernst, 2004; Ernst and Rödel, 2005). Hence, we herein restrict descriptions to relevant modifications and aspects specific to this study.

2.3. Statistical analyses

We assessed species richness as the number of species observed (S_{obs}) within a particular transect or habitat complex (primary vs. exploited forest), respectively. Species richness of a particular community as it appears in dendrograms is hence given as S_{obs}.

For all species-diversity calculations we used relative abundance values given as specimens per transect hour (th), hence taking into account variations in sampling effort between transects (Hofer and Bersier, 2001). We chose one parametric measure (Fisher's α = FA) and four commonly used non-parametric measures (Shannon index = H', and respective evenness measure = E, Simpson's index = $1/D$, Berger–Parker index = $1/d$, McIntosh's measure = MD, and respective evenness measure = ME) for comparison. Log-series distributions for FA were tested for goodness-of-fit. Diversity indices and χ^2-type goodness-of-fit tests were calculated using the software package Bio-Dap (by G. Thomas, Resource Conservation Fundy National Park, Alma New Brunswick Canada), following standard procedures (Magurran, 2004). We tested for differences between habitat complexes and disturbance states using Mann–Whitney U tests. Analyses were based on respective transect values.

Calculation of functional diversity (FD) follows Petchey and Gaston (2002a). Calculations were performed using the function Xtree written by O. Petchey. FD was standardized to vary between 1.0 (highest FD) and 0.0 (lowest FD). All analyses, except for calculations of diversity indices, were performed using the freely available software R (http://www.r-project.org).

A crucial factor in the analysis of functional diversity is the selection of parameters to be included in a model intended to identify functional groups in natural communities. All members of the community face identical challenges: dispersal (importance in less mobile taxa, such as anurans, assumed to be low), establishment and persistence, each characterized by one of a number of life history traits on which selection can take place. We therefore chose the following traits to be included in species trait matrices used to calculate FD and delimitate functional (response) groups (FRG): diel activity (diurnal, nocturnal); general habitat preference of adult frogs (arboreal, aquatic, terrestrial, fossorial); reproductive activity (offset wet season, onset wet season, peak rainy season, explosive breeder, prolonged breeder); reproductive mode (MHFR: 14 modes, TNP: 10 modes) sensu Duellman and Trueb (1994); ecomorphological guild of tadpoles (MHFR: 14 guilds, TNP: 9 guilds) sensu McDiarmid and Altig (1999). In the few cases, in which respective data were not available (three species with unknown tadpoles in TNP and two species with unknown tadpoles in MHFR), we used conservative estimations by resorting to available data of closely related species. Species trait matrices were binary (i.e., 0/1) matrices. This circumvents the problem of arbitrary weighting of particular parameters by keeping weights identical. We generated distance matrices and respective dendrograms using the unweighted pair-group clustering method (UPGMA) and Euclidean distances. Qualitative relations between FD, species richness, and composition are generally robust to changes in distance metric and clustering method (Petchey and Gaston, 2002a). The relative importance of species richness and composition for FD is controlled by the effective dimensionality of trait space and the latter is influenced by either an increase (decrease) in the number of traits, the absolute correlation between traits or the different weighting of traits. We controlled for two factors simply by choosing identical categories in all analyses, hence keeping possible correlations identical and by using unweighted traits. The number of effective traits included in the trait matrix, however, depends to a certain degree on the species that make up the communities. Due to differences in the number of occurring reproductive modes and ecomorphological guild of tadpoles, it was higher in MHFR (39 traits vs. 30 in TNP). The index is not affected, however, by the splitting of a species into two functionally identical species with the same total abundance, and thus proves to be fairly robust (Mason et al., 2005).

The relationship between taxonomic diversity and functional diversity depends on the level of taxonomic resolution. The relevance of this correlation in natural systems is subject to debate (Hooper et al., 2004). In order to guarantee that the observed patterns are not exclusively due to differences in taxonomic diversity, we controlled for phylogenetic effects. We simply calculated measures of phylogenetic diversity (PD) and tested for phylogenetic differences among anuran communities between the two eco-regions. In an effort to guarantee comparability between FD and PD we used identical algorithms. PD analyses were based on trait matrices containing binary phylogenetic information exclusively, i.e. taxonomic affiliation of a particular species from suborder down to generic level (36 categories in TNP and 41 categories in MHFR) following current taxonomy according to Frost (2002) and revisions of Faivovich et al. (2005).

Branch cut-off values for delimitation of FRGs in functional group allocation assessments were set at 1.5 on the Euclidean distance scale. The comparatively low value was chosen to guarantee high ecological resolution but is otherwise arbitrary. Choosing lower values would have resulted in an approximation to the species level and, hence would not have yielded additional information.

3. Results

3.1. Species richness and species diversity

Species richness patterns differed between the two geographic realms. Whereas species richness of primary forest communities was significantly higher in the MHFR, species richness did not significantly differ between primary and exploited forest communities in TNP (MHFR: Mann–Whitney U, $Z = 2.74$, $P < 0.05$, $N = 11$; TNP: Mann–Whitney U, $Z = 1.28$, $P > 0.05$, $N = 10$). For pooled S_{obs} values of respective communities compare Fig. 1.

Analyses of species diversity and tests for goodness-of-fit of log series distributions revealed two major patterns.

First: communities of primary forest transects were generally more diverse than those of exploited forest transects with one exception in TNP-communities (FA index). Evenness was higher in primary sites in TNP-communities only (Table 1). Range and means of indices rank at about the same order of magnitude in both realms. The same holds true for the respective primary/exploited ratios. High values indicated a reduction in species-diversity after logging (Table 1). Data followed classic log-series distributions in all cases, as confirmed by χ^2-tests, significant at the conventional $\alpha = 0.01$ level. The goodness-of-fit, however, varied. In case of TNP, exploited forest data showed a better fit ($\chi^2 = 10.87$, $p > 0.01$) than primary forest data ($\chi^2 = 15.87$, $p > 0.01$), whereas this trend was re-
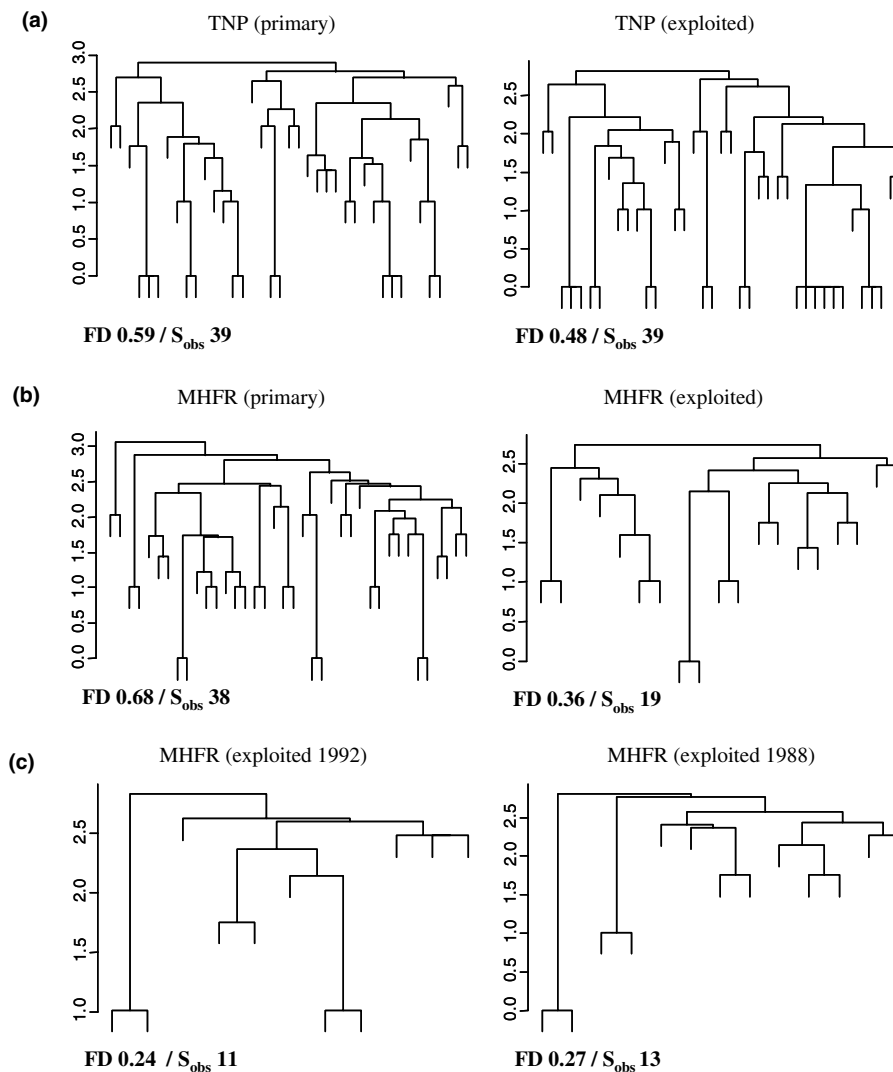
Fig. 1 – UPGMA-dendrograms (Euclidean distance) based on species trait matrices (each matrix based on all records within a particular habitat complex). Given are FD standardized to vary between 1.0 and 0.0 and S_{obs} = number of observed species for respective communities. Note different scales on distance axis. (a) TNP communities: primary forest community (left), exploited forest community (right). (b) MHFR communities: primary forest community (left), exploited forest community (right). (c) MHFR communities: exploited forest (logged in 1992) community (left), exploited forest (logged in 1988) community (right).

versed in the MHFR data, where primary forest data exhibited the better fit ($\chi^2 = 14.98$ vs. 18.82, $p > 0.01$). However, in the case of MHFR, data from two recovery states (logged in 1988 vs. 1992) were pooled. A second pattern emerged when looking at differences between the recovery states.

Species richness did not differ significantly between communities of the two recovery states (Mann–Whitney U, $Z = 1.16$, $p > 0.05$, $N = 5$). For pooled S_{obs} values of respective communities compare Fig. 1.

Second: communities of older recovery states (MHFR, logged in 1988) were not significantly more diverse than those of more recent recovery states (Table 1). Likewise evenness was not significantly higher in older recovery states. Ratios were generally high, indicating a lower diversity in younger recovery states, with one important deviation. Even though

not significant, the FA ratio was comparatively low in younger recovery states (Table 1). This deviation becomes clearer when consulting goodness-of-fit tests. Goodness-of-fit was better in older recovery states ($\chi^2 = 7.24$ vs. 17.19, $p > 0.01$). When looking at these results as a chronosequence, moving from a primary state to a 'recent' disturbance (logged in 1992) and on to an older recovery state (logged in 1988), we received the following picture. The fit to the log-series distribution was comparatively low in primary forests and even lower in more recently disturbed sites. It reaches an optimum in older recovery sites. When looking at time since disturbance, disturbed sites in TNP (disturbance event approximately 25 years ago) could be grouped along with sites that have been logged in 1988 at the MHFR, hence potentially explaining the comparatively better fit in the TNP data for exploited sites.

Table 1 – Ranges, means, and ratios in five species-diversity and two evenness indices for Mabura Hill Forest Reserve (MHFR) and Taï National Park (TNP) communities

Area	Range/mean				Ratio	
	FA(prim)	FA(exp)	FA(exp) 92	FA(exp) 88	FA(prim)/FA(exp)	FA(exp) 88/FA(exp) 92
TNP	2.1–4.8/3.5	2.3–2.7/2.4	x	x	1.5 n.s.	x
MHFR	2.3–5.6/4.1	1.3–2.0/1.7	1.7–1.9/1.8	1.3–2.0/1.7	2.4**	0.9 n.s.
	H'(prim)	H'(exp)	H'(exp) 92	H'(exp) 88	H'(prim)/H'(exp)	H'(exp) 92/H'(exp) 88
TNP	1.6–2.7/2.3	1.1–1.7/1.4	x	x	1.6*	x
MHFR	1.6–2.7/2.2	0.8–1.6/1.3	0.8–1.1/1.0	1.3–1.6/1.5	1.7**	1.5 n.s.
	E(prim)	E(exp)	E(exp) 92	E(exp) 88	E(prim)/E(exp)	E(exp) 92/E(exp) 88
TNP	0.6–0.8/0.8	0.4–0.6/0.5	x	x	1.6**	x
MHFR	0.6–0.8/0.7	0.4–0.7/0.6	0.4–0.5/0.4	0.6–0.7/0.7	1.2 n.s.	1.8 n.s.
	1/D(prim)	1/D(exp)	1/D(exp) 92	1/D(exp) 88	1/D(prim)/1/D(exp)	1/D(exp9)2/1/D(exp) 88
TNP	4.0–12.3/8.8	3.0–3.8/3.0	x	x	2.9**	x
MHFR	3.3–11.2/6.9	1.6-4.1/2.9	1.6–2.2/1.9	3.1-4.1/3.7	2.4*	2.0 n.s.
	1/d+(prim)	1/d+(exp)	1/d+(exp) 92	1/d+(exp) 88	1/d+(prim)/1/d+(exp)	1/d+(exp9)2/1/d+(exp) 88
TNP	2.9–6.8/5.0	1.8–2.7/2.1	x	x	2.4**	x
MHFR	2.0–6.0/3.8	1.3–2.8/2.1	1.3–1.6/1.4	2.4–2.8/2.6	1.8*	1.9 n.s.
	MD(prim)	MD(exp)	MD(exp) 92	MD(exp) 88	MD(prim)/MD(exp)	MD(exp) 92/MD(exp) 88
TNP	0.5–0.7/0.7	0.4–0.5/0.4	x	x	1.8**	x
MHFR	0.5–0.7/0.6	0.2–0.5/0.4	0.2–0.3/0.3	0.4–0.5/0.5	1.5*	1.7 n.s.
	ME(prim)	ME(exp)	ME(exp) 92	ME(exp) 88	ME(prim)/ME(exp)	ME(exp9)2/ME(exp) 88
TNP	0.7–0.9/0.8	0.5–0.7/0.6	x	x	1.3**	x
MHFR	0.6–0.9/0.8	0.3–0.7/0.6	0.3–0.5/0.4	0.7–0.7/0.7	1.3 n.s.	1.8 n.s.

Prim = Primary forest (TNP: N = 6/MHFR: N = 6), exp. = exploited forest TNP: N = 4/MHFR: N = 5), exp 92 = logged in 1992 (N = 2), exp 88 = logged in 1988 (N = 3). Significance levels for Mann–Whitney U-tests: * = $P < 0.05$, ** = $P < 0.01$ and n.s. = not significant). Fisher's α = FA, Shannon index = H', and respective evenness measure = E, Simpson's index = 1/D, Berger–Parker index = 1/d, McIntosh's measure = MD, and respective evenness measure = ME.

3.2. Functional diversity and functional group allocation and loss

Analogous to species-diversity, two major trends could be identified in the analysis of FD, however, with significant deviations regarding their direction.

First: communities of primary forest were functionally more diverse than those of exploited forest (MHFR: Mann–Whitney U, $Z = 2.74$, $P < 0.05$, $N = 11$; TNP: Mann–Whitney U, $Z = 1.92$, $P < 0.05$, $N = 10$). Absolute values of FD were higher in MHFR communities, despite the higher species richness in TNP communities. In the latter, species richness did not differ between primary and exploited forest sites, whereas FD differed significantly. TNP communities exhibited high species turnover (16 species recorded in exploited forest but not in primary forest). In MHFR communities, species richness differed between primary and exploited forest sites but no turnover occurred. Exploited forest communities represented an impoverished subset of primary forest communities (compare Appendix A). As a result, the discrepancy between primary and exploited sites as expressed through primary/exploited FD ratios was noticeably larger in MHFR communities (Table 2).

Second: communities of older recovery states (MHFR, logged in 1988) were functionally more diverse than those of more recent recovery states (logged in 1992; Mann–Whitney U, $Z = 1.73$, $P < 0.05$, $N = 5$), yet still significantly less diverse than those of primary forest sites (Table 2).

The comparison of functional dendrograms elucidates the differences very strikingly. Dendrograms based on data derived from exploited forest communities are by far less complex. They contain fewer branches and nodes than their primary forest counterparts (Fig. 1).

Despite differences in species richness, the number of functional (response) groups (FRG) within communities of the respective geographic realms was very similar (TNP, West Africa: 24 vs. MHFR, northern South America: 25) at the chosen branch cut-off value. In both cases, groups that were most affected (i.e. missing in exploited forest) contained species that rely on lotic or large and/or permanent lentic habitats for reproduction, whereas groups that contain species having reproductive modes that are independent from permanent open water (direct developers, phytotelmata breeders) showed the highest resilience. For tables illustrating species composition, functional group allocation and loss see Appendix A.

The analysis of phylogenetic diversity (PD) revealed only marginal differences between communities of the two eco-regions. PD values were almost identical in both cases (MHFR: mean of 0.221 in primary forest and 0.155 in exploited forest; TNP: mean of 0.222 in primary forest and 0.150 in exploited forest). Phylogenetic differences, hence do not account for the differences observed in FD and the two eco-regions can therefore be compared appropriately.

4. Discussion

4.1. A new dimension of diversity loss

Our results illustrate that simple measures of diversity, such as species richness or species diversity may not adequately reflect the real dimension of biodiversity loss after anthropogenic disturbance. In case of the West African anuran communities, species richness was identical in both, primary and exploited forest communities. Yet, functional diversity FD differed significantly. In case of the Guyanan anuran communities, the loss of FD was more pronounced. Here, species richness was also reduced more drastically but no species turnover occurred. Relative differences between FD values in the two eco-regions might be attributable to relative differences in effective trait space and therefore the importance of species richness and composition for FD. Yet, this was not tested systematically. For the same reasons, differences in FD between primary and exploited forest communities are true differences, rather than mere effects of mere changes in species richness (compare Petchey and Gaston, 2002a.).

In a recent study, Brown and Gurevitch (2004) found no statistical differences in plant species richness and species diversity in selectively logged forest sites of two different recovery states in Madagascar. However, sites that were once logged never recovered native species richness, as invasive species persisted in the communities. Hence, logging significantly altered species composition. Summerville and Crist (2002) report on similar findings in lepidopteran communities of differently disturbed forest stands in Ohio. Here, in concordance with our results from the anuran communities of TNP, species richness did not differ significantly between selectively logged and unlogged stands, whereas significant compositional differences occurred.

Common measures of biodiversity do not specifically account for these differences and may thus conceal the actual extent of biodiversity loss after disturbance. Our results

Area	Range/mean				Ratio	
	FD(prim)	FD(exp)	FD(exp) 92	FD(exp) 88	FD(prim)/FD(exp)	FD(exp) 88/FD(exp) 92
TNP	0.263–0.436/0.354	0.211–0.282/0.244	x	x	1.45*	x
MHFR	0.258–0.496/0.394	0.196–0.231/0.213	0.196–0.198/0.197	0.223–0.231/0.228	1.85*	1.16*

Table 2 – Ranges, means, and ratios in functional diversity (FD) for Mabura Hill Forest Reserve (MHFR) and Taï National Park (TNP) communities

Prim = primary forest (TNP: $N = 6$/MHFR: $N = 6$), exp. = exploited forest (TNP: $N = 4$/MHFR: $N = 5$), exp 92 = logged in 1992 ($N = 2$), exp 88 = logged in 1988 ($N = 3$). Significance level for Mann–Whitney U-tests: * = $P < 0.05$). FD was standardized to vary between 1.0 and 0.0.

indicate that conserving a large proportion of the functional traits of members (species) of a particular community may require conserving a large proportion of all species that make up the community. Not only was the extend of diversity loss greater than expected, extinctions also followed a non-random pattern. Even though this has not systematically been tested using appropriate null models, extinctions appeared to be trait dependent as has previously been shown to be the case in four natural communities, one of which being an animal assemblage (Petchey and Gaston, 2002b). Lea et al. (2005) report on similar findings in amphibian communities in Nigerian landscapes undergoing long-term degradation. They detected a shift from a predominance of forest specialists to a predominance of generalists, while species diversity remained stable or even increased. In some cases both, trait-neutral, as well as trait-based mechanisms seem to operate simultaneously to influence diversity loss (Suding et al., 2005). Even though we cannot entirely rule out its possible occurrence, we do not have evidence for trait random species loss. Trait-based mechanisms clearly appear to be more influential.

Generally, deterministic patterns of biased extinctions appear to be an intuitively correct assumption and this fact has been acknowledged in previous studies (Huston et al., 2000; Díaz et al., 2003 but compare Fonseca and Ganade, 2001), however, the order and characteristics of the diversity loss are still controversially debated. It has recently been pointed out that determinants of extinction risk differ between plants and animals and that extinctions are trophically biased (Duffy, 2003). Animal extinction was reported to be biased toward species of higher trophic levels and following this perspective, species of high functional importance to the ecosystem (e.g. Paine, 2000). Similar results were published by Petchey et al. (2004). Our results indicate that the resolution of these extinction patterns is actually more fine-grained within a particular trophic level. In case of our model system, i.e. amphibian communities consisting of mainly opportunistic feeders (Duellman and Trueb, 1994), extinctions are not primarily trophically biased. The predisposition for extinction was rather related to specific adaptations and hence functional traits of the species involved.

Not as obvious, yet even more alarming from a conservation or management perspective, was the result concerning the patterns found in different recovery states. The failure to detect significant differences in diversity of communities in different recovery states at the species-level on one hand and the observation of significant differences in FD on the other hand, is an indication for the insufficiency of traditional diversity measures that do not regard qualitative differences between species. However, these very differences, i.e. species' identity not number per se, seem to influence ecosystem functioning tremendously (see O'Connor and Crowe, 2005).

Grouping species in functional entities may simplify the system by reducing the number of distinct units and, as a result enlarges the number of individuals for each unit at the expense of resolution in ecological responses. In the light of the neutral theory of biodiversity and biogeography (Hubbell, 2001), this loss of resolution may not be a crucial factor when looking at the community level, given that community members are ecologically equivalent on a per capita basis (e.g. Bell, 2000, 2001). It may seem as if in case this quasi functional redundancy is established, the loss of a particular species will be irrelevant to ecosystem functioning. However, under the influence of disturbance, the simplification of the system may in fact be more severe and fundamental as entire functional groups are eliminated from the system, hence leading to tremendous structural impoverishment. The loss of diversity to the point that entire functional effect groups disappear will obviously have the greatest impact on ecosystem processes. This is of particular importance if groups that go extinct or become ecologically insignificant contribute to essential ecosystem services (Elmqvist et al., 2003). Functional impoverishment following anthropogenic disturbance may also be the key to understanding changes of predictability patterns in natural communities, as has recently been pointed out by Ernst and Rödel (2005). If investigations concentrate on mere changes at the species-diversity level, significant alterations will remain undetected.

The dynamics of underlying species distributions and their reaction to disturbance and subsequent recovery show that it is crucial to consider disturbance history of sites when assessing the biodiversity contained therein. Apparently, classic distributions, such as the log-series distribution regarded in this study, follow dynamics that are tremendously affected by disturbances imposed on the system. This is of vital importance for a realistic assessment of the performance power of diversity indices such as Fishers's α (FA) that assume particular distributions in a natural community. General applicability of these and similar indices is hence restricted to particular systems and/or disturbance states and generalisations should hence be made with the necessary precautions. In communities that exhibit bimodal residence time patterns (i.e. composed of resident and transient species) the fit of abundance distributions may also depend on the group membership of respective species. Abundance distributions of transients were found to match neutral model predictions (log-series), whereas residents conformed to log-normal distributions (Magurran and Henderson, 2003). These patterns are predicted whenever immigration from regional species pools and habitat heterogeneity is involved. They appear to be persistent even in patchy environments (Schwilk and Ackerly, 2005) and may hence be important in anthropogenically altered systems although the latter has not been investigates so far.

For generalizations to be meaningful it is essential that predictions have been tested in systems that differ sufficiently, yet share some key factors that make them comparable in the first place. This becomes obvious when looking at differences between patterns in communities of the two geographic realms under comparison. Despite different geographic and evolutionary histories, general patterns at higher diversity levels appeared to be equal in both realms. Nevertheless, the systems under comparison differed in very important aspects, hence possibly limiting assertions and general predictive power. Perhaps the most prominent difference being the high species turnover in the West African communities on one hand and the mere impoverishment of "primary" forest communities in exploited sites

in Guyana. These differences are also reflected in FD values and bear significant implications for conservation strategies.

The same is true with regard to the use of common species-diversity measures. The measures tested here failed to produce coherent results, both within and between studies and should, hence, only be applied with the necessary caution. Concepts for management and conservation planning will be based on incorrect or at least incomplete assumptions if the studies that they are implementing fail to address higher levels of diversity, such as functional diversity and general β-diversity patterns.

4.2. Implications for conservation strategies

The common practice of land management planning by assessing standard system descriptors of natural communities, such as species richness or species diversity bears a certain danger of inadequately representing particular taxa. Important management conclusions may not be drawn as crucial patterns remain concealed. An example is the difference in FD values between particular recovery states reported in this study. At this point, however, it would be premature to draw final conclusions based on this particular pattern. Anuran communities showed evidence of recovery i.e., communities of older recovery states were functionally more diverse than those of more recent once, yet the time span of four years may be too short to explore faunal recovery patterns, even in organisms with high population turnover rates and generation cycles, such as amphibians. Nonetheless, if applied to sites in which differences in recovery time are more distinguished or within the scope of long-term pre-/post-disturbance studies, our approach is likely to yield results of high relevance for sound management efforts and conservation. It is especially interesting as the role of disturbed systems in conserving the remaining biodiversity will most likely increase in the near future.

Alternative approaches putting more emphasis on life history studies have recently been proposed to accommodate this insufficiency (e.g. Lauck, 2005). However, as direct measurement of all aspects of an entire ecosystem or even a single community is usually far too time consuming and costly, it seems to be more important to aim at maximum flexibility rather than optimality of the method being used in order to account for varying field situations. Our analyses of two amphibian communities of differing evolutionary history illustrate that the assessment and monitoring of changes of FD after disturbance may represent an efficient tool integrating, practicability and information and optimising flexible use in various systems. In the study presented here, species loss has been shown to be largely driven by functional-based mechanisms, at least in case of severe habitat alteration due to anthropogenic disturbance. This mechanism may not be scale independent. However, rather than focusing on particular species or even susceptible functional groups, the monitoring of changes in FD after human disturbance will likely prove to be an essential conservation strategy. This is especially true as resources for long term single taxon studies are ever more limited and holistic approaches receive even more attention. Practically this may mean that efforts should be made to conserve the largest possible number of functional traits (i.e. aiming for high FD values) in order to safeguard important system parameters and guarantee proper long-term ecosystem functioning. This may require the conservation of a large proportion of all species that make up the community. Yet, this is only possible if a range of habitats and hence local communities are being conserved. Obviously, this requires the protection of large tracts of forest. This is of particular importance since amphibian diversity in primary habitats has previously been shown to be determined by the dynamics of compositionally unpredictable local communities and because local community composition in these highly dynamic systems appears to vary across the spatial range as a result of stochastic patterns of extinction and colonization events (Ernst and Rödel, 2005).

The conservation of functional traits may also be important with respect to the diversity-community invasibility hypothesis (Elton, 1958; Symstad, 2000). Recently communities with higher functional group diversity have been shown to be more resistant to invasion by an exotic species and functional traits of particular species have been proven to influence the success of invasion (Xu et al., 2004).

Land management concepts are often based on immediate conservation needs that require fast responses and practicable rapid assessment techniques. However, the complex nature of natural communities and the multiple aspects of biodiversity at different levels, make it necessary to incorporate processes acting on different organizational scales. Neglecting important community patterns and aspects, such as functional diversity, may render serious long-term conservation efforts impossible and futile.

Acknowledgements

Appendix A

See Tables A.1 and A.2.
See Figs. A.1 and A.2.

| Table A.1 – Species composition and functional group (FG) – allocation of anuran communities in TNP				
	Species	Complete	Primary	Exploited
FG 1	*Kassina lamottei*	x	x	
FG 2	*Phrynobatrachus tokba*	x	x	x
FG 3	*Cardioglossa leucomystax*	x	x	x
FG 4	*Arthroleptis sp1*	x	x	x
	Arthroleptis sp2	x	x	x
FG 5	*Hoplobatrachus occipitalis*	x		x
FG 6	*Silurana tropicalis*	x	x	x
FG 7	*Aubria subsigillata*	x	x	
FG 8	*Bufo togoensis*	x	x	x
FG 9	*Bufo taiensis*	x	x	
	Astylosternus occidentalis	x	x	x
	Bufo superciliaris	x	x	
FG 10	*Phrynobatrachus phyllophilus*	x	x	x
FG 11	*Phrynobatrachus villiersi*	x	x	x
	Ptychadena aequiplicata	x	x	
FG 12	*Aubria occidentalis*	x	x	
FG 13	*Ptychadena superciliaris*	x		x
	Ptychadena pumilio	x		x
	Ptychadena mascareniensis complex 1	x		x
	Ptychadena mascareniensis complex 2	x		x
	Ptychadena bibroni	x		x
	Ptychadena longirostris	x		x
	Amnirana albolabris	x	x	x
	Phrynobatrachus plicatus	x	x	x
	Phrynobatrachus gutturosus	x	x	
	Phrynobatrachus alleni	x	x	x
	Phrynobatrachus calcaratus	x		x
FG 14	*Phrynobatrachus fraterculus*	x	x	
	Phrynobatrachus annulatus	x	x	
	Phrynobatrachus taiensis	x	x	
FG 15	*Bufo maculatus*	x		x
	Bufo regularis	x		x
FG 16	*Phrynobatrachus accraensis*	x		x
	Phrynobatrachus liberiensis	x	x	x
FG 17	*Hemisus guineensis*	x	x	
FG 18	*Acanthixalus sonjae*	x	x	x
	Phrynobatrachus guineensis	x	x	x
FG 19	*Afrixalus vibekensis*	x	x	
FG 20	*Phlyctimantis boulengeri*	x	x	x
	Hyperolius soror	x		x
	Hyperolius nienokouensis	x	x	
	Hyperolius fusciventris	x		x
	Hyperolius lamtoensis	x	x	
FG 21	*Leptopelis hyloides*	x	x	x
	Leptopelis macrotis	x	x	
	Leptopelis occidentalis	x	x	x
FG 22	*Chiromantis rufescens*	x	x	x
FG 23	*Afrixalus dorsalis*	x		x
	Afrixalus nigeriensis	x	x	x
FG 24	*Hyperolius chlorosteus*	x	x	x
	Hyperolius sylvaticus	x	x	x
	Hyperolius zonatus	x	x	
	Hyperolius picturatus	x		x
	Hyperolius concolor	x	x	x
	Hyperolius guttulatus	x		x

Species order reflects order of appearance (branch order from left to right) in the functional dendrogram that is based on the complete community. The latter serves as a reference to illustrate functional group loss. Primary = primary forest community, Exploited = exploited forest community. Cut-off value for delimitation of functional (response) group (FRG) = 1.5 in functional dendrogram.

Table A.2 – Species composition and functional group (FG) – allocation of anuran communities in MHFR						
	Species	Complete	Primary	Exploited	Exploited 88	Exploited 92
FG 1	*Synapturanus mirandaribeiroi*	x	x			
	Ctenophryne geayi	x	x			
FG 2	*Pipa aspera*	x	x			
	Pipa pipa	x	x			
FG 3	*Hypsiboas boans*	x	x			
FG 4	*Osteocephalus oophagus*	x	x	x	x	x
	Trachycephalus resinifictrix	x	x	x	x	x
FG 5	*Hypsiboas geographicus*	x	x			
	Hypsiboas granosus	x	x	x	x	
FG 6	*Osteocephalus taurinus*	x	x	x	x	x
FG 7	*Osteocephalus leprieurii*	x	x			
FG 8	*Scinax rubra*	x		x		
FG 9	*Hypsiboas calcaratus*	x	x			
	Hypsiboas crepitans	x		x		
FG 10	*Dendropsophus minutus*	x		x		
	Dendropsophus brevifrons	x	x			
	Dendropsophus minusculus	x	x			
FG 11	*Hyalinobatrachium sp.2*	x	x			
	Hyalinobatrachium sp.1	x	x			
	Hyalinobatrachium nouraguensis	x	x			
FG 12	*Phyllomedusa tomopterna*	x	x			
	Phyllomedusa bicolor	x	x			
	Phyllomedusa vaillantii	x	x			
FG 13	*Atelopus spumarius*	x	x			
FG 14	*Colostethus sp.*	x	x	x	x	x
	Allobates femoralis	x	x	x	x	
FG 15	*Adenomera andreae*	x	x	x	x	x
FG 16	*Eleutherodactylus marmoratus*	x	x	x	x	x
	Eleutherodactylus zeuctotylus	x	x			
FG 17	*Rana palmipes*	x	x			
FG 18	*Bufo margaritifer*	x	x	x		x
	Dendrophryniscus minutus	x	x	x	x	x
FG 19	*Bufo guttatus*	x	x	x	x	x
FG 20	*Bufo marinus*	x	x	x	x	x
FG 21	*Lithodytes lineatus*	x	x			
FG 22	*Leptodactylus bolivianus*	x	x			
	Leptodactylus petersii	x	x			
FG 23	*Leptodactylus knudseni*	x	x	x	x	x
	Leptodactylus mystaceus	x	x	x		
FG 24	*Leptodactylus rhodomystax*	x	x	x	x	
FG 25	*Physalaemus sp.*	x	x	x		

Species order reflects order of appearance (branch order from left to right) in the functional dendrogram that is based on the complete community. The latter serves as a reference to illustrate functional group loss. Primary = primary forest community, Exploited = exploited forest community, Exploited 92 = community of forest logged in 1992, Exploited 88 = community of forest logged in 1988. Cut-off value for delimitation of functional (response) group (FRG) = 1.5 in functional dendrogram.
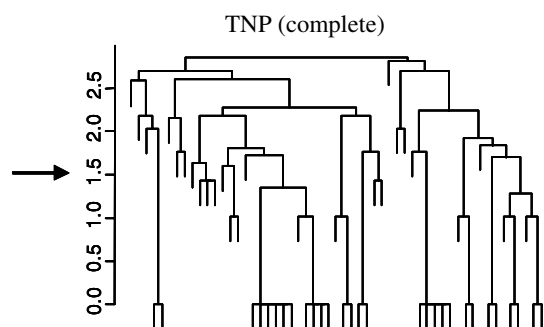
Fig. A.1 – UPGMA-dendrogram (Euclidean distance) based on complete TNP community. Arrow indicates cut-off value.
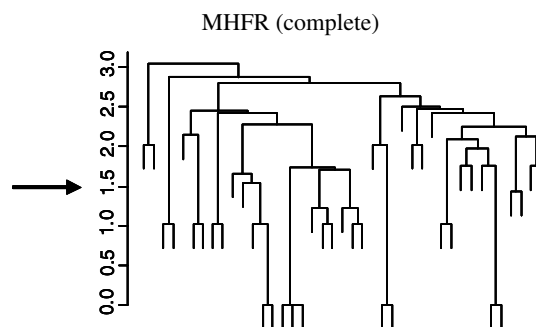
Fig. A.2–UPGMA-dendrogram (Euclidean distance) based on complete MHFR community. Arrow indicates cut-off value.

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