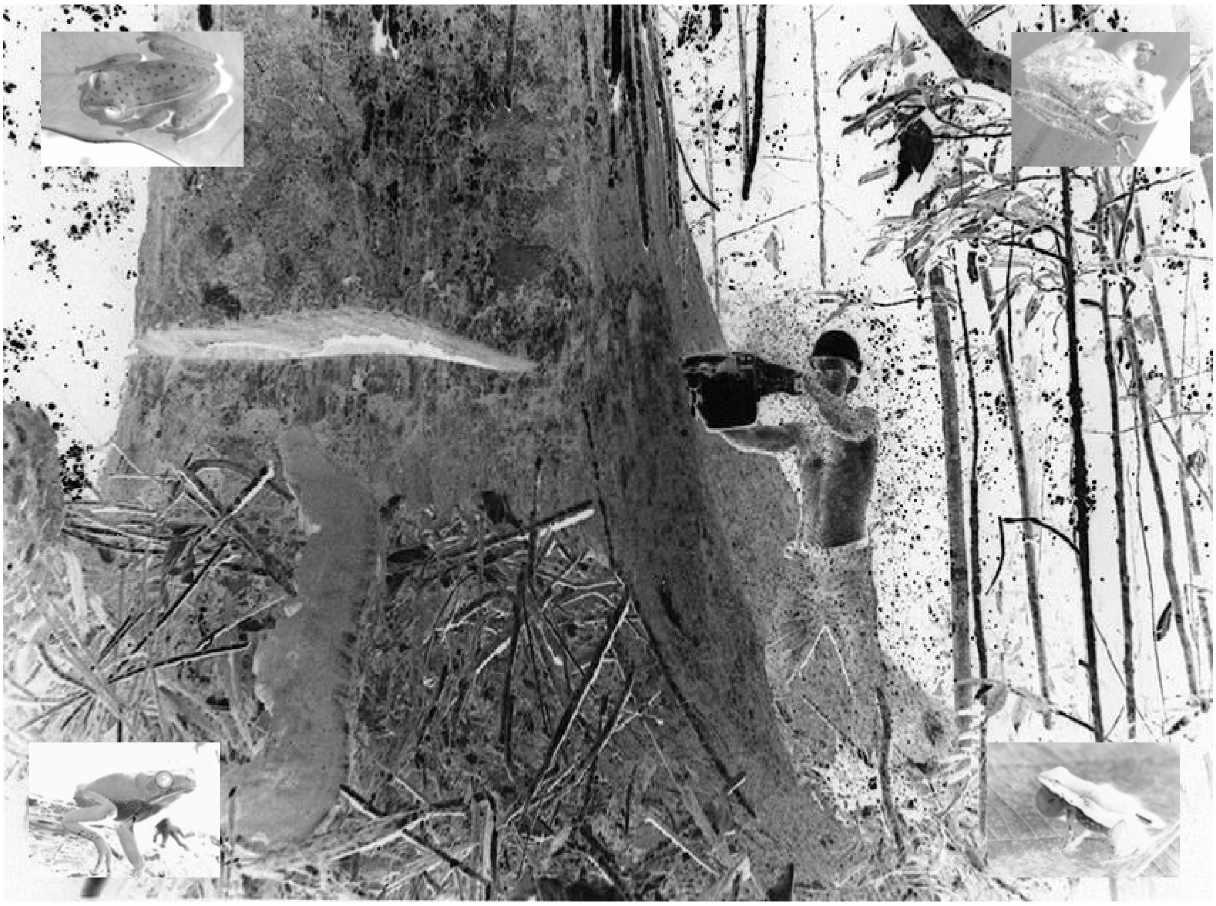
ANURAN COMMUNITIES ON THE CUTTING EDGE: ANALYSING PATTERNS AND PROCESSES IN ANTHROPOGENICALLY ALTERED TROPICAL FORESTS



Studies from the Guiana Shield and West Africa

Dissertation zur Erlangung

des naturwissenschaftlichen Doktorgrades

der Bayerischen Julius-Maximilians-Universität Würzburg

Anuran Communities on the Cutting Edge: Analysing Patterns and Processes in Anthropogenically Altered Tropical Forests

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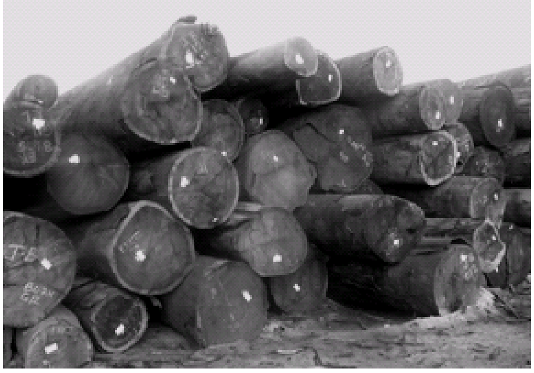
PREFACE

> **(…)"The theory of ecosystems contains an important distinction between what is complicated without any Gestalt or unifying principles (…) and what is complex (…) A multiplicity of more or less lawful, interacting factors may operate together to form a unity, a system (…) Organisms, ways of life, and interactions in the biosphere in general, exhibit complexity of such an astoundingly high level as to color the general outlook of ecologists. Such complexity makes thinking in terms of vast systems inevitable. It also makes for a keen, steady perception of the profound human ignorance of biospherical relationships and therefore of the effect of disturbances" (…)**
>
> ARNE NAESS
>
> (Phil. Founder Of Deep Ecology, 1972)

Complexity [not complication] and the effects of disturbances on complex systems are the very objects of concern addressed in the present thesis. An investigation of complex systems usually begins with the search for patterns, unifying principles if you like. In the following studies, these patterns are consequentially analysed on the basis of modern theories on biodiversity and community ecology with a special emphasise on the role of anthropogenic disturbance (logging) and its influence on general community properties.



Timber lot Mabura Hill, Guyana

R. E.

LIST OF PUBLISHED CONTRIBUTIONS

At the time of submission of this thesis, the following contributions have either been accepted for publication or were submitted to the peer reviewed journals listed in parentheses. Other contributions have previously been published in peer reviewed journals as indicated by full reference.

Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization – ***Ecotropica 10: 1-14***.

On the cutting edge – The anuran fauna of the Mabura Hill Forest Reserve, Central Guyana – ***Salamandra 41: 179-194***

Community assembly and structure of tropical leaf litter anurans – ***submitted to Ecotropica***.

Anthropogenically induced changes of predictability in tropical anuran assemblages - ***Ecology 86: 3111-3118***

Disturbance related predictability patterns of community composition in two tropical treefrog assemblages – ***not yet submitted***

The impacts of selective logging on three sympatric species of *Leptodactylus* in a central Guyanan rainforest - ***submitted to Amphibia-Reptilia***

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

Amphibian communities in disturbed forests: lessons from the Neo- and Afrotropics – ***in Tscharntke et al. (eds.):*** **Stability of tropical rainforest margins linking ecological, economic and social constraints.** ***Springer – Environmental Science Series (in press)***

CHAPTER 1

GENERAL INTRODUCTION

1.1 Communities: The search for basic patterns and elementary processes

Just as evolutionary biology can be regarded as the all-embracing and interconnecting discipline in all modern fields of biology, so can the study of communities be seen as the overarching concept in ecology, without which, patterns observed at lower organizational levels appear out of context. The following statement by Victor Shelford (1929) may hence serve as a guiding principle to be kept in mind throughout the following paragraphs of this thesis. It highlights the discipline's function as a connecting theme.

(…) "ecology is the science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associations is not properly included in the field of ecology"(…)

VICTOR SHELFORD
(Laboratory and Field Ecology, 1929)

Despite its metamorphosis from a purely descriptive discipline preoccupied with identifying and listing species found in a particular location to a "hard" analytical science with significant methodological advances that makes use of a wealth of sophisticated mathematical models and statistical tools, fundamental questions in community ecology have changed little in the past decades. And these questions are astoundingly simple: Who lives with whom and why? This in turn leads directly to another basic question and an important goal that community ecologists try to achieve, namely to understand the origin, maintenance, and consequences of biological diversity within local communities. It is this search for basic and complex community patterns and the processes that create them that drives modern community ecology. Very often these patterns and processes are simply experimentally intractable and experimental manipulations of entire communities are impossible. As community patterns are the consequence of a hierarchy of interacting processes, the information to be acquired for meaningful interpretation must come from various sources such as mathematical models, statistical tests, and experiments. However, in revealing patterns and identifying the underlying processes, community ecology will prove an indispensable tool providing the necessary knowledge in order to wisely manage ecological systems that we as biological organisms depend on, natural eco systems that are increasingly stressed and fragmented and that we have damaged through either habitat destruction or overexploitation.

Box 1.1: Community patterns – the hierarchy of interacting processes

The species composition of a given local community is the result of various hierarchically interacting processes. The upper limit on the species composition of a local community is set by the composition of the regional species pool. Membership in the regional species pool is constrained by, e.g. geological history of respective regions, and the evolutionary processes of speciation within different taxonomic groups. .Membership in the local species pool, on the other hand, is more constrained by local site filters related to e.g. natural disturbances, microclimatic factors and potential interspecific interactions.

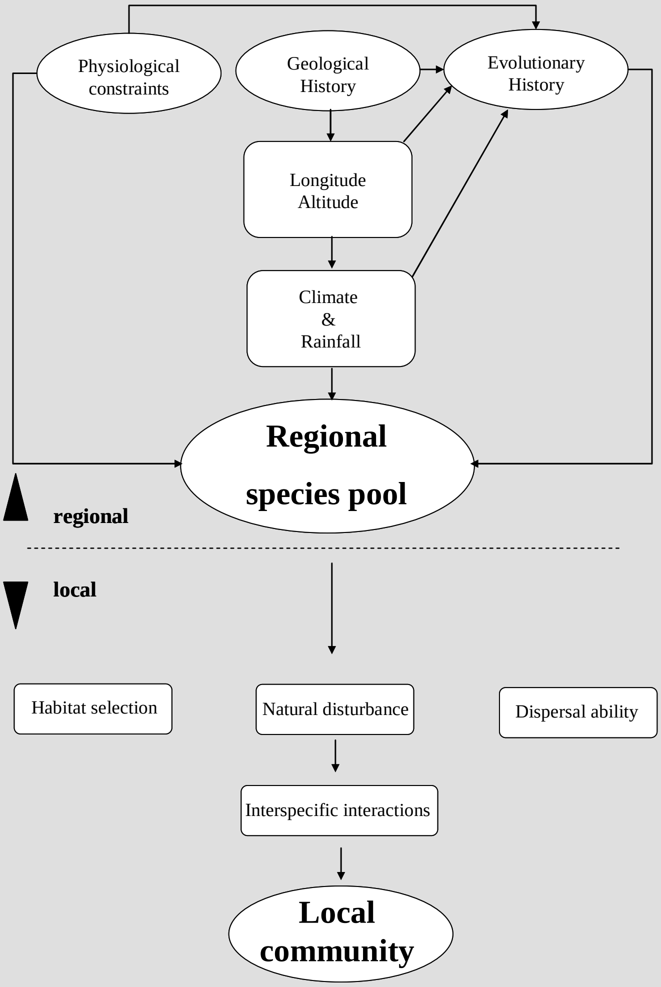
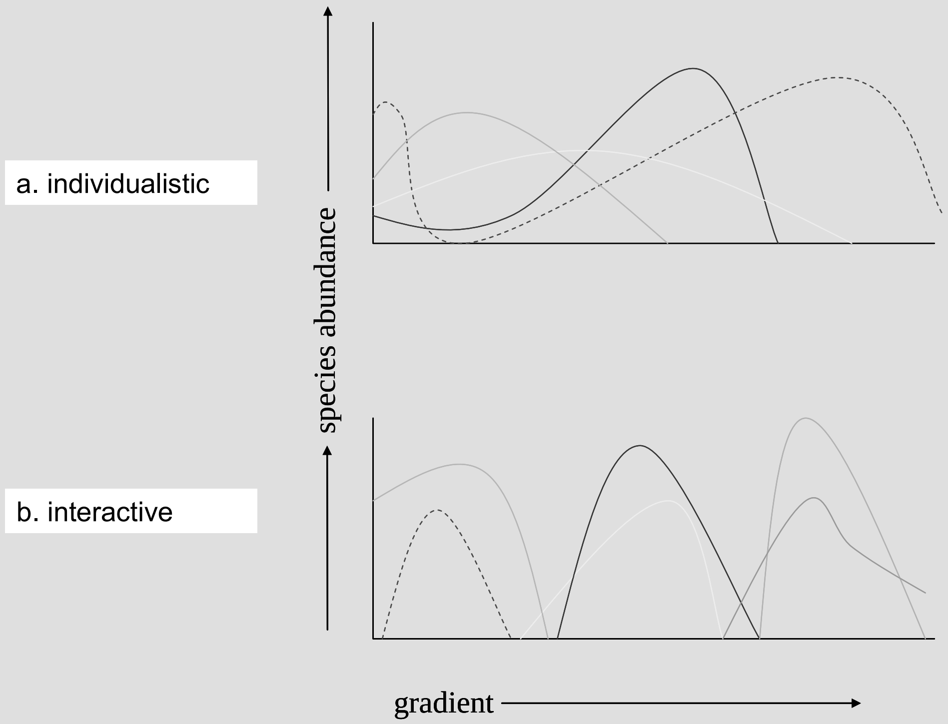


Fig.1.1: *Simplified diagram of community assembly processes (modified after Morin 1999)*

Few of the major controversies in ecology, if any, have been decisively settled. One of the central unresolved problems in community ecology is the question for the sources of species diversity within and among natural communities. Historically, explanations differ in stressing two opposing mechanisms, equilibrium mechanisms on one hand and nonequilibrium mechanisms on the other hand. It is uncertain whether the dynamics of species in natural communities conform to stable equilibria or to various kinds of nonequilibrium processes and results from various studies seem to contradict each other. The role of anthropogenic disturbances and their impact on the actual mechanisms at work has previously not been addressed directly. This is the case despite the fact that (natural) disturbance dynamics are inherent to another fundamental question that has vigorously been debated since the early controversies about the processes of temporal change [succession] among plant ecologists. The debate is ongoing and the problem has not yet been resolved ultimately. It centers on the possible ways in which communities are organized. The discussion focuses on two opposing views. Communities are either seen as integrated, repeatable, tightly structured species assemblages that have evolved as units (Clements 1916, Pianka 1973, Diamond 1975, Roughgarden 1976), or they are viewed as the result of species-specific responses to the particular set of physiological constraints imposed by particular features of the environment (Gleason 1926, Whittaker 1956, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Homes et al. 1986). In the first view, known as the interactive concept, biotic effects are considered to be the major structuring force, and the observed pattern is often interpreted to be the result of interspecific interactions (Schoener 1968, Brown and Lieberman 1973, Pianka 1973, Diamond 1975, Brown and Munger 1985, Dayan and Simberloff 1994, Smith and Remington 1996). In contrast, according to the second concept, known as the individualistic-continuum concept, particular species assemblages are thought to simply reflect the fortuitous correspondence of independent life histories of species in one place and time (Gascon 1991). Strong stochastic elements to recruitment in the component species and environmental fluctuations appear to result in variations in community composition (Hubbell 1979, Chesson and Warner 1981, Dayton 1984, Huston 1994, Allmon et al. 1998) thus reducing the possible role of competition in structuring communities through predation, as well as habitat and resource heterogeneity and simply by chance or unpredictable environmental changes. As so often in the natural sciences, pluralism may be the key in many if not all controversies in ecology. Different kinds of organisms may obey different rules and different determining factors may prevail in different environments and at different scales. A distinction between wrong and right solutions to ecological problems is hence not trivial. As Ernst Mayr (1998) put it: (…) “Many controversies may simply be true cases of pluralism” (…)

Box 1.2: Communities – independent populations or distinct species assemblages?

The graphs below show the hypothetical abundance distributions of species along an environmental gradient as expected by a.) the individualistic-continuum concept of community organization and b.) the interactive concept of community organization.



a.)

Individualistic-continuum concept sensu Gleason 1926:

'communities' are generally characterized as having species that distribute themselves over ecological gradients, independently of the distributions of other species. Particular 'communities' simply reflect the fortuitous correspondence of independent life histories in one place and time.

vs.

b.)

Interactive concept sensu Clements 1916:

communities are generally characterized by the interdependence of species' occurrence or absence. Biotic effects are considered to be the major structuring force, and the observed pattern is often interpreted to be the result of positive or negative interspecific interactions.

1.2 Two realms: The origins of similarities and differences in two tropical forests

It is nearly impossible to understand the similarities and differences between modern tropical rain forests without keeping their geological past in mind. Differences are sometimes striking (e.g. between Afrotropical and Neotropical Herpetofaunas) and seem to support the idea of independent histories. At the height of Matthew's theory of continental biogeography (Matthew 1915), Africa and South America were supposed to have had no relationships whatsoever. With the rise of Wegner's theory of continental drift (Wegner 1929) and contemporary protagonists, such as Du Troit (1937) it became widely accepted that Australia, India, Madagascar, Africa, and South America were once connected and separated from each other during the late Jurassic, Cretaceous, and early Tertiary (160 to 50 million years ago). The sequence and timing of this break-up has had a significant influence on modern biogeographical patterns (McLoughlin 2001). Today it is well established that most of the land masses that currently support tropical rain forest have a common origin in the ancient southern super continent of Gondwana (Morley 2000).

Africa had been isolated in the late Cretaceous and early Tertiary. This isolation produced an enormous radiation in an endemic mammal clade, the Afrotheria. Despite the now long-lasting (at least 20 million years) connection between Asia and Africa, faunal exchange in rain forest taxa has been limited, due to climatic constraints.

The isolation of South America lasted much longer (over 70 million years) and ended only three million years ago, when the Isthmus of Panama rose, connecting the two American continents.

Mixed forest, central Guyana

Box 1.3: Location of field studies

The field studies presented in the following paragraphs are all located in two tropical areas that share a common geological history (compare plate 1.1). Both were once part of the same pangean formation formed during the Precambrian period (4,500 – 570 million yrs. ago). The development of the Guiana Shield (to the north), the Brazil Shield (to the south), and the west African Shield (to the east) took place approximately 2,100 million yrs. ago. Roughly 2,030 million yrs later, both the South American and the African plate had been completely separated by the Atlantic Ocean.

Fig.1.2: *Location of field studies (arrows). From west to east: i) Mabura Hill Forest Reserve (MHFR), central Guyana - 05° 09.322' N, 058° 41.983' W -; ii) Taï National Park (TNP), south-western Côte d'Ivoire - 05° 50.003' N, 007° 20.536' W -.*

Taï National Park (TNP), in south-western Ivory Coast, is the largest remaining protected area of rain forest in West Africa. The study sites comprised about 30 km² of primary and exploited rain forest. 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. It comprises an area of approximately 20 km² of primary rain forest and is part of the Wappu compartment located within a 500 km² Timber Sales Agreement concession. Disturbed sites were located outside the reserve's core area, within the main logging concession. For a detailed description of MHFR and particular study sites see ter Steege et al. 1996; Ernst et al. 2005.

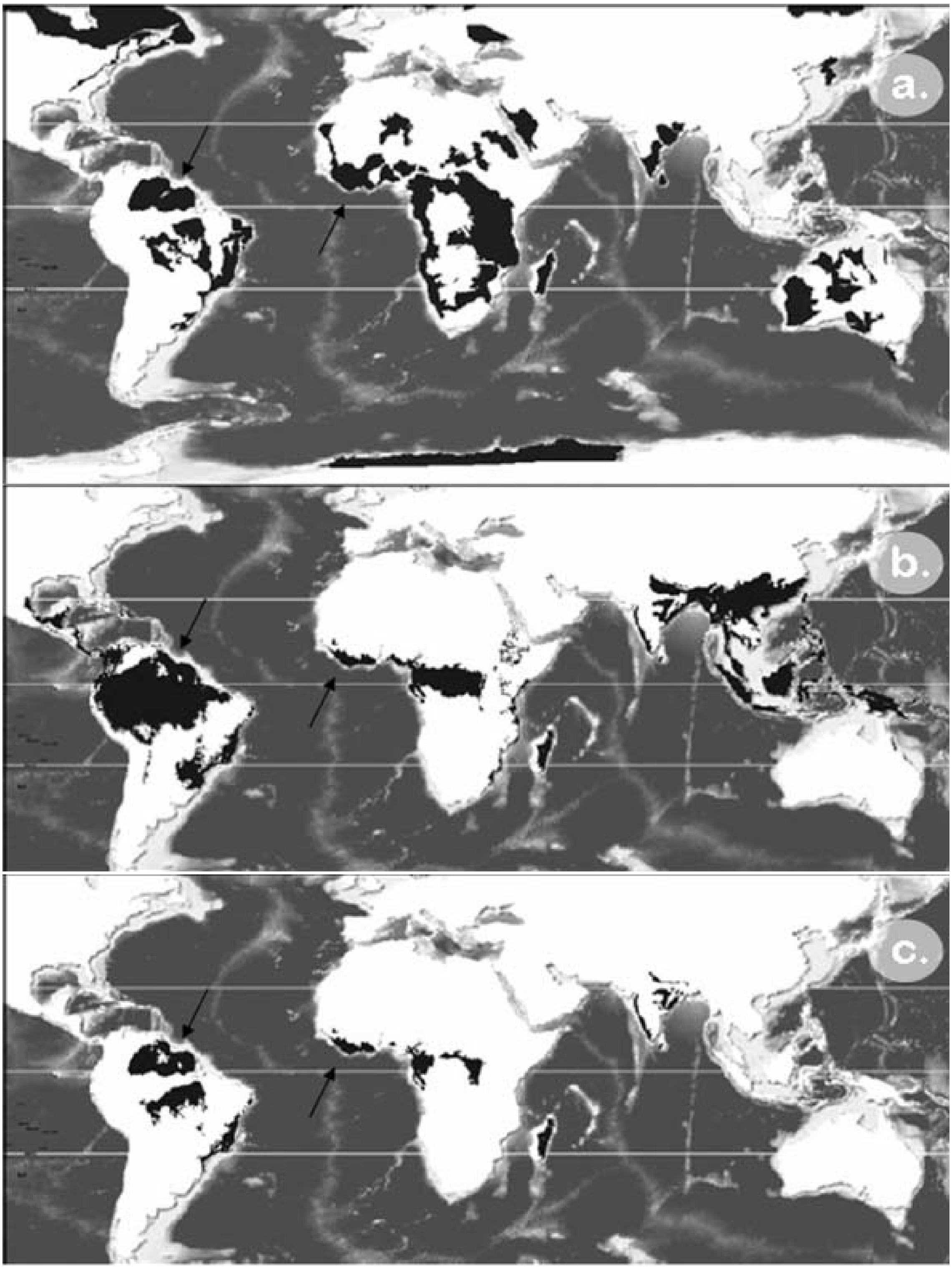


Plate 1.1: Map showing location of field studies (arrows) and a: major areas of exposed Precambrian rock, b: maximum extend of recent (sub) tropical forest cover (losses due to deforestation not included), c: major tropical forest areas situated on Precambrian formations; from Hammond (2005).

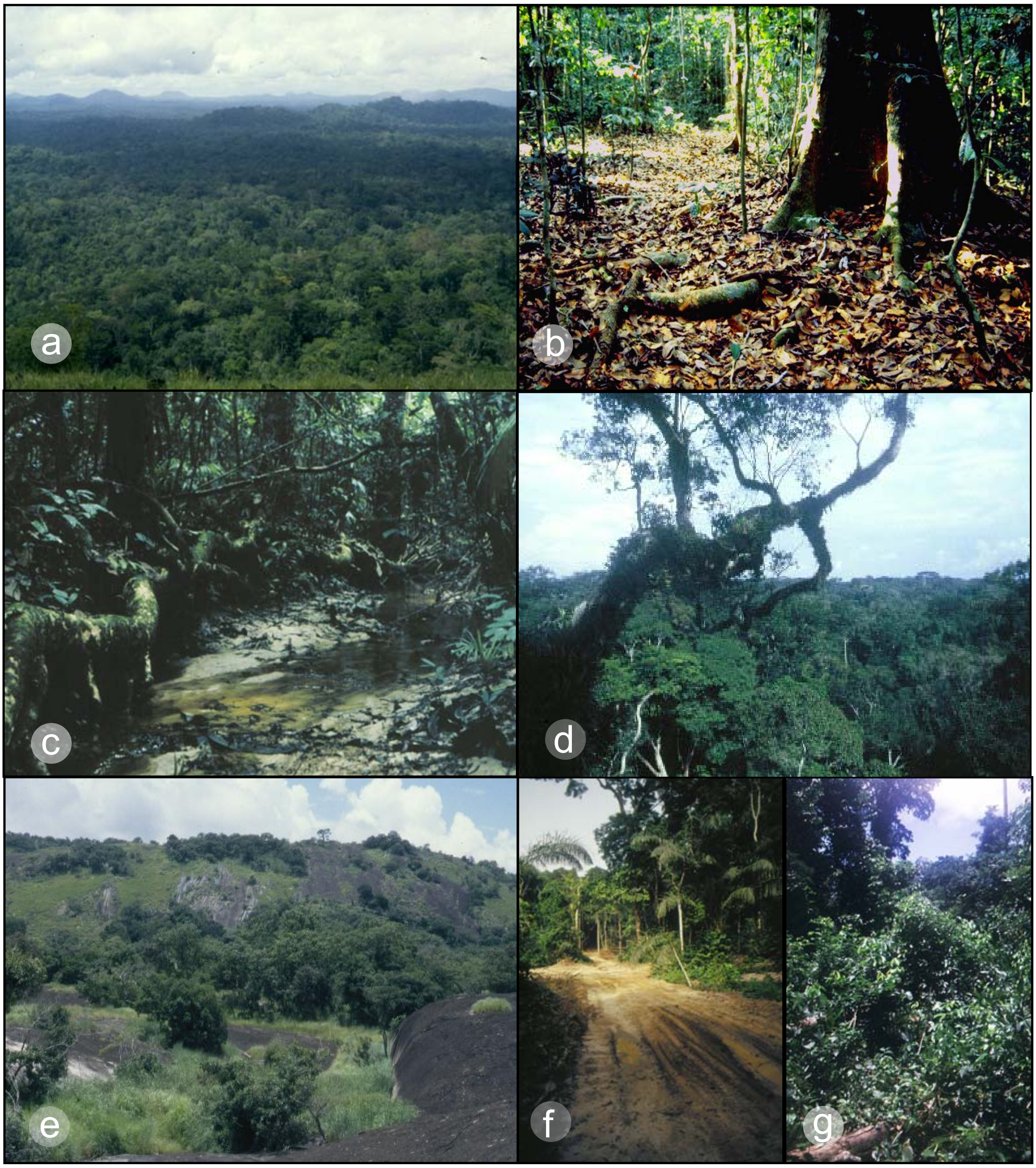


Plate 1.2: Forest habitats in southwest Côte d'Ivoire – **a**: lowland rain forest **b**: *Eremospatha macrocarpa-Diospyros mannii* type forest; **c**: creek in primary forest on quartzite; **d**: large emergent tree in primary forest; **e**: granitic outcrop (inselberg) vegetation; **f**: logging road; **g**: secondary forest app. 10 yr. after logging.

Plate 1.3: Forest habitats in central Guyana – **a**: lowland rain forest (mixed forest); **b**: upland mixed forest; **c**: black water creek in mixed forest on laterite; **d**: Mora forest on brown sand; **e**: black water creek in Wallaba forest on white sand; **f**: mixed Greenheart forest; **g**: Mixed Morabukea forest.

Plate 1.4: Logging in central Guyana – **a**: bucking Purpleheart; **b**: Purpleheart stump; **c**: skidder damage; **d**: slider damage; **e**: haling road 15 yr. after logging ; **f**: understory in mixed Greenheart forest 15 yr. after logging; **g**: gap in mixed Greenheart forest 15 yr. after logging.

1.3 The cutting edge: Logging and the history of anthropogenic disturbance

Tropical forests cover 6 % of the planet, however, an estimated area of 142, 000 km^2 is lost every year equalling 1 % of the total tropical forest area. Most extant tropical rain forests have been logged or will be logged in the near future (Whitmore 1997). Logging intensities, however, vary. They can range from single tree removals with only one tree removed every few hectares (e.g. mahogany, *Swietenia macrophylla* in South America) to high intensity logging of more than 15 trees removed per hectare (e.g. dipterocarps in southeat Asia), or even clear felling with total removal of entire stands. The most common form of timber extraction from tropical forest is selective logging. This kind of logging aims at the extraction of a limited number of tree species with high commercial value, which generally comprise only a small proportion of the trees present in a given area. Technological advances and an increasing demand for wood products, however, resulted in a substantial increase in the number and intensity of logging operations world wide (Dawkins and Philip 1998). The term 'selective logging' has hence become misleading, because, even though only a small percentage of the trees are felled for timber today still, a larger percentage is killed or damaged during logging operations (e.g. Jonsson and Lindgren 1990). Logging damage may thus be random much like natural disturbance. Logging mimics natural disturbance as it creates canopy openings and debris piles that are comparable to the natural Chablis found in mature rain forests. Yet, the scale and intensity of the disturbance caused may be different as compared to natural disturbances. Estimated annual rates of gap formation in natural forests range between 1 -2 % (Hartshorn 1990, van der Meer and Bongers 1996). Low-dynamical forests, such as the tropical rain forest of Guyana (ter Steege and Hammond 2001), fall well below these rates (0.4 %, van Dam and Rose 1997). Gaps created by logging are frequently larger than natural tree fall gaps and usually more gaps per ha can be found (van der Hout 1999). Large parts of forest landscapes are affected at the same time, even if logging operations are restricted to small patches, while natural disturbance, with the exception of large scale disturbances, such as fires or hurricanes, will only affect smaller parts at a time. Another important deviation from natural disturbance patterns is the level of selectivity.

In any case, logging has direct impacts on the biotic and a-biotic conditions of the forest (Uhl and Vieira 1989, Johns 1997, Vitt et al. 1998). As mentioned above, the direct impacts of selective logging include the removal of harvested trees and associated damage to the residual stand but it also leads to significant disturbance of the soil and catchments hydrology caused by the extraction using heavy machinery.

Box 1.4: Logging in Guyana – The History of Anthropogenic Disturbance

Commercial timber extraction has been practiced in Guyana for over 200 years (Vieira 1980), however, deforestation rates have remained consistently low (Burgess 1993). Yet, declines in harvestable timber volumes in Southeast Asia and West Africa caused multinational timber companies to draw their attention to South American countries, still rich in terms of forestry resources, such as Guyana (Colchester 1994). Traditional logging practices have not been much different from those in other parts of the tropics. Uncontrolled, selective logging was carried out until 1871 when first attempts were made to regulate cutting. Nowadays, the forests of Guyana are classified in four categories, State Forests, State Lands, Amerindian Lands and Private Property. With a total of 13.8 million hectares, State Forests currently comprise the largest portion of the total forest area. Permissions for concessions varying in size from patches smaller than 8,000 ha (State Forest Permission) to areas larger than 24,281 ha (Timber Sales Agreement) are given out to timber companies that often log uncoordinatedly, but almost always without much care for the remaining stand or future yields (van der Hout 1999). The officially granted extraction rate is 20 m^3 ha^{-1} and actual extraction rates usually range between 10-20 m^3 ha^{-1}(ter Steege 2001). However, rates often do not exceed 13 m^3 ha^{-1}, due to limited occurrence of commercially interesting species (GFC 2004). Yet, in some areas actual extraction rates may very well exceed these values and the control of illegal logging operations may be problematic. Timber harvesting has traditionally focused on only a few commercial species. One species in particular, the endemic *Chlorocardium rodiei* (Greenheart), constituted 70 % of the country's timber exports (ter Steege et al. 1996). However, recently efforts have been made to promote the diversification of forest products. By 2004, Greenheart represented only 17 % of all log exports (GFC unpubl.). Log production has risen from an average annual output of 160,000 m^3 yr^{-1} between 1981 and 1992 to 520,000 m^3 yr^{-1} in 1997. Van der Hout (1999) estimated that if extraction continued at the same rate and intensity, all allocated forest areas will have been logged within the next 40 years. Large parts of the allocated area, however, are unsuitable for timber extraction, either because they are non-productive in terms of commercial species, or because access is difficult. Pressure on forested areas not yet allocated, hence increases and accessible forest could thus be used up in less than 40 years. The increase in extraction rates has only recently come to a halt. According to an official market report log production rates (this excludes chainsaw lumber, roundwood, split wood, and fuelwood, all of which show increases in production) have decreased, reaching an annual output of 236,215 m^3 in 2003 (GFC 2003).

Fig.1.3: *log market Mabura Hill, Central Guyana*

Unlike most forms of natural disturbance, logging creates new habitats through soil compaction that in combination with increasing solar radiation due to an open canopy, leads to alterations in the hydro regime. Forest understoreys are characterized by strong vertical and horizontal gradients in light availability (Poorter and Arets 2003) with irradiance levels of 1-2 % of full sunlight under closed canopy. In tree fall gaps, however, irradiance levels can reach up to 25 % (Chazdon and Fetcher 1984). Although gap formation will locally change a multitude of microclimatic and edaphic parameters, increased light availability and hence intensified solar radiation is the most obvious change (van Dam 2001).

Forest recovery after logging depends highly on the severity of the impact. High logging intensities may have a disastrous effect on forest recovery (e.g. Chai and Udarbe 1997) and intensive exploitation may simply cause devastation (Nepstad et al. 1999). Selectivity is yet another problem as the selective removal of large reproductive trees may have severe consequences for regeneration (van Ulft 2004) and hence population development (Tilman et al. 1994). The overall impact on biodiversity and the forest ecosystem is difficult to quantify. Even though the conservation value of secondary and logged forests is recently obtaining more and more recognition (Chazdon 1998, Peña-Claros 2001), the long-term capacity to support biodiversity is still insufficiently known for tropical forests that are managed for timber (Arets 2005). As timber harvesting is currently the most common use of tropical forests (Johns 1996) and forest management will be one of the major determinants of global biodiversity in the next 50 yrs., assessing the effects of logging activities on biodiversity and general ecosystem functions is of primary importance to conservation (compare Fimbel et al. 2001). Information about recovery time, impacts of different management practices and logging intensities are of outmost importance in order to adjust the requirements of management plans for conservation purposes.

Large canopy gap, Mabura Hill, Guyana

Box 1.5: Disentangeling diversity components – Limitations of taxonomic diversity as surrogate for functional diversity

Disentangeling the different components in diversity analyses remains a problematic task. Species richness has been the most common measure of diversity in biodiversity-ecosystem functioning studies, based on the assumption that species' deliniations both embody functionally significant information and are distinct. The multitude of alternate species concepts (compare Hey 2001) highlihts the limitations of this taxonomically based diversity measure. Species delimitation is usually based on genetic or morphological traits. However, organisms with distinctly different phylogenetic background may very well share similar functional traits. Whether species richness adequately reflects functional diversity in natural systems partially depends on patterns of community assembly (Hooper et al. 2004). Strong correlations between species richness and functional diversity are likely if species are assembled at random (e.g. if disturbance leads to a predominance of stochastic colonization, Fridley 2001) or if functional trait complementarity is an important assembly factor (Weiher and Keddy 1998, Kelt and Brown 1999). In case where strong environmental filters determine community assembly and communities are hence non-random assemblages from regional species pools (Diaz and Cabido 2001) functional diversity may not be linearly correlated with species richness. In this case available niche space is simply more finely divided as more species are added (Schmid et al. 2002). Another important aspect with respect to the relationship between species richness and functional diversity is certainly the level of taxonomic resolution within a given community. At the α 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. In this case it seems intuitively appropriate to assume that the most taxonomically varied community is the more diverse. Measures of taxonomic diversity can be used in conjunction with species richness, however, only if the phylogeny of the community of interest is reasonably well resolved. A number of taxonomic diversity measures have been developed in the past (e.g. Pielou 1975, Faith 1992, 1994, Izsák and Papp 2000, Ricotta, 2002), yet they face similar problems as their species diversity counterparts. As an alternative, taxonomic distinctness measures have been proposed that have fewer limitations (Clarke and Warwick 1998, Warwick and Clarke

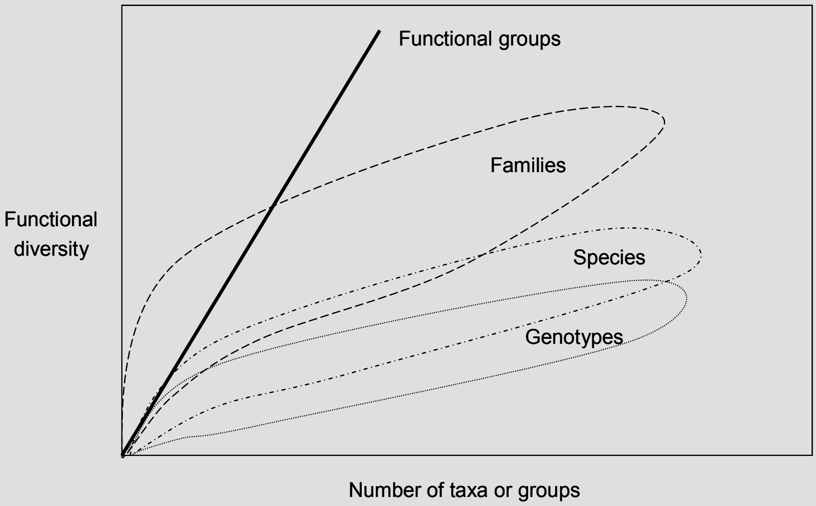


Fig.1.4: *Hypothetical relationship between richness of taxa and total amount of trait variation after Hooper et al. 2004*

1998). With respect to functional trait diversity, randomly adding higher taxonomic entities (e.g. genera, families, etc.) would, on average, add more functional diversity than adding lower taxonomic entities (e.g. genotypes, species). However, this relationship is highly process-dependend and closely linked to species-specific variations and plasticity. Whether species richness or diversity adequately reflects functional diversity hence largly depends on these factors. Recently the development of continuous measures of functional diversity (Petchey and Gasston 2002a,b) has added a new approach that merits consideration. In any case, functional traits are more directly related to ecosystem processes and assessing functional rather than species diversity will likely lead to a better understanding of diversity effects on ecosystem properties.

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1.4 Set up of thesis

Objectives and main questions

The general objectives of the present thesis are

(i) to analyse and elaborate the basic or general organization patterns in a complex multi species system, with an emphasis on individualistic-continuum vs. interactive concepts;

(ii) to assess and explain the impact of anthropogenic disturbances, mainly logging, on general community patterns, and

(iii) to shed light on the key factors and processes that lead to alterations in the general patterns.

I mainly address four sets of questions (A-D) by testing respective sets of hypothesis associated with underlying concepts.

(A) ***H_1*:** the anuran communities under investigation behave as integrated communities *sensu* Clements 1916. Interspecific interactions and niche partitioning are important structuring factors.

***H_0*:** the anuran communities under investigation behave as individualistic species associations *sensu* Gleason 1926. Species-specific responses to the environment are the major structuring factors.

(B) ***H_1*:** the anuran communities under investigation are predictable based on environmental parameters.

***H_0*:** the anuran communities under investigation are *not* predictable based on environmental parameters.

(C) ***H_1*:** the predictability pattern is constant with regard to disturbance state of the system.

***H_0*:** the predictability pattern changes with regard to disturbance state of the system.

(D) ***H_1*:** species diversity and functional diversity in the anuran communities under investigation are *not* positively or negatively affected by anthropogenic disturbances, i.e. logging.

***H_0*:** species diversity and functional diversity in the anuran communities under investigation are positively or negatively affected by anthropogenic disturbances, i.e. logging.

A sneak preview

This thesis is organised along two main themes. After a general introductory chapter (chapter 1), a section on general methodology and an introduction to the model systems studied (chapter 2) the first theme moves from general patterns (chapter 3) to underlying processes (chapter 4). A second theme running through both chapters carries from undisturbed systems to disturbed systems. An Integration and synthesis follows in chapter 5. This chapter also addresses implications for conservation management of anthropogenically altered tropical forests. The thesis concludes with a final summary (in German) highlighting the major results.

Chapter 2 is an introduction to the methodology and the two systems (i.e. anuran communities) being studied. It provides an evaluation of sampling methods and gives recommendations for standardization. Data on composition and structure of the two anuran communities, as well as detailed study site descriptions are all included this chapter.

Chapter 3 concentrates on patterns of community structure, composition, and predictability. The first case study takes a close population level look at the natural or ‘ground’ state of diverse tropical leaf litter anuran communities in pristine and disturbed habitats, whereas the second study takes the question one step further by investigating predictability patterns on a community level. To test for general patterns, the community level approach is consequently applied to a different segment of the entire community, namely arboreal anurans.

Chapter 4 aims at unveiling the processes highlighted in chapter 3. Likely candidates for pattern changes are being singled out and studies concentrate on a functional group and population level. The first case study looks at the direct impacts of selective logging on three sympatric anuran species that exhibit very peculiar reproductive strategies. The second study abstracts the species-specific approach by looking at the behaviour of different entities of the community, namely functional groups, under the influence of anthropogenic disturbance.

Chapter 5 finally integrates ‘patterns’ and ‘processes’ and discusses the mechanisms leading to the observed changes. Implications for land management planning are being addressed and recommendations for harvesting routines are presented.

Formatting and layout remark: each published contribution included in this thesis is reproduced in its original and journal specific style and format. Likewise, accepted and submitted contributions, as well as those that are to be submitted in the near future are presented in respective journal or book formatting. Even though all chapters are linked by a common theme, each contribution can be referred to as a self-contained and independent article.

CHAPTER 2

METHODS AND MODEL SYSTEMS

Measuring and monitoring amphibian diversity in tropical forests. I. an evaluation of Methods with recommendations for standardization

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MEASURING AND MONITORING AMPHIBIAN DIVERSITY IN TROPICAL FORESTS. I. AN EVALUATION OF METHODS WITH RECOMMENDATIONS FOR STANDARDIZATION

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Abstract: The need for standardization of field methods within and across studies has been recognized by the majority of ecologists throughout the world. However, comparable studies based on a standardized protocol are still scarce. We provide a guideline for effectively sampling and monitoring tropical forest amphibians and give recommendations for standardization. Based on a four-year study on amphibians in Taï National Park, Côte d'Ivoire, we evaluate commonly used techniques, and offer a catalogue of efficient techniques, along with suggestions for improvement of particular methods, with regard to study objectives and specific amphibian guilds. For simple short-term surveys we recommend visual and acoustic encounter surveys, accompanied by opportunistic trapping. The transect design introduced here proved to be most adequate for representative sampling and appeared to be appropriate for most studies that involve multivariate data. It is especially useful for long-term studies. Transects furthermore provide an effective method of investigating at least leaf litter frogs, not only at their breeding sites but also throughout the whole range of habitats used by them, thus generating a much more complete picture of an amphibian community than is possible with other methods. *Accepted 4 February 2004.*

Key words: *Tropical amphibian monitoring, standardization, method evaluation, Taï National Park, West Africa.*

INTRODUCTION

In theory there is no disagreement about the necessity to standardize ecological field methods and data acquisition in order to guarantee comparability between different studies, as well as to enhance the power of predictions resulting therefrom. The need for standardization of techniques across and within studies has continuously been emphasized by several authors (e.g., Heyer *et al.* 1994, Adis *et al.* 1998). Those who are involved in community ecological field research know well that this is a crucial factor when it comes to generalizing results in order to make them accessible to those who urgently need scientific guidelines to back up their practical efforts. This becomes especially important when looking at phenomena such as the well known world-wide amphibian decline, which seems to have affected even populations in pristine habitats and continues to affect or even wipe out whole populations with terrifying rapidity (Houlahan *et al.* 2000, Kiesecker *et al.* 2001, Pounds 2001). In these cases synergistic efforts are urgently needed, calling for unified methods and data output (Alford & Richards 1999, Parris 1999, DAPTF 2002).

However, in reality there still is a lack of studies that can be compared without reservations, especially studies that were conducted in different parts of the world, although precisely this kind of comparison is

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essential for academic and practical purposes alike. Given the lack of time for the development of effective conservation programs, standardization of methods that yield broad-scale comparative data is now needed more than ever. A number of recently published regional field monitoring manuals for amphibian surveys (Latin America: Lips *et al.* 2001, Africa: Howell 2002) reflect this need. The intention of this paper is thus to provide a guideline to choosing effective and comparable methods for the monitoring of tropical forest amphibian assemblages in general. We thereby evaluated several methods that are already commonly used and present a set of techniques that, on the basis of our experience in the field as well as with consecutive data analyses, proved to be most effective for forest amphibians. We report on our experiences with already existing methods and with methods that we thought needed modifications to enhance their effectiveness and to enable the use of new statistical analysis methods. All evaluations and recommendations are based on a study of tropical amphibian assemblages conducted over four years (1999–2002) in Taï National Park, Côte d'Ivoire. We aim to present a methodology that i) provides quantitative and qualitative data useful for rapid surveys as well as long-term monitoring programs, that ii) is easy to handle, also for para-ecologists, iii) is efficient concerning time and money, and iv) has a low environmental impact. Thus widely used techniques, such as standard plot sampling (Allmon 1991, Vonesh 2001, Doan 2003) or total removal plots (Barbault & Trefaut Rodrigues 1978, 1979a, b; Rodda *et al.* 2001) were *a priori* excluded from testing, as they may result in severe disturbance to the system under investigation.

MATERIAL AND METHODS

Study site

The study was conducted in Taï National Park (TNP), situated in western Côte d'Ivoire (5°08'-6°07'N, 6°47'-7°25'W). TNP is the largest remaining protected area of rain forest in West Africa. It can be characterized as humid tropic seasonal (Riezebos *et al.* 1994, Parren & de Graaf 1995, Richards 1996). Precipitation is distributed across two more or less distinct periods. A minor rainy season lasts from March/April to July, followed by a short dry season in July/August. The major rainy season stretches from September to October. The core dry season lasts from November until February/March. Mean annual precipitation in the study area was 1806 mm during 1988–2002 (± 297 mm; data: Taï Monkey Project). Daily temperatures vary between 20 and 33° C. The mean annual temperature is about 25° C (Rompaey 1993). Our study site was located 23 km southeast of the small town of Taï and comprised about 30 km^2 of primary and secondary rain forest around the Station de Recherche en Ecologie de Taï (SRET, 5°50'N, 7°20'W). Parts of the habitats on the park's periphery were subject to more or less intense logging and cultivation until 1998 (P. Formenty pers. comm. and unpubl. map "Projet OMS Forêt de Taï"). Our study sites are either pristine forest areas or have not been logged or cultivated since 1978. Floristically the TNP belongs to the Guinean-Congo-Region (Guillaumet 1967, Lawson 1986, PACPNT 2000). TNP is part of the Upper Guinea forest block, that stretches west of the Dahomey Gap from Ghana into Sierra Leone and Guinea (Schiøtz 1967, Poynton 1999). More detailed descriptions of TNP are provided by Rompaey (1993), Riezebos *et al.* (1994) and PACPNT (2000).

Selection of sites and design of sampling units

We chose sites within existing macrohabitats (primary/secondary forest) to establish a total of ten rectangular transects (six in primary forest, four in secondary forest). Each had a north-south extension of 200 m and an east-west extension of 100 m. For data acquisition the complete transect length of 600 m was subdivided in 25 m subunits (24 subunits/transect). Every subunit was marked with numbered colored flag-tape. Transect paths were kept open so that walking at a constant speed was possible at all times. We avoided extensive cutting and thus manipulation of important habitat features. The starting coordinate for each transect always marked the southeast corner to ensure identical geographic orientation between sampling units. Transects were arranged in pairs, thus ensuring that all habitat types of a certain area within the very inhomogeneous forest were covered. The minimum distance between adjacent transects was 200 m. The maximum distance between transects was 6.3 km. The rectangular transect design is a combination of two widely used standard techniques. The first, known as quadrat sampling (plot design), consists of a series of small squares (quadrats) that are laid out at randomly selected sites within a habitat then thoroughly searched for amphibians. The second, known as transect sampling, uses linear transects instead of squares. Whereas quadrat sampling can be used to determine the species present in a homogenous area, as well as their relative abundances and densities, transect sampling can provide similar data across habitat or disturbance gradients (Jaeger 1994, Jaeger & Inger 1994). Compared to linear transects, rectangular ones provide the possibility of easily up- or downscaling data without neglecting local habitat diversity (e.g., for comparison of local with regional species pools). For a discussion of the advantages of rectangular sample units over quadratic or circular ones see Krebs (1989) and McCune & Grace (2002).

Sampling methods and sampling effort

Habitat characterization. To assess habitat preferences of particular species (e.g., to assign them to particular guilds), and to investigate correlations of species assemblages with environmental variables, we characterized all habitats using several variables that were recorded at two defined points within each 25 m subunit (beginning and midpoint). These parameters included vegetation density in four strata (canopy: > 20 m, lower tree stratum: 3–10 m, bush and shrub stratum: 0.5–1.5 m, understory: < 0.5 m), divided into seven categories corresponding to particular densities. Edaphic parameters were registered as general substrate types according to Lieberoth (1982). A simplified method originally developed by Braun-Blanquet (1964) for determination of vegetation coverage in vegetation analyses was used to estimate the percentage of leaf litter coverage. In addition, the vegetation of all 25 m segments within a distance of about 100 cm left and right of the transect was recorded by counting the number of plants belonging to a certain category (diameter at breast height, dbh). We assumed that the number of plants with small dbh is greater in degraded, secondary forests, whereas primary forests show increasing numbers of plants of larger dbh (Chatelain *et al.* 1996, Pearman 1997). Definitions of habitat variables are summarized in Table 1. In order to quantify the availability of potential aquatic breeding sites, every aquatic habitat (lentic and lotic) located at a maximum distance of 25 m from either side of the transect was recorded with respect to type, surface and depth. Additionally, substrate moisture was determined in four categories during every transect walk.

Standardized visual transect sampling (SVTS). Sampling was performed independent of prevailing weather conditions. Usually four to six transects per day were sampled during daytime. A maximum of four transects was patrolled at night. Repeated controls of identical transects on consecutive days were avoided to ensure independence of samples. Transects were intensively patrolled at a constant speed (0.30–0.35 m/s), thereby recording all amphibians within a distance of 100 cm from either side of the path. As far as possible all individuals were captured. Specimens heard but not seen within this distance were not searched for and not included in the SVTS data sets (see below). In addition to species identity we recorded sex and snout-vent-length (SVL) of every individual, thus providing data that are useful to test for sex- or age-specific differences in habitat use, both in time and space.

Sampling was interrupted for the duration of the recording in order not to overestimate locations in which animals had previously been captured. To avoid duplicate recordings, captured frogs were marked by

TABLE 1. Categories of habitat variables measured on transects; dbh = diameter of plants at breast height; vegetation density was measured in four strata (see text).

	definition			
category	vegetation density	substrate types	dbh [cm]	leaf cover (%)
1	absent	forest soil	0–5	0–20
1.5	transition			
2	gaps predominating	arenaceous forest soil	6–10	21–40
2.5	transition			
3	closed areas predominating	loamy soil	11–20	41–60
3.5	transition			
4	closed	arenaceous soil	21–50	61–80
5		sabulose soil	> 50	81–100
6		muddy soil		
7		swampy soil		

toe clipping (Donnelly *et al.* 1994, Henle *et al.* 1997). Recaptures were excluded from the analyses. Individuals below nine mm SVL were not marked due to their small size. Coding schemes used for individual recognition were not applied. Removal of additional toes may decrease the recapture rate of marked individuals by more than 6–18 % for each additional toe removed after the first (Parris & McCarthy 2001). Thus, individual marking should be restricted to studies in which individual recognition is indispensable. At capturing sites a thorough description of the microhabitat was recorded, following the characterization routine used for general habitat description.

Standardized acoustic transect sampling (SATS). Since in the majority of frog species males use species-specific calls to advertise their position to potential mates and rivals (Wells 1977), this behavior can be exploited for acoustic monitoring. Audio strip transects represent a commonly used method for acoustic monitoring (Zimmerman 1994). Counts can be used to estimate relative abundance of calling males, species composition, as well as breeding habitat use and breeding phenology of species (Zimmerman 1994). Furthermore, this technique allows the detecting of cryptic species that, despite their potential abundance, may be underestimated when exclusively using visual techniques.

Throughout transect walks a combination of visual and acoustic techniques was applied at all times, keeping the transect routine identical for both techniques. As opposed to visual sampling, during SATS it was often impossible to determine individual parameters, other than sex and species. Likewise microhabitat description was not always possible. In those cases, habitat analyses can be based on data obtained from the general habitat characterization for single transects or segments. The width of the acoustic transect depends on the ability to detect each species' advertisement call. For that reason a maximum recording distance of 12.5 m to either side of the transect was defined, thus creating 25 m x 25 m acoustic sampling plots. Calls from greater distances cannot be unambiguously identified and the chance of duplicate recordings in neighboring segments increases. In the transect corners, only calls coming from the right-hand side in the first segments were registered (i.e., beginning with segment 1: segment 1, 8, 12 and 20). For both SVTS and SATS, data can be expressed in numbers of individuals per time and surface units. From February 1999 to December 2000 we compiled 382.5 hours of transect sampling. This corresponds to 765 transect walks.

Visual (VES) and acoustic (AES) encounter surveys. Due to the simplicity of the method, VES and AES are frequently used for rapid assessments and the evaluation of larger areas. An area or habitat is searched systematically for individuals in a defined time period. The resulting data are expressed in numbers of individuals of a certain species found in an area per unit time. For practical reasons "man-hours" can be used, which can be adjusted to the complexity of the habitats being sampled. This technique has been formalized as the time-constrained technique of Campbell & Christman (1982), and as the time-constrained searches of Corn & Bury (1990). It can be used to determine the species richness of an area and the species composition of a local assemblage, and to estimate relative abundances of species within an assemblage (Crump & Scott 1994). According to Corn & Bury (1990), VES can only provide information on the presence or absence of a species in an area but are inadequate for determining abundances.

In concordance with these authors the methods were only used as a qualitative or semi-quantitative tool within the scope of our studies. We used these methods continuously in all habitats of the study area including the transect areas. VES and AES thus could be used to evaluate if the randomly chosen transects represented the regional species pool, and also for evaluating if species that are rarely found on a transect belong to a particular local species pool or represent single migrating specimens that have habitat preferences not covered by the transects. Total VES- and AES-effort was kept comparable to the time spent on SVTS and SATS surveys throughout the entire study period.

Trapping with pitfall or funnel traps along drift fences. Pitfall traps with drift fences were installed in two of the primary forest transects from March to April 1999, and additionally in only one of these transects from January 2001 to September 2002. This device is useful to determine species richness of epigaeic organisms (Corn 1994). Capture success may vary greatly between species (Corn & Bury 1990, Dodd 1991). Anurans that are strong jumpers (e.g., *Ptychadena* species) are more difficult to trap than terrestrial species that lack these abilities (e.g., *Bufo* species). Drift fences consisted of durable green plastic gauze, 0.5 m high and stapled vertically onto wooden stakes. An array of fences and traps consisted of a central trap (buckets:

275 mm deep, 285 mm top diameter, 220 mm bottom diameter) and two triangular fence segments (total length 16 m). Each segment was tightened around a plastic bucket with an opening angle of 45°. The ends of each segment were flanked with additional plastic buckets, one on either side. Duct tape was used to reduce the diameter of the buckets and construct funnel-like openings in order to impede escaping from traps. Traps were checked at least on a daily basis.

In the course of this study, funnel traps (see Branch & Rödel 2003) were installed in a primary forest transect from 18 to 27 September 2002, and in a forest fragment (Paulé-Oula 2) outside TNP from 30 August to 12 September 2002 (A. Hillers *et al.*, unpubl. data). They were checked at least every morning. Additionally, we applied that method during a herpetological survey of the Haute Dodo and Cavally forests, which are situated south and west of TNP respectively (Rödel & Branch 2002, Branch & Rödel 2003). The data from pitfall and funnel traps can be expressed as number of individuals per trap-day. Pitfall trapping time summed to a total of approximately 4000 trap-days. Funnel traps summed to a total of 384 trap-days.

Data from each sampling method were compared with each other and to a list of species records that we gathered through January 1999 to September 2002 for the forest parts of the SRET region (Appendix 1). Sampling success is referred to as number of species within families recorded, using a particular sampling method. In addition, results were analyzed for leaf litter, arboreal, fossorial and aquatic species independent of families, as sampling success and efficiency may vary with regard to the particular biology of a species.

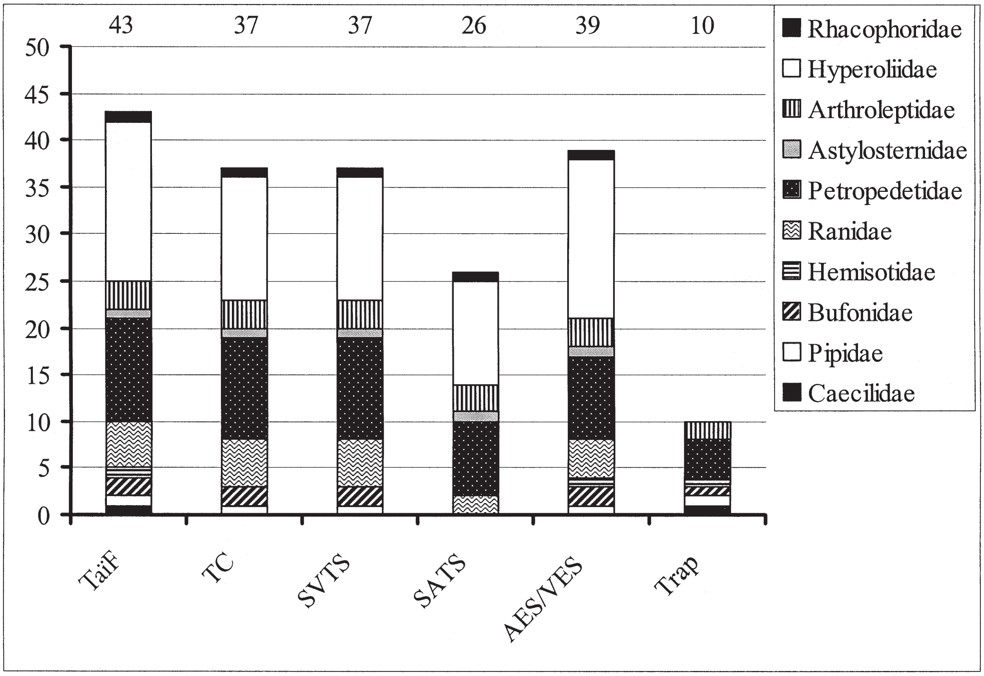

FIG. 1. Number of species per family recorded using different sampling methods. TaïF = all species recorded with all methods in forest habitats around SRET station; TC = species recorded during transect walks (SVTS and SATS combined); SVTS = species recorded during visual transect walks; SATS = species recorded during acoustic transect walks; AES/VES = visual and acoustic encounter surveys (only species that have been recorded in forest habitats around SRET station); Trap = pitfall and funnel traps. Numbers above bars represent total number of species recorded with the respective method.

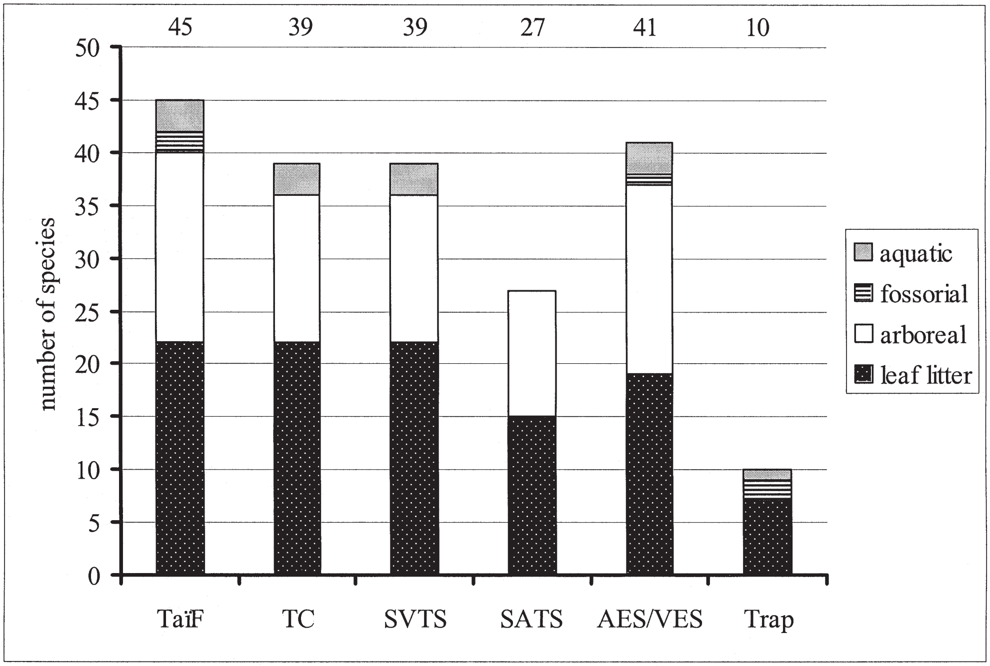

FIG. 2. Number of species per amphibian guild recorded using different sampling methods. For abbreviations see Fig. 1; two species were each listed in two guilds (compare Appendix). Numbers above bars represent total number of species recorded with the respective method.

RESULTS

In total, 56 amphibian species are known to occur in TNP (Schiøtz 1967, Perret 1988, Rödel 2000, Rödel & Ernst 2000, 2002; Rödel *et al.* 2003, see Appendix 1). Using all methods we recorded 50 species in the region of the SRET (89.3 % of TNP species). Failure to detect particular species in this region was most probably due to their general scarcity (e.g., *Bufo superciliaris*) or simply absence in the area under investigation (e.g., *Phrynobatrachus calcaratus*, *Hyperolius guttulatus*), rather than actual sampling method insufficiency. Seven species (*Bufo maculatus*, *B. regularis*, *Hoplobatrachus occipitalis*, *Ptychadena pumilio*, *P. bibroni*, *P. mascareniensis*, and *P.* sp.) were recorded exclusively outside forest habitats (e.g., clearing around SRET) and thus ignored in the analysis. Taking all methods into account, 43 species were recorded in forest habitats within the study region (Fig. 1, Appendix 1).

Sampling success and data quality varied between different methods, and between different amphibian families or guilds (Figs. 1, 2). Families containing only a few species in the TNP area showed the highest recording rates. Sampling efficiency in families containing higher numbers of genera and/or species was only marginally lower, thus making overall sampling success very high (Tab. 2; compare Appendix 1). During transect sampling (SVTS, SATS) we recorded a total of 15007 individual amphibians belonging to 37 species (86.0 % of TaïF) in eight families. Three leaf litter species (*Amnirana occidentalis*, *Phrynobatrachus fraterculus*, *P. annulatus*) were exclusively recorded during transect walks. VES/AES revealed 39 forest species (90.7 %) of nine families. Four arboreal frogs were exclusively recorded with these methods (*Hyperolius picturatus*, *H. nienokouensis*, *H. fusciventris*, *Phlyctimantis boulengeri*). Ten species (23.2 %) were recorded with pitfall and funnel trapping. Two fossorial species were exclusively detected either with VES and pitfall traps (*Hemisus* sp.) or pitfalls only (*Geotrypetes seraphini*).

Effectiveness in detecting species within given families differed significantly between methods (Friedman test; χ^2 = 19.199, df = 5, p = 0.002, N = 10; tested for TaïF, TC, SVTS, SATS, AES/VES, Trap).

TABLE 2. Percentage of species within an amphibian family or guild that were recorded using a particular method. Reference is the number of species that were recorded using all methods in forested habitats around the SRET station (TaïF). For other abbreviations see text and Fig. 1.

Family / guild	TaïF	TC	SVTS	SATS	AES/VES	Trap
Caecilidae	1	0.0	0.0	0.0	0.0	100.0
Pipidae	1	100.0	100.0	0.0	100.0	100.0
Bufonidae	2	100.0	100.0	0.0	100.0	50.0
Hemisotidae	1	0.0	0.0	0.0	100.0	100.0
Ranidae	5	100.0	100.0	40.0	80.0	0.0
Petropedetidae	11	100.0	100.0	72.7	81.8	36.4
Astylosternidae	1	100.0	100.0	100.0	100.0	0.0
Arthroleptidae	3	100.0	100.0	100.0	100.0	66.7
Hyperoliidae	17	76.5	76.5	64.7	100.0	0.0
Rhacophoridae	1	100.0	100.0	100.0	100.0	0.0
leaf litter	22	100.0	100.0	68.2	86.4	31.8
arboreal	18	77.8	77.8	66.7	100.0	0.0
fossorial	2	0.0	0.0	0.0	50.0	100.0
aquatic	3	100.0	100.0	0.0	100.0	33.3

We could not detect a statistical difference in sampling efficiency between different amphibian guilds using the methods employed (Friedman test; $\chi^2 = 10.294$, df = 4, p = 0.067, N = 4; tested for TaïF, TC, SVTS, SATS, VES/AES, Trap). Schaich & Hamerle *post hoc* multiple comparisons revealed no significant differences between methods at $\alpha = 0.05$, neither between given family or guild. However, this was most probably due to the small overall sample size and high heterogeneity of species numbers in families and guilds (Bortz *et al.* 1990).

VES and AES revealed highest species numbers. Quantification of these data, other than based on time units, was difficult as detectability of species varied considerably with (e.g.) vegetation density. In contrast, transect walks made it possible to search for amphibians in a very comparative way. A distance of 1 m (visual) and 12.5 m (acoustic) proved to work equally well in all habitats investigated. Diurnal ground-dwelling frogs were best recorded quantitatively using SVTS. Most arboreal frogs could be recorded with SVTS, but that concerned mostly single specimens. With the exception of *Acanthixalus sonjae*, which is mute, quantitative data for all arboreal species were best assembled with SATS. Likewise, nocturnal leaf litter frogs (arthloeptids, asytlosternids) were best recorded with SATS.

The traps proved to be inadequate in qualitative and quantitative sampling since even small species such as *Phrynobatrachus villiersi* (SVL: 10–15 mm) managed to escape regularly (several direct observations). In Haute Dodo and Cavally forests we captured 38 % of the recorded amphibian species (16 of 42) with a combination of pitfall and funnel traps. Most specimens were captured with funnel traps (0.47 specimens per trap-day in contrast to 0.03 specimens per trap-day in pitfall traps). Trapping success was highest in leaf litter frogs (56.5 % of recorded leaf litter frogs), but very low in arboreal species (6.7 % of recorded arboreal species). As in TNP, the fossorial *Geotrypetes seraphini* was recorded with pitfall traps only. All other species were recorded with VES/AES (Rödel & Branch 2002, Branch & Rödel 2003). In TNP funnel traps were ineffective. We only captured a few leaf litter frogs; all were recorded using other methods as well, in a primary forest transect with none in the forest fragment (Hillers *et al.*, unpubl. data). No additional species were detected with funnel traps.

As aquatic sites were only taken into account, when being a part of the transect line itself, presence and abundance of purely aquatic species and tadpoles of all species were underestimated with all methods used here.

DISCUSSION

Choice of methods should reflect the best compromise between i: practicability, ii: specific aims, iii: efficiency, and iv: environmental impact. Standard plot sampling and total removal plots were not tested, as they impose a severe disturbance on the system under investigation and thus were not suitable to our goals. In addition, these methods do not seem to sample a given fauna adequately well (Allmon 1991, Vonesh 2001, Doan 2003). Compiling data on presence and abundance of aquatic species and tadpoles was outside the scope of this study and these species and stages were inadequately sampled with all methods used here. Simple presence/absence data of aquatic species and stages can best be gathered by direct observation (surfacing individuals) and with dip-netting. Methods of collecting quantitative data for aquatic amphibians and for tadpole assemblages have been described by Shaffer *et al.* (1994), Olson *et al.* (1997) and Rödel (1998a). Migrating pipid frogs can also be easily recorded with pitfall and funnel traps.

The methods tested within this study proved to perform with varying degrees of efficiency. VES and AES yielded highest species numbers. However, a combination of SVTS and SATS, as well as SVTS alone, were nearly as successful in detecting species. According to Pearman *et al.* (1995) a simple comparison of species numbers may not be sufficient to evaluate the efficiency of different sampling methods. They suggest using relative species richness within taxonomic entities, such as species groups, genera or families, as an adequate measure. The percentage of species within supraspecific taxonomic units, determined by using a particular sampling method, can then be compared to the real conditions in an area or habitat. In this study this has been done by determining relative species richness with reference to families or guilds.

The differences in efficiency of visual versus acoustic sampling varied between taxa. Some taxa, such as species of the genus *Acanthixalus*, which are mute (Drewes 1984, Schiøtz 1999, Rödel *et al.* 2003), could be detected exclusively using visual sampling methods. SVTS was generally the best method for detecting diurnal leaf litter frogs. Nonetheless, in order to sample particularly secretive leaf litter species, such as the very abundant *Arthroleptis* sp.1, *Arthroleptis* sp.2, *Cardioglossa leucomystax*, or *Phrynobatrachus alticola*, acoustic sampling appeared to be indispensable since these species were more readily detected by their calls than by sight. This was also true for most of the arboreal species belonging to the families Hyperoliidae and Rhacophoridae, and will likewise hold true for other arboreal anurans throughout the tropics, such as the Hylidae. In general SATS was very efficient in detecting nocturnal leaf litter frogs and treefrogs but less successful in detecting diurnal leaf litter frogs, and failed to detect aquatic and fossorial species. Pitfall trapping was only useful in detecting fossorial species that were not encountered during transect walks. We found no additional species and only very few specimens by funnel trapping.

Although the combination of AES and VES provided an adequate approximation to real conditions (see also Doan 2003), this only holds true if species numbers alone are considered. When including relative abundance measurements these methods were insufficient. The combined transect sampling methods provided a close approximation to the real presence and abundance of species, whereas visual sampling appeared to be superior to acoustic sampling. The advantage of transect sampling was especially obvious when focusing on leaf litter species. Therefore transect sampling can be considered to be the method of choice when sampling leaf litter anurans, but is certainly just as well suited for the investigation of tropical anuran assemblages in general.

The methods VES and AES in combination with pitfall traps with drift fences were useful in sampling additional, especially arboreal and fossorial, species not encountered during transect sampling, but appear not to be appropriate when standardized quantitative sampling is required. We found it impossible to quantify VES and AES other than in relation to time. Whereas transect walks provide the possibility of monitoring amphibians in a very comparative way, data acquisition varies considerably depending on habitat type in VES and even AES. Thus even time-based quantification of these data is questionable. We found it more realistic to apply a (clearly subjective) measure for habitat complexity on which to base collection effort during VES/AES, spending more time in complex, inaccessible areas than in areas that are easy to monitor. However, VES and AES are useful tools for the compilation of species inventory lists, e.g., during rapid assessment surveys (for recent West African examples see Rödel & Branch 2002, Rödel 2003, Rödel & Ernst 2003). Although widely used and recommended, especially in long-term field studies within temperate regions (e.g., Bury & Corn 1987, Semlitsch *et al.* 1996), pitfall traps and drift fences proved to be the least effective method. Donnelly *et al.* (2001) report on similar experiences using this method in a herpetological survey in Guyana. They collected only six species (out of a total of 132 species of amphibians and reptiles being recorded), none of them uniquely found by this method. Burger *et al.* (2004) had high trapping success with pitfalls in Gabon when considering numbers of individuals. However only two species, the fossorial *Hemisus perreti* and the aquatic *Silurana epitropicalis*, accounted for 72.6 % of all individuals captured with this method. Data from both trapping methods can, in theory, be quantified in relation to time, e.g., as trapping success per trap per time unit. However trapping success depends very much on choice of site, experience of investigator and prevailing weather conditions (see Branch & Rödel 2003). A comparison of trapping data with data other than those of the observer in question seems to be difficult. When considering the relatively high costs and time investment due to the high level of maintenance required (Parris 1999), one should test the efficiency at a particular site in advance before installing these traps on a broad scale. In our experience, this method cannot be recommended for standardized sampling of tropical anurans.

SVTS and SATS have been proven to be the only methods that provided quantitative data on forest amphibians with regard to space and time. With the exceptions of aquatic and fossorial species they provided data that cover the whole community very well. SVTS and SATS provided data on species and habitats und thus may reveal changes in composition and species abundance, as well as environmental changes. Data can be used for comparisons between habitats, seasons and years.

Costs with regard to time spent for data acquisition was highest in trapping and in transect walks. Traps have to be checked at least daily. If the investigation is interrupted for some time, traps have to be uninstalled or closed and reopened when starting again. Transect walks are time intensive. It is advisable to perform them randomly independent of prevailing weather conditions. Thus data should be gathered throughout a whole season to obtain a thorough knowledge of the local fauna. However, in consecutive field seasons, the frequency of sampling can be reduced when general phenological traits of the species recorded have been clarified. VES and AES are less time consuming; however, generalization of data with regard to phenology or abundances is less possible.

VES and AES had probably the lowest environmental impact. The impact of traps and drift fences was difficult to judge. Theoretically it might well be that trapping will result in dislocating at least some species from the area where traps have been established. Transects will have an environmental impact, if not on amphibians then on other organisms. We observed (e.g.) that leopard (*Panthera pardus*) tracks

TABLE 3. Effectiveness of methodology in regard to type of data required, amphibian guild and environmental impact. QS/TR = quadrat sampling/total removal sampling (data from Allmon 1991, Parris 1999, Rodda *et al.* 2001, Vonesh 2001, Doan 2003); for other abbreviations see text and Fig. 1.

	TC	SVTS	SATS	AES/VES	Trap	QS/TR
leaf litter frogs	+++	+++	++	+++	+	+++
arboreal frogs	++	++	++	+++	–	–
fossorial amphibians	–	–	–	+	+++	–
aquatic frogs	+++	+++	–	+++	+	–
qualitative data	+++	+++	+++	+	+	+++
quantitative data	+++	++	++	+	–	+++
environmental impact	low	low	low	very low	medium	very high
costs (time)	high	high	high	low	very high	high
costs (material)	low	low	low	very low	low	low
utility (ecology)	very high	high	high	low	very low	very low
utility (conservation)	very high	high	high	high	low	low

were more often seen on the transect path than in undisturbed forest. This might affect densities of other mammals including possible seed dispersers with, in the worst case, consequent long-term effects on forest structure. After using transects intensively for some time, a well visible path becomes established that at least in primary forests remains so for years. Transect cutting and the use of transects should therefore be done with the necessary precautions.

Advantages and disadvantages of different methods are summarized in Tab. 3. For simple short-term surveys we recommend VES and AES, possibly accompanied by opportunistic trapping. The presented transect design proved to be adequate for representative sampling and appeared to be appropriate for most studies involving multivariate structure data. SVTS and SATS are especially useful for long-term studies. Furthermore transects provide an effective method of investigating leaf litter frogs in particular, not only on their breeding sites but throughout the whole range of habitats used by them, thus generating a much more complete picture of an amphibian community than is possible with other methods. However, for specific questions (*cf.* Lips *et al.* 2003) transects should be supplemented by specifically investigating aquatic breeding sites with the appropriate set of standardized techniques (Heyer *et al.* 1994, Olson *et al.* 1997, Rödel 1998a).

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APPENDIX. List of amphibian species recorded in Taï National Park (TNP); TaïF = species recorded in forest habitats around the SRET station; G = species recorded in southern TNP (Guiroutou, 5°25' N, 7°10' W); SRET = species recorded with VES/AES on the clearing around the SRET station; TC = all species recorded on transects; TP = all species recorded on transects in primary forest; TS = all species recorded on transects in secondary forest; VES/AES = species recorded via visual and acoustic encounter surveys in forest habitats near SRET, other than transects; Trap = species recorded with pitfall and funnel traps; l = leaf litter species; a = arboreal species; f = fossorial species; aq = aquatic species; [1] = known from TNP (Schiøtz 1967, Perret 1988) but not recorded by us; [2] = determination not possible at present time; [3] = *Phrynobatrachus guineensis* is a leaf litter frog but reproduces in small water-filled tree holes (Rödel 1998b); [4] = *Acanthixalus sonjae* lives aquatically in large water filled tree holes but forages in surrounding vegetation (Rödel *et al.* 2003); [5] = treated as full species and not as subspecies of *Hyperolius fusciventris* due to sympatric occurrence in TNP (see Rödel & Branch 2002); [6] = recorded north of area under investigation.

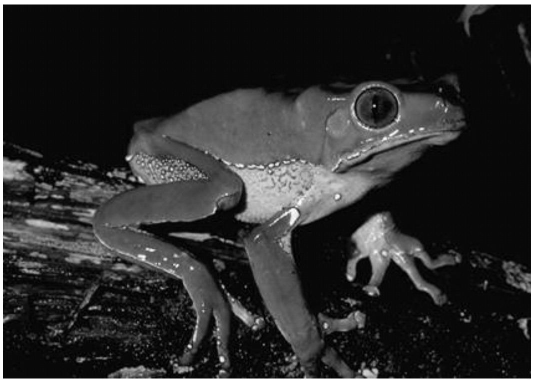
species	TaïF	G	SRET	TC	TP	TS	VES/AES	Trap	guild
Gymnophiona									
Caecilidae									
Geotrypetes seraphini	1	0	0	0	0	0	0	1	f
Anura									
Pipidae									
Silurana tropicalis	1	1	0	1	1	0	1	1	aq
Bufonidae									
Bufo regularis	0	1	1	0	0	0	0	0	l
Bufo maculatus	0	1	1	0	0	0	0	0	l
Bufo togoensis	1	1	0	1	1	1	1	1	l
Bufo taiensis	1	0	0	1	1	0	1	0	l
Bufo superciliaris	0	1	0	0	0	0	0	0	l
Hemisotidae									
Hemisus sp.[2]	1	0	0	0	0	0	1	1	f
Ranidae									
Hoplobatrachus occipitalis	0	1	1	0	0	0	0	0	aq
Amnirana albolabris	1	1	0	1	1	1	1	0	l
Amnirana occidentalis	1	1	0	1	1	1	0	0	l
Aubria occidentalis	1	0	0	1	1	0	1	0	aq
Ptychadena pumilio	0	1	1	0	0	0	0	0	l
Ptychadena bibroni	0	0	1	0	0	0	0	0	l
Ptychadena mascareniensis	0	0	1	0	0	0	0	0	l
Ptychadena superciliaris	0	1	0	0	0	0	0	0	l
Ptychadena aequiplicata	1	1	0	1	1	1	1	0	l
Ptychadena longirostris	1	1	1	1	0	1	1	0	l
Ptychadena sp.[2]	0	1	1	0	0	0	0	0	l
Petropedetidae									
Phrynobatrachus accraensis	1	1	1	1	0	1	1	0	l
Phrynobatrachus gutturosus	1	1	0	1	1	0	1	0	l
Phrynobatrachus fraterculus	1	0	0	1	1	1	0	0	l
Phrynobatrachus guineensis[3]	1	1	0	1	1	1	1	0	l, a
Phrynobatrachus phyllophilus	1	1	0	1	1	1	1	1	l
Phrynobatrachus liberiensis	1	1	0	1	1	1	1	0	l
Phrynobatrachus alticola	1	1	0	1	1	1	1	0	l
Phrynobatrachus alleni	1	1	0	1	1	1	1	1	l
Phrynobatrachus plicatus	1	1	1	1	1	1	1	1	l

Appendix continued

species	TaïF	G	SRET	TC	TP	TS	VES/AES	Trap	guild
Phrynobatrachus calcaratus	0	1	0	0	0	0	0	0	l
Phrynobatrachus taiensis[1]	0	0	0	0	0	0	0	0	l
Phrynobatrachus villiersi	1	1	0	1	1	1	1	1	l
Phrynobatrachus annulatus	1	0	0	1	1	0	0	0	l
Astylosternidae									
Astylosternus occidentalis	1	1	0	1	1	1	1	0	l
Arthropleptidae									
Cardioglossa leucomystax	1	1	0	1	1	1	1	0	l
Arthroleptis sp. 1[2]	1	1	1	1	1	1	1	1	l
Arthroleptis sp. 2[2]	1	1	0	1	1	1	1	1	l
Hyperoliidae									
Leptopelis hyloides	1	1	1	1	1	1	1	0	a
Leptopelis occidentalis	1	1	0	1	1	1	1	0	a
Leptopelis macrotis	1	1	0	1	1	1	1	0	a
Hyperolius concolor	1	1	1	1	1	0	1	0	a
Hyperolius guttulatus[6]	0	0	0	0	0	0	0	0	a
Hyperolius picturatus	1	1	1	0	0	0	1	0	a
Hyperolius sylvaticus	1	1	0	1	1	1	1	0	a
Hyperolius zonatus	1	1	0	1	1	1	1	0	a
Hyperolius fusciventris[5]	1	0	1	0	0	0	1	0	a
Hyperolius lamtoensis[5]	1	1	0	1	1	0	1	0	a
Hyperolius nienokouensis	1	1	0	0	0	0	1	0	a
Hyperolius wermuthi[1]	0	0	0	0	0	0	0	0	a
Hyperolius chlorosteus	1	1	0	1	1	1	1	0	a
Afrixalus dorsalis	1	1	1	1	0	1	1	0	a
Afrixalus nigeriensis	1	1	0	1	1	1	1	0	a
Afrixalus vibekae	1	0	0	1	1	0	1	0	a
Kassina lamottei	1	1	0	1	1	0	1	0	l
Phlyctimantis boulengeri	1	0	0	0	0	0	1	0	a
Acanthixalus sonjae[4]	1	0	0	1	0	1	1	0	a, aq
Rhacophoridae									
Chiromantis rufescens	1	1	0	1	1	1	1	0	a
total 56 species in TNP	43	41	16	37	33	28	39	10	

On the cutting edge – The anuran fauna of the Mabura Hill Forest Reserve, Central Guyana

R. Ernst, M.-O. Rödel & D. Arjoon



Phyllomedusa bicolor Mabura Hill, Guyana

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On the cutting edge – The anuran fauna of the Mabura Hill Forest Reserve, Central Guyana

RAFFAEL ERNST, MARK-OLIVER RÖDEL & DEOKIE ARJOON

Abstract. Data on herpetofaunal communities in Guyana are very limited. However, it is of utmost importance that existing information is made available for policy makers at an early stage in the process of developing and planning protected areas. The study presented here provides first time information and essential data on anuran diversity, composition and endemism of the Mabura Hill Forest Reserve. So far, 41 anuran species, belonging to eight families, were recorded between November 2002 and September 2004, including a number of rare, secretive or unusual species rarely recorded in field surveys and thus hardly represented in collections, as well as several taxa new to science or species of uncertain taxonomic status. Two species represent interesting range extensions and are new records for the country. The status of the anuran fauna is discussed with regard to faunas of comparable sites in the Guianan region of northern South America and with respect to general conservation issues. The exceptional taxonomic composition of the Mabura Hill assemblage emphasizes the high conservation relevance of the site.

Key Words. Amphibia: Anura; communities; conservation; diversity; Central Guyana; South America.

Introduction

The forests of the Guiana Shield, particularly those of the Co-operative Republic of Guyana, have had among the lowest deforestation rates of the world, with very little change over the past decades (LANLY 1982, LUNING 1987, BURGESS 1993, BRYANT et al. 1997). The study site at Mabura Hill is part of the Guianan Shield Frontier Forest (sensu BRYANT et al. 1997), one of the four remaining extensive pristine forested areas left in the world (Amazon, Congo, Papua New Guinea and Guiana Shield). Historically, pressures on natural resources in these forests have been relatively low (HADEN 1999, OJASTI 1996) and therefore, the Guianan Shield Frontier Forests represent one of the highest per capita forested areas in the world (CARTER & ROSAS 1997). However, rapid economic and social changes increase pressures on these relatively well-conserved forest ecosystems. Guyana is at a crossroads concerning decisions and trade-offs among utilization, conservation and preservation of its forests and thus substantial parts of the country's biodiversity.

Whereas the local phytodiversity has been covered extensively (e.g. EK 1997), knowledge of the faunal diversity in general and the herpetofaunal diversity in particular is still very limited. Even basic biological and ecological data inevitable for sound conservation projects and urgently needed by policy makers at an early stage in the process of developing and planning protected areas are most often lacking. The amphibian fauna of the Guiana Shield region is moderately diverse but comprises a high number of endemic species. The Guyana Highlands have recently even been identified as a previously overlooked biodiversity hotspot on grounds of species richness and endemism (ORME et al. 2005, POSSINGHAM & WILSON 2005). The taxonomy of most groups is relatively well known (but compare note added in proof) and the different species are often tightly connected to certain species-specific types of habitats. Yet, reasonably good species inventories for Guyana are still scarce. So far surveys and collection expeditions either have focused on highland faunas (e.g. MACCULLOCH & LATHROP 2002, NOONAN &

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Bonett 2003) or sites already regarded as high priority conservation areas, such as Iwokrama Forest (Donnelly et al. 2005). Despite their potential importance, a number of smaller lowland forest sites, particularly in Central Guyana, have been largely neglected. In this study we provide first time information and essential data on amphibian diversity, community composition and endemism of the Mabura Hill Forest Reserve (MHFR), Central Guyana. In addition we comment on the status of species that are considered particularly rare or secretive or represent new country records and undescribed taxa. We also address their conservation status in the light of current threats imposed by selective logging. Detailed life-history and ecological data will be presented in a separate publication.

Study site

The Mabura Hill Forest Reserve is situated approximately 20 km south-east of the township of Mabura Hill, Central Guyana (5°13' N, 58°48' W, Fig. 1). It comprises an area of approximately 2000 ha of primary rain forest (see ter Steege et al. 1996) and is part of the Wappu compartment located within a 503,415 ha Timber Sales Agreement concession granted to Demerara Timbers Limited (DTL). The MHFR was established in late 1987 through a mutual agreement between Demerara Woods Limited (a predecessor of DTL) and the Forest Project Mabura Hill (a joint research project of the Universities of Guyana and Utrecht). It has been managed by the Research Unit, now Planning and Research Development Division, of the Guyana Forestry Commission, since January 2002. This area within the country's main forestry belt is part of a geological formation known as White Sands Plateau. It is gently undulating but occasionally penetrated by Laterite-covered dolerite dykes from the Pre-Cambrian Plateau, forming ridges and hills (ter Steege et al. 1996, van Kekem et al. 1997). Soil types belong to one of two major groups, clayey Plinthosols on one hand and a group of sandy and loamy soils of various types on the other hand (Jetten 1994, van Kekem et al. 1997). The climate in the area can be described as hot and humid with an annual mean daily average temperature of 27 °C and an average annual precipitation of 2,700 mm, respectively. Rainfall follows a bimodal pattern with maxima in May-July and in December (Jetten 1994, ter Steege et al. 1996). The vegetation is classified as Evergreen Rain Forest (Mixed Forest, see Fig. 2) and Dry Evergreen Forest (ter Steege 1993, ter Steege et al. 1996). Major forest types present in the concession are represented within the reserve and forest types vary across soil types and drainage types (ter Steege 1993, Jetten 1994, Ek 1997). The acidic soils of the Mabura Hill region are poor in nutrients and thus typical of deeply weathered soils in the humid tropics (van Kekem et al. 1997). A second site (Pibiri Reserve) located in the same general area (5°02' N, 58°38' W) has only briefly been investigated during several short visits. Detailed descriptions of particular sites surveyed at the MHFR are presented in Appendix 1.

Methods

Field data were acquired between November 2002 and September 2004 following the research routine established by Rödel & Ernst (2004). Quantitative faunistic data collection was carried out employing standardized visual transect sampling (SVTS) and standardized acoustic transect sampling (SATS). Sampling was performed both day and night and independent of prevailing weather conditions. A total of twelve rectangular transects was established (seven in primary forest, five in exploited forest, Fig. 1). The complete transect length of 600 m was subdivided in 25 m subunits (SUs; 24 SUs / transect). For brief site descriptions and GPS-co-ordinates see Appendix 1. A complete list of recorded species and their habitat associations is provided in Tab. 3 and Appendix 2. Forest types present within the study area

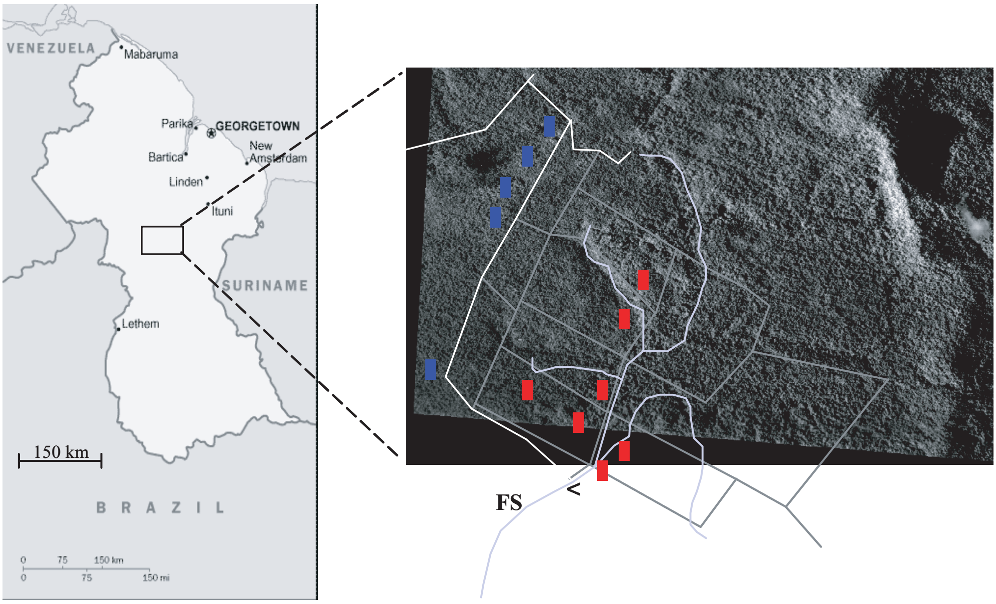

Fig. 1. Map of Guyana (left) with Mabura Hill area (box) and aerial photography of MHFR (right, not to scale) with location of transects (red rectangles = primary sites, blue rectangles = exploited sites), access road (white), trail system (dark grey), and creek drainage (light grey). FS = Field Station.

varied across soil types and drainage types (TER STEEGE et al. 1996, JETTEN 1994, EK 1997). Therefore, logging intensity differed between sites with regard to the presence of commercially valuable species. To circumvent this bias, transects covered all existing major forest types.

For a detailed description and discussion of the transect design, definition of habitat variables and data acquisition routine see RÖDEL & ERNST (2004). A total of 7,799 individuals of anurans belonging to 30 species were registered during 393.5 hours of transect sampling, equaling a total of 787 transect walks. In analyses, covering amphibian monitoring programs on transects in East Africa, West Africa, Madagascar and Borneo, VEITH et al. (2004) have recently shown that ≥ 20 independent transect walks seem to be necessary to achieve a species saturation. Every MHFR transect has been walked independently at least 65 times. It thus is justified to assume that the local species assemblages have been sufficiently sampled.

Fig. 2. Typical aspect of an evergreen rain forest (mixed forest), central Guyana.

Standardized transect sampling methods were supplemented by qualitative techniques, such as visual and acoustic encounter surveys (VES and AES), opportunistic sampling of major habitat types, as well as the installation of pitfall traps and drift fences (HEYER et al. 1994). These supplementary methods yielded additional records. Only qualitative methods have been employed during investigations at Pibiri Reserve. Museum acronyms referred to in the text are as follows: AMNH = American Museum of Natural History, New York; USNM = National Museum of Natural History, Washington, D.C.

Results and Discussion

Sampling results

AES proved to be an important tool, especially for most arboreal species that vocalize frequently but are rarely encountered otherwise [e.g. *Osteocephalus oophagus* Jungfer & Schiesari, 1995, *Phrynohyas resinifictrix* (Goeldi, 1907), *Hyalinobatrachium* spp.]. Yet, 39 amphibian species belonging to eight families were recorded employing VES, whereas AES only yielded 35 species, belonging to seven families. Among those, however, were two species not recorded during VES. SVTS and SATS together (transects) yielded 30 species belonging to six families. Seven species belonging to four families were recorded using pitfall traps and drift fences. One species, *Ctenophryne geayi* Mocquard, 1904, was exclusively recorded using this method (Fig. 3). SVTS and SATS are indispensable whenever quantitative data are needed. VES and AES are especially useful for simple short term surveys. However, they do not yield adequate quantitative data. Due to their high level maintenance required, pitfall traps and drift fences can only be recommended if studies are not time constrained. They do not provide quantitative data for most anurans but may be useful for recording secretive and/or fossorial species not sampled otherwise. These results corroborate the findings and methodological recommendations of our previous study on amphibian communities in West Africa (Rödel & Ernst 2004).

Sampling efficiency

Species accumulation curves show how many new species were added each month of investigation (Fig. 4). The curve reaches saturation, indicating that sampling time was sufficient to record most of the occurring species. Hence, even if sampling time would be increased, the chance of adding new species would be relatively low. Calculations of the approximate total numbers of amphibians occurring at the site corroborated these results (Fig. 4). We used the presence/absence data based Jack-knife 1 and Chao2 estimators (program: BiodivPro from the Natural History Museum, London) to allow di-

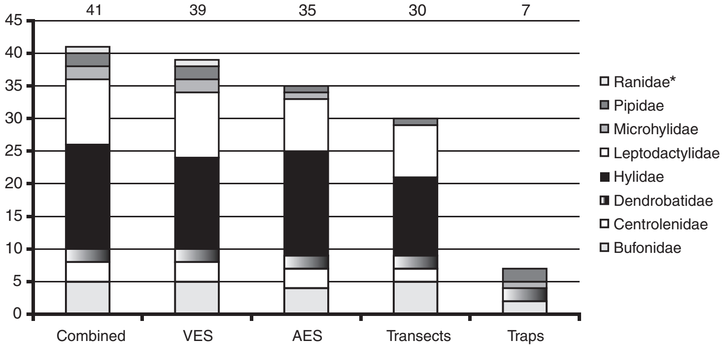

Fig. 3. Number of frog species recorded using a particular sampling method. VES = visual encounter surveys; AES = acoustic encounter surveys; Transects = acoustic and visual transect sampling; Traps = pitfall traps with drift fences; Combined = VES, AES, Transects + Traps. Figures above bars represent total number of species recorded with the respective method. * = recorded at Pibiri only.

rect comparisons with other faunal studies that most often do not provide relative abundance data. Estimated species numbers were very close to the actual number of species observed.

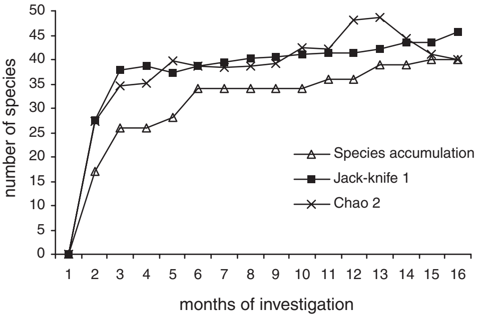

Fig. 4. Species accumulation, Jack-knife1, and Chao 2 estimator curves for the anurans of the MHFR. Estimated species richness for anurans Jack-knife 1: 46, recorded: 40 (87.0 %); Chao 2: 40, recorded: 40 (100.0 %).

Taxonomic remarks and range extensions

At least two taxa that were recorded have not yet been formally described scientifically, *Physalaemus* sp. and *Colostethus* sp.; the latter has previously been referred to as *Colostethus beebei* (Noble, 1923) (e.g. Lescure & Marty 2000). *C. beebei*, however, is a species restricted to the Guiana Highlands (Pakaraimas and perhaps Venezuela). It differs from *Colostethus* sp. in morphological and ecological aspects (compare Bourne et al. 2001). Its local name, the "golden frog", refers to the distinct bright yellow color of reproductive males, not exhibited in *Colostethus* sp. The holotype of *C. beebei* (AMNH 18683, type locality: "near Kaeiteur Falls, British Guiana") fits the description of frogs from populations found at Kaieteur National Park (R. Reynolds pers. comm.). These frogs are clearly distinct from populations of *Colostethus* sp. found at the MHFR (R. Ernst unpubl data).

Physalaemus sp. (Fig. 5) is the first known member of the genus occurring in Guyana. Only one other species, *P. petersi* (Jimenez de la Espada, 1872), has been recorded from French Guiana (Born & Gaucher 2001, Lescure & Marty 2000).

The taxonomy of an additional group of frogs, namely the three members of the genus *Hyalinobatrachium,* are currently subject of phylogenetic analyses conducted in cooperation with S. Castroviejo and co-workers from the Department of Evolutionary Biology at Uppsala University. First results indicate that the species herein referred to as *Hyalinobatrachium* sp. 1 is new to science and will be described elsewhere. It resembles *H. taylori* (Goin, 1968) but differs from the later in a number of morphological and advertisement call characteristics as well as on the basis of molecular genetics (R. Ernst et al. unpubl.). The status of *Hyalinobatrachium* sp. 2 (Fig. 6) could not be clarified as yet. It resembles *H. ignioculus* Noonan & Bonett, 2003 recently described from the Highlands of Guyana (Noonan & Bonett 2003). This species, however, may prove to be a junior synonym of *H. crurifasciatum* Myers & Donnelly, 1997 (S. Castroviejo & J. Ayarzagüena

	primary							exploited				
year of logging	no logging							1992		1988		
transect	P 1	P 2	P 3	P 4	P 5	P 6	P 7	S 1	S 2	S 3	S 4	S 5
S_{obs}	26	22	13	15	8	23	29	9	9	11	10	9
complete	30							14				

Tab. 1. Total number of species observed (S_{obs}) in transects (P = primary forest; S = exploited forest) and in habitat complexes combined = complete (entire study period).

Fig. 5. Amplectant pair of *Physalaemus* sp. constructing foam nest.

Fig. 7. Male *Synapturanus mirandaribeiroi.*

Fig. 6. Male *Hyalinobatrachium* sp. 2, guarding clutch.

Fig. 8. Male *Pipa aspera.*

pers. comm.). The record from the lowland rainforest site at MHFR would thus be the easternmost record of the species that has so far been reported from montane environments of Venezuela and western Guyana. The third species recorded, *H. nouraguensis* Lescure & Marty, 2000 was previously only known from the type locality in French Guiana. It thus represents a first country record for Guyana. The status of *H. nouraguensis*, however, is uncertain and it may prove to be a junior synonym of *H. iaspidiensis* Ayarzagüena, 1992 (S. Castroviejo & J. Ayarzagüena pers. comm.), a species recorded from Estado Bolivar and Estado Delta Amacuro, Venezuela (Ayarzagüena 1992, Señaris & Ayarzagüena in press). The Guyana record would thus represent a distributional gap link between known populations.

Another first country record is represented by *Hyla brevifrons* Duellman & Crump, 1974, a small hylid of the *Hyla parviceps*-group. This species has previously also been reported from French Guiana (Lescure & Marty 2000). These records are especially interesting since species of the *H. parviceps*-group are known to have their distributional centers in the Upper Amazon Basin of Colombia, Ecuador, and Peru. Widely scattered populations of *H. brevifrons* are also known from the Madeira and Amazon River regions in Amazonas State, Brazil. The Guyana and French Guiana records are thus the most northern records of the species.

The remaining 34 anurans comprise some remarkable, rare, secretive or unusual species rarely recorded in field surveys and thus hardly represented in collections. Among

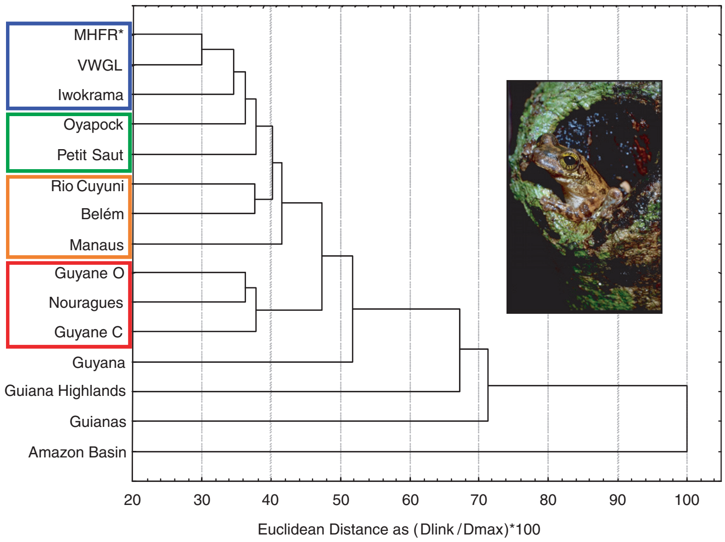

Fig. 9. Community composition and relatedness of anurans in northern South America and central Amazonia. Dendrogram based on presence-absence data (unweighted pair group average, Euclidean Distance). Calculations performed using the freely available software R (http://www.r-project.org). Blue = Guyana locations; green = eastern French Guianan locations; orange = Central Amazonian and Venezuelan forest locations; red = Guiana, biogeographic regions sensu Lescure & Marty 2000; cluster at bottom of dendrogram = large biogeographic realms or sites with high endemism (Guiana Highlands). Inlet picture, male *Osteocephalus oophagus*, a phytotelmata breeding species frequently encountered in disturbed forest sites. Own data: Mabura Hill Forest Reserve (MHFR* = including Pibiri record of *R. palmipes*; R. Ernst unpubl. data), Variety Woods and Greenheart Ltd.-Concession (VWGL; R. Ernst unpubl. data); literature data: Guianas (Hoogmoed 1979, IUCN et al. 2004); Guiana Highlands (Duellman 1999, McCulloch & Lathrop 2002); Guyana (IUCN et al. 2004, Jungfer & Böhme 2004); Amazon Basin (Duellman 1999); Belém (Crump 1971); Rio Cuyuni (Duellman 1997); Manaus (Zimmerman & Rodrigues 1990); Oyapock (Duellman 1997); Petit Saut (Duellman 1997); Nouragues (Born & Gaucher 2001); Guyane (O)riental and Guyane (C)entral (sensu Lescure & Marty 2000); Iwokrama Forest (D. Arjoon & G. Watkins pers. comm. of unpubl. data, Donnelly et al. 2005 and unpubl. data).

those is a rare microhylid, *Synapturanus mirandaribeiroi* Nelson & Lescure, 1975 (Fig. 7), which was only recorded during a period of three weeks in November 2002. However, throughout this short period, calling males were very abundant locally. The species has never been recorded at other occasions, even when climatic conditions, i.e. temperatures and rainfall, were comparable. A single specimen of a second microhylid, *Ctenophryne geayi*, was recorded during the peak rainy season of 2004. We have no hints for successful reproductive events during that period. A country record of the rare pipid *Pipa aspera* Müller, 1924 (Fig. 8) that was based on a single juvenile specimen from the Takutu Mountains, Mazaruni-Potaro (USNM-284392) was confirmed at the MHFR, where it represented the most abundant pipid species.

Species composition and biogeographical patterns

A total of 40 anuran species belonging to seven different families was recorded during the 16 month study period. One additional

Index	P 1	P 2	P 3	P 4	P 5	P 6	P 7	S 1	S 2	S 3	S 4	S 5	primary	exploited
Shannon H' Log Base 10	1.13	0.89	0.83	0.71	0.63	1.04	**1.18**	0.36	0.47	0.70	**0.71**	0.58	1.17	0.70
Shannon Hmax Log Base 10	1.42	1.34	1.11	1.18	0.90	1.36	**1.46**	0.95	0.95	**1.04**	1.00	0.95	1.48	1.15
Shannon J' (evenness)	0.80	0.66	0.75	0.60	0.70	0.76	**0.81**	0.38	0.50	0.67	**0.71**	0.61	0.79	0.61
Fisher's Alpha	4.77	4.21	2.28	2.84	1.92	4.96	**5.82**	1.87	1.68	**1.97**	1.78	1.26	4.31	1.89
Berger-Parker (1/d)	5.29	3.80	3.32	1.96	2.07	3.52	**6.02**	1.28	1.59	2.44	**2.84**	2.54	6.13	3.20
Simpsons Diversity (1/D)	10.10	5.34	5.41	3.29	3.25	7.08	**11.22**	1.59	2.18	3.74	**4.14**	3.08	11.04	4.10
Hill's Number H1	62.44	27.67	23.02	15.10	11.64	45.09	**72.74**	4.79	6.92	14.80	**15.25**	9.91	69.38	14.62

Tab. 2. Diversity indices for each transect (P = primary forest; S = exploited forest) and for *primary* and *exploited* transects combined (entire study period). Highest index-values within particular habitat complex in bold letters.

species [*Rana palmipes* (SPIX, 1824)] was recorded at the Pibiri site, only 30 km south of the MHFR. It is thus highly likely that the species also occurs at the MHFR, raising the total species number to 41. Species differed greatly in their abundance and hence were recorded in varying frequencies. The anuran species most commonly encountered were (in order of number of individual records, excluding tadpole records): *Osteocephalus oophagus* (1,750), *Eleutherodactylus marmoratus* BOULENGER, 1900 (1,228), *Dendrophryniscus minutus* (MELIN, 1941) (1,182), *Colostethus* sp. (1,025), *Allobates femoralis* (BOULENGER, 1884 "1883") (457). In terms of species richness, the MHFR is as species rich as, e.g. the well known site of the Iwokrama Forest (compare DONNELLY et al. 2005), when looking at the number of species at a given site. The same probably holds true with regard to alpha diversity, i.e. the diversity (species richness and abundance distributions) within a single site. Yet, this has not been tested as no comparable quantitative data were available for Iwokrama. Fifty-one species of amphibians have been recorded at Iwokrama, compared to 40 (+1) at the MHFR. However, the area of Iwokrama Forest comprises various clearly distinct habitat types, such as lowland rainforests, highland forests, savannas, Muri Scrub, seasonally flooded marsh forests, etc., which in turn are likely to harbor clearly distinct herpetofaunas. When excluding all non-forest species, the number of species recorded drops to 38 (35 when regarding anurans exclusively, i.e. excluding caecilians) at Iwokrama Forest and to 37 at the MHFR, respectively. In addition, the composition of the MHFR is very unique and clearly distinct from that of the Iwokrama Forest. Eleven species recorded at the MHFR are not known to occur at Iwokrama Forest. This indicates that the Essequibo River may be an effective biogeographical barrier at least for less mobile taxa, such as most amphibians. In a general comparison of amphibian communities of other northern South-American and Central Amazonian sites that have been studied previously (literature data), the assemblage of the MHFR groups along with assemblages of two other Central Guyanan sites, namely those of the Variety Woods and Greenheart Ltd-Concession at Upper Berbice and of the Iwokrama Forest, with closer links to the first. Interestingly, the Central Guyana cluster has close affinities to two locations (Petit Saut and Oyapock) that are part of the biogeographical region of Guyane Oriental sensu LESCURE & MARTY (2000). However, both of the larger biogeographical regions, Guyane Oriental and Central sensu LESCURE & MARTY (2000), as well as the French Guianan location of the Réserve des Nouragues form a clearly separated cluster (Fig. 9). These patterns indicate that the biogeographical classification of LESCURE & MARTY (2000) may not hold, especially as more sites within the region are being studied extensively and new species records are added. The Amazonian species *H. brevifrons* and *R. palmipes* have previously not been recorded east of a suggested biogeographical demarcation line that runs north-south connecting the locations of Iracoubo and Saül, French Guiana. This was interpreted in favor of the validity of the suggested classifica-

taxa	primary	secondary	BT	FS	Access-Rd	W-Fall	MHFR	restricted to			habitat			CITES & Red List status
								SA	AM	GU	F	S	D	
Amphibia – Anura														
Bufonidae														
Atelopus spumarius	1						1			1	1			vulnerable A3ce
Bufo guttatus	1	1		1	1	1	1		1		1		1	
Bufo margaritifer	1	1		1	1		1	1			1		1	
Bufo marinus	1	1		1	1		1	1^{a}			1	1	1	
Dendrophryniscus minutus	1	1					1		1		1		1	
Centrolenidae														
Hyalinobatrachium nouraguensis	1						1			1	1			
Hyalinobatrachium sp. 1	1						1			1?	1			
Hyalinobatrachium sp. 2	1					1	1			1?	1			
Dendrobatidae														
Colostethus sp.	1	1	1	1	1		1			1	1		1	
Allobates femoralis	1	1	1	1	1		1		1		1		1	CITES App.II
Hylidae														
Hyla boans	1						1	1			1			
Hyla brevifrons	1						1		1		1			
Hyla calcarata	1						1		1		1			
Hyla crepitans					1		1	1				1	1	
Hyla geographica	1						1		1		1			
Hyla granosa	1	1					1		1		1		1	
Hyla minuscula	1						1			1	1			
Hyla minuta					1		1	1			1		1	
Osteocephalus leprieurii	1						1		1		1			
Osteocephalus oophagus	1	1		1			1		1		1		1	
Osteocephalus taurinus	1	1					1		1		1		1	
Phrynohyas resinifictrix	1	1		1			1		1		1		1	
Phyllomedusa bicolor	1						1		1		1			
Phyllomedusa tomopterna					1		1		1		1		1	
Phyllomedusa vaillantii	1						1		1		1			
Scinax ruber				1			1	1			1		1	
Leptodactylidae														
Adenomera andreae	1	1		1			1		1		1		1	
Eleutherodactylus marmoratus	1	1		1	1		1			1	1		1	
Eleutherodactylus zeuctotylus	1						1			1	1			
Leptodactylus bolivianus	1						1	1			1			
Leptodactylus knudseni	1	1		1	1		1		1		1		1	
Leptodactylus mystaceus	1		1				1		1		1			
Leptodactylus petersii	1						1		1		1			
Leptodactylus rhodomystax	1	1					1		1		1		1	
Lithodytes lineatus	1						1	1			1			
Physalaemus sp.	1				1		1			1?	1		1	
Microhylidae														
Ctenophryne geayi	1		1				1	1			1			
Synapturanus mirandaribeiroi		1						1			1	1		
Pipidae														
Pipa aspera	1		1				1			1	1			
Pipa pipa	1		1				1		1		1	1		
Ranidae														
*Rana palmipes**								1			1			
total	**36**	**14**	**6**	**11**	**11**	**2**	**40**	**10**	**20**	**11**	**40**	**3**	**19**	**2**

Tab.3. Presence, distribution, habitat association, and conservation status of the anurans of the MHFR. BT = drift fences with bucket traps; FS = Field Station; Access-Rd = White Sand access road to field station; SA = South America; AM = Amazonia; GU = Guianan Region; F = forest; S = savannah; D = disturbed habitats; additional site abbreviations and detailed descriptions see study sites, 1^{a} = range extends SA; * = recorded at Pibiri only.

Fig. 10. Amplectant pair of *Atelopus spumarius*.

tion. The Guyanan records hence do not confirm this assumption. The actual pattern may be more complex than previously assumed.

Effects of logging

Preliminary results of the analyses of anuran community patterns in primary versus exploited sites indicate a general decrease in species richness (Tab. 1) and species diversity (Tab. 2) with increasing disturbance, i.e. moving from primary to old secondary (logged in 1988) and more recently disturbed (logged in 1992) forest sites. Assemblages in these habitats have been subjected to a different disturbance regime due to logging, generally producing more restrictive environments, especially with respect to microclimatic parameters. As species generally do not occur in areas that tax their physiological limits, the number of potential "true" forest species that can successfully colonize is a priori being reduced. The remaining set of species thus consists of either highly adapted species, resulting in stronger species-habitat relations than would be detected in primary forest habitats, or it consists of species that exhibit a broad-scale physiological tolerance. Increases in abundance after disturbance regularly occur among those species with wide ecological tolerances and large geographical ranges (Hamer et al. 1997, Spitzer et al. 1997). In a study on small mammals and bats in a fragmented landscape in French Guiana, generalists were found to be the best survivors (Granjon et al. 1996).

In case of the anuran communities of the MHFR, those species that had the highest abundance levels in exploited forest sites, exhibited specialized reproductive modes, i.e. the majority belonged to groups that are independent of open water (direct developers, e.g. *Eleutherodactylus marmoratus* or phytotelmata breeders, e.g. *Osteocephalus oophagus*). These specializations enable these species to cope with conditions, and to colonize habitats, not suitable for other species.

A transition from stochastically organized communities in primary forest sites to deterministically organized communities in secondary forest sites, as has recently been observed in west African anuran leaf litter communities (Ernst & Rödel in press), was also observed in the MHFR communities (R. Ernst unpubl.). This transition in predictability patterns indicates that logging not only affects system descriptors, such as species richness, abundance, and diversity, but may also alter the system's dynamics.

Conservation status of the amphibian fauna of the MHFR

The species richness of the region under investigation can be considered moderate, especially when compared to other neotropical sites. Endemicity on the other hand is comparatively high. Ten species can be considered Guianan Region endemics (sensu Hoogmoed 1979, compare Tab. 3 and Appendix 2). *Atelopus spumarius* Cope, 1871 (Fig. 10) has recently been recognized as a species complex (Lötters et al. 2002) and the status of the central Guyanan populations is currently the subject of a revision (S. Lötters pers comm.). Individuals of the MHFR will likely prove to be distinct from those of central Amazonian populations. The number of endemics would thus increase to 11. Except for one species just recently listed as vulnerable (the aforementioned *Atelopus spumarius*), none of the amphibian species recorded is currently considered threatened or included in the Red List 2001 (Hilton-Taylor 2001, CITES 2003, IUCN et al. 2004). Neither is their international trade monitored or regulated by inclusion in CITES appendices (one exception, see below). However, members of the genus *Phyllomedusa* are regularly caught for the pet trade and thus may be prone to severe population decreases. The same holds true for a number of dendrobatid frogs. Several species of this family are listed under CITES appendix II. Among them is one species (*Allobates femoralis*), recorded in the MHFR. The other species of the family Dendrobatidae that has been recorded during the study (*Colostethus* sp.) is currently not included in any of the lists. Recently, populations of several amphibian genera have been reported to undergo sudden and dramatic population declines or even to be facing extinction. In the Neotropics, this especially includes toads of the genus *Atelopus* (Lips 1997, Ron et al. 2003, Lötters et al. 2004). This may be understood as part of a global biodiversity crisis affecting amphibians in general. Possible reasons include increased solar radiation, climatic change associated with El Niño southern oscillation (ENSO) events, but also environmental contaminations, the spread of the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*), the latter especially in higher elevation species that occur in undisturbed habitats (Ron 2005), direct human impact, and habitat destruction, due to, for example logging. Almost all Andean *Atelopus* are now being grouped as "Critically Endangered" and two even as "Extinct" (IUCN 2003, IUCN et al. 2004). The status of lowland species' populations, of which the only species of *Atelopus* (*Atelopus spumarius*) recorded at the MHFR is a member, has recently been defined as stable (La Marca et al. 2005) but the actual status of these populations has not yet been clarified. A current study conducted in a comparable area in Suriname addresses these questions (W. Hödl & M. Luger pers. comm.). The sizable population (so far the largest population recorded within Guyana) at MHFR still seems to be stable, as indicated by the number of individuals recorded. However, reproduction was not confirmed and only two amplectant pairs were found during the entire study period. The loss of further habitat, especially permanent creek sites, may drastically affect these populations and eventually lead to their extinction. It is hence of utmost importance to preserve these pristine forest sites not only to guarantee the long-term viability of particular species or populations at risk, but also to maintain one of Guyana's most precious resources as a whole, its biodiversity.

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Appendix 1

Description of particular sites surveyed. P = primary forest transect, S = exploited forest transect, BT = drift fences with bucket traps, FS = Field Station. GPS-coordinates for transects represent the respective south-east corner coordinate.

site	GPS-coordinate	description
P1	N 5° 09.2003'; W 58° 41.8590'	Mixed forest on gravelly clay laterite (Leptosols) hill slope, low lying segment touching Maiko creek.
P2	N 5° 09.2454'; W 58° 41.7921'	Mixed forest on gravelly clay laterite (Leptosols) hill slope, low lying segment riverine floodplain forest on alluvial soils
P3	N 5° 10.1231'; W 58° 41.5004'	Well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
P4	N 5° 10.1334'; W 58° 41.5667'	Poorly drained mixed forest on brown sand (ferralic Arenosols) with pegasse (terric Histosols) and white sand (albic Arenosols) segments, dissected by small black water creek
P5	N 5° 10.0066'; W 58° 42.2536'	Palm-swamp forest on peaty soils (Histosoils)
P6	N 5° 09.7131'; W 58° 41.7969'	Riverine floodplain forest on alluvial soils connecting with Maiko creek, transcending in well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
P7	N 5° 09.4540'; W 58° 41.8928'	Riverine floodplain forest on alluvial soils connecting with Maiko creek, transcending in well-drained mixed forest on brown sand (ferralic Arenosols) hill slope
S1	N 5° 09.6484'; W 58° 42.7071'	Well-drained mixed forest on white sand (albic Arenosols), logged in 1992 with an extraction rate of 19.5 trees (app. 57 m^3) ha^{-1}
S2	N 5° 10.6700'; W 58° 42.3685'	Well-drained mixed forest on white sand (albic Arenosols), logged in1992 with an extraction rate of 19.5 trees (app. 57 m^3) ha^{-1}
S3	N 5° 10.8805'; W 58° 42.1953'	Well-drained mixed forest on brown sand (ferralic Arenosols), transcending into poorly-drained mixed forest with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m^3) ha^{-1}
S4	N 5° 10.9712'; W 58° 42.1690'	Well-drained mixed forest on white sand (albic Arenosols) with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m^3) ha^{-1}
S5	N 5° 11.1096'; W 58° 42.1416'	Well-drained mixed forest on brown sand (ferralic Arenosols), transcending into poorly-drained mixed forest with ephemeral creek, logged in 1988 with an extraction rate of 19.5 trees (app. 57 m^3) ha^{-1}
BT1	N 5° 09.2699'; W 58° 42.0025'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
BT2	N 5° 09.3207'; W 58° 41.9494'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
BT3	N 5° 09.7636'; W 58° 42.0145'	Mixed forest on gravelly clay laterite (Leptosols) hill slope
BT4	N 5° 09.4572'; W 58° 41.8574'	Riverine floodplain forest on alluvial soils connecting with Maiko creek
W-Fall	N 5° 09.3767'; W 58° 41.5587'	Waterfall and flood terraces, laterite bottom black water creek, plateau with dry evergreen low forest
FS	N 5° 09.3217'; W 58° 41.9826'	Large clearing near Maiko creek, at the southern side of the MHFR

Appendix 2

Summary of site records and geographic distribution of the amphibian species recorded during the study period at the MHFR. Nomenclature follows Frost (2002, with updates) and IUCN et al. (2004). Species names are followed by a list of localities from which they were recorded (see Appendix 1 for more details). Distributions according to IUCN et al. (2004).

Country Abbreviations: **AG**: Antigua and Barbuda ; **AR**: Argentina; **AU**: Australia; **BB**: Barbados; **BO**: Bolivia; **BR**: Brazil; **BZ**: Belize; **CO**: Colombia; **CR**: Costa Rica; **DO**: Dominican Republic; **EC**: Ecuador; **GD**: Grenada; **GF**: French Guiana; **GP**: Guadeloupe; **GT**: Guatemala; **GY**: Guyana; **HN**: Honduras; **HT**: Haiti; **JM**: Jamaica; **KN**: St. Kitts and Nevis; **LC**: St. Lucia; **MQ**: Martinique; **MX**: Mexico; **NI**: Nicaragua; **PA**: Panama; **PE**: Peru; **PR**: Puerto Rico; **PY**: Paraguay; **SR**: Suriname; **SV**: El Salvador; **TT**: Trinidad/Tobago; **UY**: Uruguay; **VC**: Saint Vincent & the Grenadines; **VE**: Venezuela; **VI**: U.S. Virgin Islands.

Bufonidae: *Atelopus spumarius* Cope, 1871 (P1, P2, P6, P7). Distribution: BR, CO, EC, GF, GY, PE, SR; *Bufo guttatus* Schneider, 1799 (P1, P2, P3, P4, P5, S2, S4, P6, P7, W-Fall). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Bufo margaritifer* (Laurenti, 1768) (P1, P2, P3, S1, S2, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PA, PE, SR, VE; *Bufo marinus* (Linnaeus, 1758) (P1, P4, S1, S5, P6, P7). Distribution (Neotropical Realm only): AG, BB, BO, BR, BZ, CO, CR, DO, EC, GD, GF, GP, GT, GY, HN, HT, JM, KN, LC, MX, NI, PA, PE, PR, SR, SV, TT, VC, VE, VI; *Dendrophryniscus minutus* (Melin, 1941) (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR. **Centrolenidae:** *Hyalinobatrachium* sp. 1 (P1, P2, P4, P6, P7); *Hyalinobatrachium* sp. 2 (W-Fall); *Hyalinobatrachium nouraguensis* Lescure & Marty, 2000 (P1, P2, P6, P7). Distribution: GF. **Dendrobatidae:** *Allobates femoralis* (Boulenger, 1884 “1883”) (P1, P2, P3, S3, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Colostethus* sp. (P1, P2, P3, P4, P5, P6, P7, S1, S3, S4, S5). Distribution: GF, GY, SR. **Hylidae:** *Hyla boans* (Linnaeus, 1758) (P1, P2, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PA, PE, SR, TT, VE; *Hyla brevifrons* Duellman & Crump, 1974 (P2, P7). Distribution: BR, CO, EC, GF, PE; *Hyla calcarata* Troschel, 1848 (P1, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Hyla crepitans* Wied-Neuwied, 1824 (FS). Distribution: BR, CO, GF, GY, HN, PA, SR, TT, VE; *Hyla geographica* Spix, 1824 (P1, P4, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE; *Hyla granosa* Boulenger, 1882 (P1, P2, P4, P5, S3, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Hyla minuscula* Rivero, 1971 (P1, P7). Distribution: BR, CO, GF, GY, SR, TT, VE; *Hyla minuta* Peters, 1872 (FS). Distribution: AR, BO, BR, CO, EC, GF, GY, PE, PY, SR, TT, UY, VE; *Osteocephalus leprieurii* (Duméril & Bibron, 1841) (P1, P7). Distribution: BO, BR, CO, GF, GY, PE, SR, VE; *Osteocephalus oophagus* Jungfer & Schiesari, 1995 (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BR, CO, GF; *Osteocephalus taurinus* Steindachner, 1862 (P1, P2, P3, P4, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Phrynohyas resinifictrix* (Goeldi, 1907) (P1, P2, P3, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, PE, SR, VE, *Phyllomedusa bicolor* (Boddaert, 1772) (P1, P2, P6, P7). Distribution: BO, BR, CO, GF, GY, PE, SR, VE; *Phyllomedusa tomopterna* (Cope, 1868) (FS). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Phyllomedusa vaillantii* (Boulenger, 1882) (P1, P2, P3, P4, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Scinax ruber* (Laurenti, 1768) (FS). Distribution: BO, BR, CO, EC, GF, GY, LC, MQ, PA, PE, PR, SR, TT, VE. **Leptodactylidae:** *Adenomera andreae* Müller, 1923 (P1, P2, P3, P6, P7, S2, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Eleutherodactylus marmoratus* Boulenger, 1900 (P1, P2, P3, P4, P5, P6, P7, S1, S2, S3, S4, S5). Distribution: BR, GF, GY, SR, VE; *Eleutherodactylus zeuctotylus* Lynch & Hoogmoed, 1977 (P1, P7). Distribution: BR, CO, GF, GY, SR, VE; *Leptodactylus bolivianus* Boulenger, 1898 (P1, P4, P6, P7). Distribution: BO, BR, CO, CR, EC, GF, GY, NI, PA, PE, SR, TT, VE; *Leptodactylus knudseni* Heyer, 1972 (P1, P2, P3, P4, P6, P7, S1, S2, S3, S4). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Leptodactylus mystaceus* (Spix, 1824) (P2, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, PY, SR, VE; *Leptodactylus petersii* (Steindachner, 1864) (P1, P2, P4, P5, P6, P7). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Leptodactylus rhodomystax* Boulenger, 1884 “1883” (P2, P3, P4, P6, P7, S3, S4, S5). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Lithodytes lineatus* (Schneider, 1799) (P1). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE;

Physalaemus sp. (P7; FS). Distribution: GY. **Microhylidae:** *Ctenophryne geayi* MOCQUARD, 1904 (BT1). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, VE; *Synapturanus mirandaribeiroi* NELSON & LESCURE, 1975 (P7). Distribution: BR, CO, GF, GY, SR, VE. **Pipidae:** *Pipa aspera* MÜLLER, 1924 (P1; P2; P7). Distribution: GF, SR; *Pipa pipa* (LINNAEUS, 1758) (P1; P7; BT1; BT4). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE. **Ranidae:** *Rana palmipes* SPIX, 1824 (Pibiri). Distribution: BO, BR, CO, EC, GF, GY, PE, SR, TT, VE.

Note added in proof

The family Hylidae has recently undergone major systematic revision [see FAIVOVICH, J., C.F.B. HADDAD, P.C.A. GARCIA, D.R. FROST, J.A.CAMPBELL & W.C. WHEELER (2005): Systematic review of the frog family Hylidae, with special reference to Hylinae: Phylogenetic analysis and taxonomic revision. – Bull. Amer. Mus. Nat. Hist., **294:** 1-240]. This work has been published too recently to be considered in our study. We therefore decided to retain the conventional nomenclature of FROST (2000) until taxonomic changes have been widely established. However, we provide a brief list of taxa (relevant to the present study) that underwent taxonomic changes (Table below).

Current name	New name	New group assignment
Hyla boans	*Hypsiboas boans*	*Hypsiboas semilineatus* group
Hyla geographica	*Hypsiboas geographicus*	*Hypsiboas semilineatus* group
Hyla calcarata	*Hypsiboas calcaratus*	*Hypsiboas albopunctatus* group
Hyla crepitans	*Hypsiboas crepitans*	*Hypsiboas faber* group
Hyla granosa	*Hypsiboas granosus*	*Hypsiboas punctatus* group
Hyla brevifrons	*Dendropsophus brevifrons*	*Dendropsophus parviceps* group
Hyla minuscula	*Dendropsophus minusculus*	*Dendropsophus microcephalus* group
Hyla minuta	*Dendropsophus minutus*	*Dendropsophus minutus* group
Phrynohyas resinifictrix	*Trachycephalus resinifictrix*	

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CHAPTER 3

PATTERNS

The 'ground' state - general community patterns

Community assembly and structure of tropical leaf litter anurans

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Phrynobatrachus alleni, Taï-NP, Côte d'Ivoire

COMMUNITY ASSEMBLY AND STRUCTURE OF TROPICAL LEAF LITTER ANURANS

Raffael Ernst and Mark-Oliver Rödel

Abstract

We tested two traditional views of community organization relating to the individualistic-continuum versus the interactive concept using anuran leaf litter assemblages of primary and secondary forest habitats in Taï National Park (TNP), Ivory Coast as model system. Based on biotic data and species occurrence patterns, the relative importance of either of these concepts was assessed. Null model tests of niche and size overlap revealed that the observed multivariate structure was only weakly influenced by biotic interactions and therefore most likely is not the sole result of present species interactions. Non-metric-multidimensional-scaling and quadratic regression analyses showed that particular species responded to certain habitat characteristics, in particular the absence and presence of specific breeding sites and tree size classes, the latter being an index of forest degradation. This corresponded to a discrimination of four major functional response groups within the leaf litter community. However, the strength of these species-specific responses, and therefore the allocation to one of these response groups, varied throughout seasons. Thus, our results indicate that differing individual life histories, rather than interspecific interactions were likely to explain the observed pattern. The leaf litter anuran assemblages of TNP can be best described as a collection of loosely interacting individuals responding to particular sets of physiological constraints imposed by a particular location, rather than as tightly integrated and highly interacting set of species.

Key Words: Amphibia, Anura, community composition, individualistic concept, interactive concept, leaf litter, rainforest, West Africa.

Introduction

Interspecific interactions are usually complex in natural communities and as the number of species increases, so does the potential number of interactions. Interactions can be both, positive (facilitation) or negative (typically competition and predation). Yet, abiotic factors might be just as important in structuring communities and determining the distribution and abundance of species (e.g. Beadle 1966, Clark & McLachlan 2003). However, general rules of community assembly remain elusive. There is an ongoing debate about the way in which communities are organized, and a wide spectrum of opinions exists. Both tradeoff-based theories of interspecific competition (Huisman & Weissing 1999, Chesson 2000, Rees *et al.* 2001) and neutral theories (Bell 2001, Hubbell 2001) have been suggested as potential explanations for the assembly, dynamics, and structure of ecological communities. The main discussion focuses on two opposing views. Communities are either seen as integrated, repeatable, tightly structured species assemblages that have evolved as units (Clements 1916, Pianka 1973, Roughgarden 1976), or they are viewed as the result of species-specific responses to the particular set of physiological constraints imposed by particular features of the environment (Gleason 1926, Rotenberry & Wiens 1980, Wiens & Rotenberry 1981, Homes *et al.* 1986). The dispute is personified by Frederick Clements and Henry Gleason (Clements 1916, Gleason 1926). Clements' holistic view stresses interdependence of the composite species in a community. In contrast Gleasonian 'communities' are generally characterized as having species that distribute themselves over ecological gradients of conditions, independently of the distributions of other species. In the first view, biotic effects are considered to be the major structuring force, and the observed pattern is often interpreted to be the result of positive (Bertness & Callaway 1994, Callaway 1997) or negative (Schoener 1968, Brown & Munger 1985, Dayan & Simberloff 1994, Smith & Remington 1996) interspecific interactions. The second concept implies that particular species assemblages simply reflect the fortuitous correspondence of independent life histories of species in one place and time (Ter Braak & Prentice 1988, Gascon 1991). At an extreme, even the very existence of any general assembly rule has been debated (McIntosh 1995).

Strong stochastic elements to recruitment in the component species and environmental fluctuations result in variations in community composition (Hubbell 1979, Chesson & Warner 1981, Dayton 1984, Huston 1994, Allmon *et al.* 1998). The possible role of competition in structuring communities is being reduced through predation (e.g. Azevedo-Ramos *et al.* 1999, Hero *et al.* 2001), as well as habitat and resource heterogeneity and simply by chance or unpredictable environmental changes. Where competition is inferred to be the major structuring factor, studies concentrated on niche relations among species (Brown & Lieberman 1973, Pianka 1973, Vitt & Carvalho 1995, Caldwell & Vitt 1999), and any observed structure was assumed to be the result of competition. By contrast, several methods of direct or indirect gradient analysis have been used to examine the covariance structure of matrices of species distribution vectors as a function of environmental characteristics (Whittaker 1956, Parris & McCarthy 1999). In the integrated community view, vectors for many species are correlated in time or space such that discrete units can be observed. In the individualistic view of species associations, these vectors are uncorrelated and repeatable units are not necessarily being observed. By analyzing single species vectors, species-specific correlates of distribution can be found. Historically, the debate has been specifically vivid among plant ecologist and animal studies were comparatively underrepresented. However, general applicability of results across various taxa is always desirable in ecological studies. We therefore chose a leaf litter amphibian fauna for our analyses. They have been shown to be especially appropriate for investigations concerning factors that influence community structure (Gascon 1996), for they comprise a significant proportion of the amphibian fauna at any given site (app. 25-30 %; Allmon 1991) and because standardized methods exist for estimating their species richness and abundance (Heyer *et al.* 1994, Rödel & Ernst 2004). Amphibians in general also comprise a significant portion of the vertebrates of tropical forests throughout the world, where they are important, both as predators and as prey (Inger 1980ab, Duellman 1990).

Most of the studies on tropical amphibian assemblages address either community questions of resource partitioning, focusing e.g. on niche breadth and overlap (e.g. Crump 1974, Inger & Colwell 1977, Duellman 1978, Toft 1982, Inger *et al.*1987, Lima & Magnusson 1998), or occurrence patterns and habitat use (e.g. Gascon 1991, Parris & MacCarthy 1999, Neckel-Oliveira *et al.* 2000, Parris 2004). To our knowledge no study combined the two approaches by testing the respective assumptions based on the same set of data. In this study we analyze the relevance of either of the outlined concepts. We take a niche and size overlap based null model approach to determine the importance of competition in community organization. To test for individualistic or ubiquitous relationships to environmental parameters and, hence the predictive value of these factors with regard to species occurrences, we use non-metric-multidimensional-scaling analyses and a successive quadratic regression model. This particular approach focuses on predictor variables related to site-specific environmental factors, which may affect species' presence and abundance in different ways. As species presence may change over time, as a result of simple accumulation or dispersal, successional processes or environmental variation (Nurnberger 1996, Giaretta et al. 1999, Brooks 2000), we analyzed data with respect to season, thus addressing temporal variation as explanatory variable. Additionally, since virtually all types of ecological interactions have been shown to vary with changes in the abiotic environment (e.g. mutualism: Bronstein 1994, competition: Connell 1983), we performed all null-model tests of interspecific interactions with regard to disturbance state of the habitat (i.e. primary versus secondary forest).

Materials and Methods

Study site and data acquisition

The field work was conducted in Taï National Park (TNP), south-western Ivory Coast. TNP is the largest remaining protected area of lowland rainforest in West Africa. For a detailed description of the study area, see Riezebos *et al.* (1994). The field data were acquired between February-May and September-December 1999, and May-September 2000. Wet season data, months having precipitation sums above 100 mm, included data from February, April, May, September-November 1999, March-June and September 2000. Dry season data included March, December 1999, and July-August 2000. Study sites were chosen at random within existing macrohabitats (i.e. primary / secondary forest). Although anthropogenic disturbance (selective logging, coffee and cacao plantations) stopped approximately 25 years ago, past human influence was still visible in this area, e.g. absence of a closed canopy. None of our study sites have been logged or cultivated after 1978.

We tested a variety of different methods for their value in representatively assessing the anuran leaf litter fauna of TNP. Standardized visual and acoustic encounter surveys along established transects proved to be by far the most effective one (Rödel & Ernst 2004, Veith et al. 2004). Therefore we established a total of ten rectangular transects (six in primary forest, four in secondary forest; minimum distance between neighbouring transects = 200 m, maximum distance between transects = 6.3 km). The complete transect length of 600 m was subdivided in 25 m subunits [SUs], (24 SUs / transect). SUs have been tested for spatial autocorrelation and proved to be independent, thus preventing pseudoreplication in the analyses (see Ernst & Rödel 2005 for the two approaches used to test for spatial autocorrelation and respective results).

We recorded all frogs present in a band of 100 cm to either side of the transect path. In case of acoustic sampling we recorded all calling individuals within a distance of 12.5 m to either side of the path, thus creating a 25 x 25 m acoustic sampling plot. To avoid duplicate recordings we marked captured frogs by clipping the most distal part of one toe. Recaptures were excluded from analyses. We characterized all 25 m SUs using variables that were recorded at two defined points (beginning and midpoint of each SU). These variables included vegetation density in four strata, divided into seven categories. We assigned soil to one of seven categories. Substrate moisture was determined in four categories during every transect walk. Leaf litter coverage was assigned to five categories (accuracy: 20 %). The vegetation of all 25 m SUs within a distance of about 100 cm left and right of the transect was recorded by counting the number of plants within each of five stem diameter at breast height groups (dbh1 – dbh5). Dbh-categories can be taken as a measure for forest degradation, assuming that the number of plants with small dbh is greater in degraded, secondary forests, whereas primary forests show increasing numbers of plants of larger dbh (Chatelain *et al.* 1996, Pearman 1997). In order to quantify the availability of potential aquatic breeding sites, we registered every aquatic habitat located at a maximum distance of 25 m from either side of the transect (lentic or lotic, surface and depth). The habitat variables that we considered in the analyses were: substrate type, substrate moisture, leaf litter coverage, four vegetation strata, five dbh-groups, lotic habitats, and lentic habitats (total of 14 variables). For a detailed description of the transect design, the monitoring routine and habitat parameter definitions see Rödel & Ernst (2004) and Ernst & Rödel (2005).

With respect to niche overlap analyses it has bee argued that microhabitat, diet, and temporal activity time are the three most important niche axes, and that most differentiation occurs along the first two of these axes (Schoener 1974). The 70 niche parameters that we used for the niche overlap analyses, therefore included all habitat variables (see above) at each site where an individual frog was caught, and species specific data relating to: reproductive mode (non-aquatic direct development, semiaquatic nidiculous tadpoles, phytotelmata, spawn in lotic sites, spawn in lentic sites), webbing (pronounced, present, absent), toes (enlarged to discs, enlarged but not forming discs, not enlarged), activity (diurnal, nocturnal) and species and gender specific mean snout-vent-length (SVL, accuracy of dial callipers: ± 0.1 mm).

We registered a total of 11,678 individuals of leaf litter anurans belonging to 24 species of six families during 382.5 hours of transect sampling (765 transect walks, 18,360 25 m SUs being sampled). Detecting probability was not tested but seemed to be independent of frogs' sizes. Capture probability varied according to size of frogs and climatic conditions, but generally was higher than 90 %. Frogs were more likely to escape after rain and larger frogs were more likely to escape than smaller ones. In a comparative analysis, covering amphibian monitoring programs on transects in East Africa, West Africa (including 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). We walked every TNP transect independently at least 41 times. We thus take it as justified that the local species assemblages have been almost completely recorded. This assumption was further supported by comparing the anuran species and their abundances recorded during transect walks, with the overall results of the TNP amphibian fauna recorded throughout four years of almost continuous field work including a variety of different methods (see Rödel & Ernst 2004). For a complete species listing, abbreviation of scientific names of particular species appearing in tables and figures, and a summary of relative abundances of all leaf litter frogs recorded during transect walks see Appendix 1.

Overlap analysis

According to conventional niche theory, interspecific competition should lead to a reduction in the niche overlap of competing species. Niche overlap analyses are an appropriate tool for the quantification of actual niche overlap between pairs of species. However, it is not enough to show that species differ in their use of resources in a way that reduces niche overlap. Even in the absence of competition, species will differ in their utilization of resources (Connell 1980). Null hypothesis tests by means of null model analyses are therefore an indispensable prerequisite and an important tool in the search for ecologically significant patterns (Gotelli & Graves 1996). We therefore calculated niche overlaps choosing a null model approach.

For niche overlap analyses we used data obtained from visual as well as acoustic transect sampling. The analysis comprised only the seven most abundant species (n ≥ 40) in comparisons between habitat complexes (primary vs. secondary forest habitats), and the 14 most abundant species (n ≥ 40) in seasonal comparisons (entire study period vs. dry season vs. wet season), respectively. The data that we used in size overlap analyses comprised species and gender specific mean SVL-measurements that we took ad libitum throughout the entire study period (transect walks + opportunistic visual surveys in other parts of the Taï forest, see Rödel & Ernst 2004). Only mean SVL-measurements of species and/or sexes with a sample size of more than five individuals were used, leaving a total of 18 species included in the analysis. When analyzing data of males, 15 species were considered. Analyses of females considered 14 species, respectively (see Appendix 1). Ordinations were performed using data obtained from visual transect sampling exclusively, because these provide the most detailed information on microhabitat parameters potentially correlated with species occurrence. Since it was not possible to distinguish two *Arthroleptis* species morphologically, we treated them as a single species whenever data obtained from visual transect sampling were analyzed. According to results of niche overlap analyses, this was a justifiable simplification, as both species were similar with respect to niche partitioning. Separation of the two species was possible with acoustic records. We used relative abundance values referring to number of transect hours (th) for species related calculations, hence taking into account variations in sampling effort between transects (time-based density measures; Hofer & Bersier 2001). Whenever we pooled categorical data such as different habitat parameters, the respective modes were used for calculation. In niche-overlap analyses, resource states are expressed as percent of usage. We transformed "skewed" variables that did not have a normal distribution (Kolmogorov-Smirnov and Shapiro-Wilk tests) by taking their logarithm or analyzed them by using non-parametric tests. To avoid the problem of zero-log calculations after log-transformation of data, all figures were calculated as log x + 1.

Null model tests of interspecific interactions

In order to elucidate the importance of interspecific interactions, namely competition, in structuring the assemblage, we performed niche and size overlap analyses using the program EcoSim version 7.0 Acquired Intelligence Inc. and Kesey-Bear. We used Pianka's (1973) index and a randomization algorithm (RA3), which retains the niche breadth of each species, but randomizes (1000 iterations), which particular resource states are utilized.

Fixed resource categories such as morphometric parameters that represent unique species-specific features were defined as "hard zeros", representing resource categories that cannot ever be used by a particular species, regardless of whether species interactions are important and therefore are never reshuffled or randomized. In addition to pairwise comparisons of niche overlap indices we compared the observed mean niche overlap to the overlap in the simulated communities, in order to assess whether it was greater than or less than expected by chance ('pseudocommunity analysis', Winemiller & Pianka 1990). The outcome of this null model test provides information on patterns of competition and resource allocation. Determining dietary preferences or forage ratios of frogs would have required the killing of a great number of individuals. Methods such as stomach flushing to obtain stomach contents would be to invasive and potentially lethal in most of the species, having comparatively small SVLs, as well (most frogs < 30 mm SVL). Non invasive faeces analyses do not mirror the real prey spectrum. Hard bodied prey items, i.e. beetles and ants, will be overestimated in these analyses (compare e.g. Rödel 1995). We hence searched for an alternative method to judge the importance of competition for food. Diets of many of the species dealt herein, or close relatives of them, have been investigated by previous workers. All of them have been shown to be opportunistic feeders, feeding on a variety of prey items mostly predictable by the frogs' habitats and frogs' sizes (Inger & Marx 1961, Barbault 1964). Hence, we chose frogs' body sizes (SVL) as an indirect index to average prey size (Pacala & Roughgarden 1982, Caldwell 1996, Pough *et al.* 1998, Caldwell & Vitt 1999, but see Lima & Magnusson 1998 for a contradicting example).

Since SVL is a continuous measurement, dietary overlap, expressed as size overlap was calculated in a separate analysis. We used two different overlap metrics, minimum segment length and variance in segment length. Whereas minimum segment length tests the hypothesis that there is a critical minimum separation necessary for coexistence, the variance in segment length tests the hypothesis that species sizes are evenly spaced, even if there is no particular minimum separation. Variance in segment length is most appropriate for analyses of size overlap in animal communities. The minimum segment length on the other hand is most appropriate for analyses of phenological overlap in plant or animal communities (Gotelli & Entsminger 2001). For details on the calculation algorithms and null model assumptions see Gotelli & Entsminger (2001).

Analysis of species' response to environmental parameters

We applied non-metric multidimensional scaling (NMDS) using the program PC-ORD for Windows version 4.17 MjM Software Design to describe particular species' responses to environmental factors, thereby asking for the environmental factors associated with sites used by individual species (McCune & Grace 2002). NMDS appears to provide a better fit to ecological data than may be obtained using other ordination techniques (Kenkel & Orloci 1986). For a general description of the method and iterative algorithm see Kruskal (1964), and Van Deun & Delbeke (2000). In order to minimize the possibility of finding a local minimum rather than global minima and to determine the appropriate dimensionality and statistical significance, we constructed an initial configuration with a method suggested by Legendre & Legendre (1998). We used the Sørensen (Bray-Curtis) distance and the following settings for thorough preliminary runs: maximum number of iterations: 400; instability criterion: 0.00001; starting number of axes: 6; number of real runs: 40; number of randomized runs: 50. We used the resulting configurations as starting coordinates in consecutive ordinations, thereby applying the suggested dimensionality. Since most species showed unimodal rather than linear response to habitat parameters we chose a quadratic regression model using ordination scores obtained from NMDS performed with habitat parameter matrices as independent and log-transformed relative species abundance values as dependent variables. The model thus fits a parabola to log-transformed abundances, therefore actually fitting a Gaussian response curve to the original abundance data. For details see Jongman *et al.* (1995). The regression analyses were calculated with SPSS for Windows 10.0, SPSS Inc.

Results

Null model tests of interspecific interactions

The analysis of the recorded niche parameters revealed high observed mean overlaps, compared to relatively low simulated mean overlaps in both, primary and secondary forest habitats. In all cases the observed overlap was significantly greater than the expected overlap index, p(observed ≥ expected) < 0.001; p(observed ≤ expected) = 1.000 (Table 1). This indicates no competition, based upon the underlying assumptions. The observed variances were generally significantly greater than the means of the simulated variances in both, primary and secondary forest habitats, p(observed ≥ expected) < 0.001; p(observed ≤ expected) = 1.000 (Table 1). These results were consistent throughout both seasons.

		Observed mean	Simulated mean	Standardized effect size	Observed variance	Simulated variance
1	Complete	0.616	0.363	37.866	0.011	0.004
	Dry season	0.581	0.351	34.816	0.012	0.004
	Wet season	0.615	0.360	38.452	0.011	0.004
2	Primary	0.682	0.358	23.615	0.016	0.004
	Secondary	0.584	0.374	16.080	0.021	0.004

Table 1 Results of niche overlap randomization test (1000 iterations) of pairwise species comparison; (1) complete: primary and secondary forest habitats were analyzed as pooled sample (14 most abundant species, n ≥ 40); (2) primary, secondary: data from wet and dry season were analyzed as pooled sample (seven most abundant species, n ≥ 40). Standardized effect size = (Observed mean - Simulated mean) / (Standard deviation of simulated means). 95% confidence intervals for the standardized effect size: -1.96-1.96.

Size overlap analyses revealed that the observed minimum segment length was never significantly larger than that predicted by the null model [males, the entire assemblage: p(observed ≥ expected) = 1.000 in; females: p(observed ≥ expected) = 0.545], thus not supporting the existence of a critical minimum and rather indicating convergence in body size, perhaps because of common environmental or foraging constraints. The variance in segment length showed an overall tendency for evenly spaced body sizes. This resulted in significantly smaller variances than expected by chance [p(observed ≤ expected) < 0.05].

Analysis of species' response to environmental parameters

Preliminary NMDS runs, performed in order to minimize stress values and find initial starting coordinates suggested a three dimensional (3-d) solution. In all cases, the 3-d solution provided significantly more reduction in stress than expected by chance, accepting a probability of Type I error <0.05 (Table 2). Three ordination axes explained 95 % of the variance when considering data from both seasons. The efficiency was even greater when looking at dry (96 %) and wet (97 %) season data separately (Table 3).

		Stress in real data			Stress in randomized data			
	Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
Complete	3	13.484	20.092	55.718	14.125	19.535	34.795	0.032
Dry season	3	12.309	15.166	21.745	13.980	17.058	29.475	0.032
Wet season	3	8.516	8.691	9.171	9.570	9.995	10.647	0.032

Table 2 Stress in relation to dimensionality (number of axes). Randomized data based on Monte Carlo test (50 randomized runs).

	Axis	Increment	Cumulative
Complete	1	0.019	0.019
	2	0.912	0.931
	3	0.022	0.953
Dry season	1	0.001	0.001
	2	0.020	0.021
	3	0.935	0.956
Wet season	1	0.855	0.855
	2	0.091	0.946
	3	0.023	0.969

Table 3 Coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space (explained variance). Distance measure: Sørensen (Bray-Curtis).

A first interpretation of the ordination is provided by the calculation of correlation coefficients for each matrix column (species and habitat variables) with each of the ordination axes. These coefficients express the linear (Pearson's r = parametric) and rank (Kendall's τ = nonparametric) relationships between the ordination scores and the individual variables used to construct the ordination. Joint plots provide a graphical representation of the relationship between habitat variables and ordination scores (Fig. 1 a-c). In all cases, correlation with ordination axes was sufficiently strong in only seven of 14 tested habitat variables. These comprised all five vegetation dbh-groups, as well as abundance of potential aquatic breeding habitats (lentic and lotic).

Variables contributed to the three ordination axes (referred to as NMDS 1–3) to varying degrees. Since axes values range from zero to one, negative correlations have to be interpreted as an increased impact of the respective variable moving towards zero or decreased impact moving towards one, respectively. Thus, negative and positive correlations represent a continuum along ordination axes, moving from high impact to low impact and vice versa. In the analysis of the complete set of data, NMDS 1 combines attributes emphasizing small dbh-groups and increasing availability of potential (lentic) aquatic breeding habitats. NMDS 2 was mainly characterized by a combination of the smallest dbh-group, along with decreasing availability of lotic breeding habitats.

Lentic breeding habitat availability in combination with an increase in larger dbh-groups had a major impact on NMDS 3. Specific results of correlations with ordination axes are given in Appendix 2.

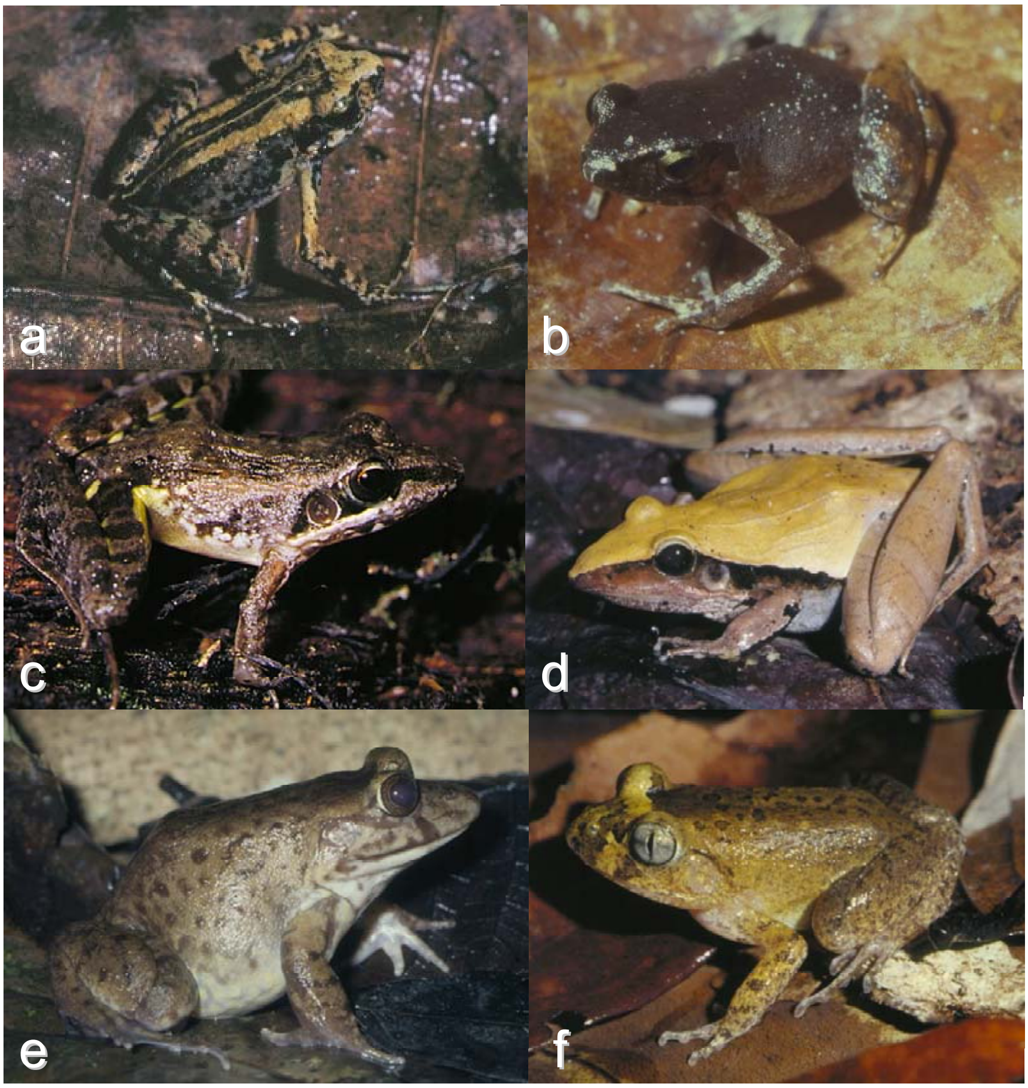

Figure 1 Typical representatives of the major functional groups within Taï National Park's leaf litter frogs: a & b represent species with direct development; c-f represent species with aquatic larval stages; a, c & e predominantly occur in primary forest; b, d & f predominantly occur in secondary forest; a & d reproduce in lentic habitats; e & f reproduce in lotic habitats; a: *Arthroleptis* sp. 1; b: *Arthroleptis* sp. 2; c: *Ptychadena aequiplicata*; d: *Ptychadena longirostris*; e: *Aubria subsigillata*; f: *Astylosternus occidentalis*.

Some shift concerning the influence of particular variables on ordination axes occurred, when taking into account dry season data exclusively. NMDS 1 was more impacted by a decrease in the availability of lotic breeding sites along with a decrease in small dbh-groups. Availability of lentic breeding habitats most influenced NMDS 2.

Increases in large dbh-groups and a decrease in small dbh-groups contributed to the axis to a lesser degree. NMDS 3 was more impacted by lotic, as opposed to lentic, breeding habitats (Appendix 2).

When we took into account wet season data exclusively, the contribution of particular variables to single ordination axes shifted as well. Potential aquatic breeding habitat availability (lotic sites), and small dbh-groups contributed to NMDS 1.

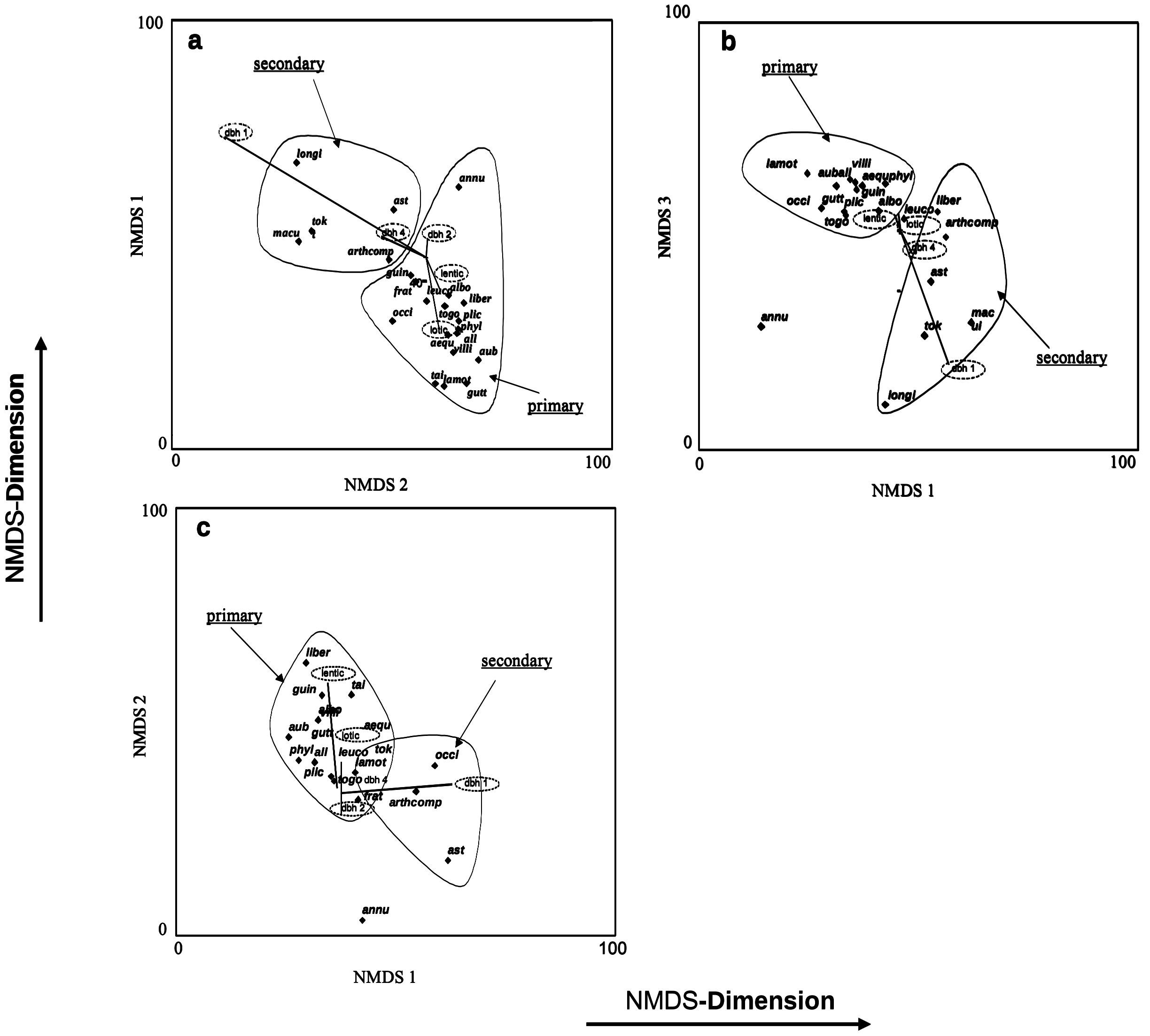

Figure 2 Typical results of NMDS ordinations on species relative abundance and habitat parameters based on Sørensen distance; (a) entire study period; (b) dry season; (c) wet season. Axes are scaled to the longest axis, thus providing accurate portraits of the similarity relationships among points. Angles and lengths of radiating vectors indicate the direction and strength of relationships of habitat parameters (stippled ellipses) with ordination scores. Ellipsoids indicate species associated with primary and secondary forest sites, respectively. For abbreviations and definition of seasons see Material and Methods and Appendix 1.

NMDS 2 was mainly characterized by decreasing aquatic breeding habitat availability (lentic habitats), as well as the lower dbh-groups. NMDS 3 was almost completely determined by the impact of dbh-groups 2 and 3. Aquatic breeding habitat availability had little influence on NMDS 3 (Appendix 2). Generally, the location of species' centroids in niche space was largely determined by NMDS axis reflecting factors related to dbh groups and aquatic breeding site availability. In other words, the presence or absence of a particular species appears to be determined by these very factors. The analyses of species' response to environmental factors by means of quadratic regression revealed that correlations were significant in a number of cases, thus indicating that individual species respond to particular environmental factors (Appendix 3).

NMDS-plots, as well as results of the regression analyses therefore form the basis for our definition of four major functional response groups (Fig. 1, Appendix 1). The most prominent discrimination was between species that were restricted to or most abundant in secondary or primary forest habitats, respectively (Fig. 2 a). This separation, was most pronounced during the dry season (Fig. 2 b), but became less distinct during the rainy season (Fig. 2 c). A second, less pronounced, discrimination existed between species that depend on aquatic breeding habitats for reproduction and those that do not depend on these habitats. The first of these two response groups was furthermore subdivided into species that were associated with lotic habitats, as opposed to those associated with lentic habitats.

Discussion

Importance of interspecific interactions

A major criticism addressing the interpretation of gradient analyses in the light of the individualistic-continuum concept is the supposed assumption that interactions among species should be similar at all points along environmental axes, and that groups of species should be associated at all points on a gradient if interdependence is to be accepted, yet interactions have been shown to vary over time and on abiotic gradients (Callaway 1997). Variations in the strength of interspecific interactions have been observed among others in plants (Connell 1983), neotropical anurans (Toft 1980), and North American lizards (Dunham 1980). Competition has also been shown to be more intense under benign abiotic conditions that permit rapid resource acquisition than under abiotically stressful conditions (Bertness & Hacker 1994). We accounted for to these points by testing for seasonal and disturbance gradient related shifts in competitive patterns. Our results for both the entire assemblage, as well as the assemblage separated by primary and secondary habitats, indicated no competition among species, regardless of seasonal changes. The observed overlap was high between most species, regardless of season or habitat complex. Hence, there was no direct evidence indicating that the intensity or existence of interspecific competition may vary according to changes in environmental conditions. The high observed variances in resource use can be interpreted as an indication of some internal guild structure (Winemiller & Pianka 1990), thereby corroborating the a priori designation of a leaf litter anuran guild and furthermore implying the existence of "sub-guilds" or functional groups, most probably based on species-specific responses to environmental parameters. Anurans in the assemblage are most likely feeding on a wide variety of small arthropods (compare Barbault 1974). Based on the predominant view in herpetological literature that most leaf litter anurans are opportunistic feeders (e.g. Inger & Marx 1961, Duellman & Trueb 1986), we assume that food partitioning is not one of the major factors structuring the assemblage (Hofer *et al.* 2004).

Although some species seem to respond to particular habitat parameters and thus show different habitat preferences, limitation of these habitats is difficult to quantify and may change throughout the season, with potentially higher impact within secondary forest habitats. The relatively high structural heterogeneity of the environment (Ernst & Rödel 2005), though, is likely to produce a great amount of habitats that can be used by different species and, thereby, may prevent species from competing. These findings correspond with recently developed stochastic niche theories. These predict that stochastic niche assembly creates communities in which species dominate approximately equally wide "slices" of the habitat's spatial heterogeneity. The niche widths then generate realistic distributions of species relative abundance for which there are strong correlations among species traits, abundance, and environmental conditions (Tilman 2004). In consideration of the integrated community view it can be argued that the anuran species that make up the leaf litter assemblage of TNP can coexist due to the absence of, or very low pressure from interspecific competition and that the structure of the assemblage is most probably not or only weakly influenced by biotic interactions, with the exclusion of predation and parasitism, which have not been investigated in this study. This corresponds with results from a study at Mount Kupe, Cameroon, where competitive interactions were assigned a minor importance in limiting amphibian distributions (Hofer *et al.* 1999, 2000). These results have recently been confirmed by Sanderson (2004).

Environmental factors determining habitat selection

Our results indicated that different species react differently (positive or negative) to the same set of environmental predictor parameters represented through particular NMDS-axes. Similar results have been reported from pond invertebrates in Northumberland, U.K. (Jeffries 2003). For the leaf litter anuran assemblages of TNP this means that different species occur in different habitats. Taking into account the most influencal parameters, habitat degradation (indicated through dhb-categories) and breeding site availability, the species could be sorted into four distinct functional groups. The rainy season observation of a comparatively weaker separation between species primarily inhabiting primary versus secondary forest sites can be explained by the increased precipitation, resulting in more favorable conditions in secondary habitats, as compared to the conditions during the dry season, when humidity drops and availability of aquatic habitats decreases. Indeed an increased occurrence of "primary forest species" in secondary habitats during the rainy season was observed.

A similar explanation may hold true for the observation of the same trend among species that are associated with lotic or with lentic habitats. The enhanced discrimination between these groups during the dry season may have been an effect of general reduction in aquatic breeding habitat availability during that period, thus resulting in the aggregation of species that depend on these habitats at the remaining sites. This resulted in an amplified contrast in the NMDS-ordination. Some species seemed to be indifferent to aquatic site availability, instead reproducing whenever and wherever suitable habitats are present. Thus, they can be considered opportunistic breeders. In conclusion, individual species responded to the habitat and predominantly occurred in sites having certain environmental attributes. Species-specific responses to habitat characteristics varied throughout the season. These variations were most probably influenced by the availability of open water, especially in secondary forest habitats. Due to their altered vegetation structure, they are microclimatically less stable than primary forest habitats, in which a closed canopy functioned as climatic buffer. The strength of these species-specific habitat requirements, although significant in a number of cases, was generally relatively weak and varied considerably between species. This suggests that these factors are not very good predictors of exact sites used by each species. They probably simply describe a set of habitat characteristics within which a species might be encountered. This may, at least, be true for the majority of species that were analyzed, apart from those that display reproductive strategies depending on very special breeding sites (Rödel *et al.* 2004, Rudolf & Rödel 2005).

Integrated communities or individualistic species associations?

Linking the observed structure to causative agents remains a problematic task in the analyses of species assemblages. Whether the observed structure is the result of present or past species interactions (Pianka 1973, Diamond 1975, Dayan & Simberloff 1994), or simply the correspondence of independent life histories due to selective pressures from predators, or responses to environmental characteristics (Heyer 1973, Wiens 1973, Homes *et al.* 1986; Gascon 1991, Parris & MacCarthy 1999, Eterovick & Sazima 2000), cannot be easily decided. However, descriptive studies are useful tools in revealing correlative patterns. As can be inferred from the discussion above, interspecific interactions, in general, and competition, in particular, do not seem to influence the structure of the recent leaf litter anuran assemblage to a considerable amount. This, in addition to the failure to detect single ubiquitous environmental predictor parameters and the observation of positive and negative correlations with different species and the same sets of these predictors indicates that species are responding individualistically.

Hence, the leaf litter anuran assemblage of TNP can best be described as a collection of loosely interacting individuals responding to the particular set of physiological constraints imposed by a particular location. Our results are, thus adding more weight to individualistic concepts of community organization and therefore underline the importance of historical and stochastic events in the assembly of particular communities. Deterministic explanations supporting conventional niche theory may thus be challenged if these patterns prove to be consistent.

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Appendix 1 Relative abundance matrix of species recorded in primary and secondary forest habitats during the study in TNP, as considered in niche analyses. The size overlap analyses comprised measurements taken within and outside transects, listed are only specimens that have been recoded on the transects. Relative abundance is given as individuals per transect hour. *Arthroleptis* sp. 1 and *A.* sp. 2 form an artificial taxon, as considered in NMDS and regression analyses; - = no record; § = considered in habitat complex comparisons; * = considered in seasonal comparisons; i/th primary = individuals per transect hour in primary forest transects; i/th secondary = individuals per transect hour in secondary forest transects; i/th total = total number of individuals during whole study period in all habitats; total # of specimens = absolute number of individuals recorded in this study; total # of transect walks = 765 (one transect walk = app. 30 min). Functional groups: a^1: restricted to primary forest sites; a^2: most abundant in primary forest sites; b^1: restricted to secondary forest sites; b^2: most abundant in secondary forest sites; c^1: not depending on aquatic habitats (direct developers); c^2: breeding in small aquatic habitats (phytotelmata or small depressions); d^1: depending on larger lotic habitats for reproduction; d^2: depending on lentic habitats for reproduction.

Taxa	i/th primary	i/th secondary	i/th total	total # of specimens	Functional group
Bufonidae					
Bufo maculatus (macu)	-	0.011	0.003	1	b^1
B. taiensis (tai)	0.004	-	0.003	1	a^1; d^1
B. togoensis (togo)*	0.197	0.097	0.173	66	a^2; d^1
Ranidae					
Aubria subsigillata (aub)	0.017	-	0.013	5	a^1; d^1
Amnirana albolabris (albo)*	0.200	0.086	0.173	66	a^2; d^2
A. occidentalis (occi)	0.007	0.011	0.008	3	a^1; d^2
Ptychadena aequiplicata (aequi)*	0.383	0.011	0.293	112	a^1; d^2
P. longirostris (longi)	-	0.011	0.003	1	b^1; d^2
Petropedetidae					
Phrynobatrachus accraensis (acc)	-	0.011	0.003	1	b^1
P. alleni (all)§*	5.596	0.538	4.366	1670	a^2
P. annulatus (annu)	0.007	-	0.005	2	a^1
P. fraterculus (frat)	0.010	0.011	0.011	4	a^2
P. guineensis (guin)*	0.162	0.075	0.141	54	a^2; c^2
P. gutturosus (gutt)*	0.225	-	0.170	65	a^1
P. liberiensis (lib)§*	2.567	4.344	2.999	1147	b^2
P. plicatus (plic)*	1.157	0.118	0.905	346	a^2; d^2
P. phyllophilus (phyl)*	1.247	0.161	0.983	376	a^2; c^2

P. tokba (tok)§*	0.649	19.796	5.305	2029	b^2; c^1
P. villiersi (villi)*	1.810	0.376	1.461	559	a^2; c^2
Astylosternidae					
Astylosternus occidentalis (ast)	0.004	0.022	0.008	3	b^2; d^1
Arthroleptidae					
Arthroleptis sp.1 (arthcomb)§*	7.081	10.753	7.974	3050	a^2; c^1
A. sp.2 (arthcomb)§*	3.610	2.570	3.357	1284	b^2; c^1
Cardioglossa leucomystax (leuco)§*	2.501	0.344	1.977	756	a^2; d^1
Hyperoliidae					
Kassina lamottei (lamot)*	0.266	-	0.201	77	a^1; d^2
total	27.700	39.344	30.531	11,678	

Appendix 2 Pearson (r) and Kendall (τ) correlations with ordination axes; dbh = diameter at breast height; lentic and lotic breeding sites.

		Axis 1		Axis 2		Axis 3	
		r	*τ*	*r*	*τ*	*r*	*τ*
Entire study period	dbh 1	-0.015	-0.057	0.959	0.956	0.138	0.198
	dbh 2	0.537	0.460	-0.008	-0.001	-0.523	-0.439
	dbh 3	-0.062	-0.015	0.118	0.099	0.067	0.057
	dbh 4	-0.170	-0.130	0.133	0.133	0.031	0.012
	dbh 5	-0.140	-0.157	0.025	0.015	0.258	0.003
	lentic	0.313	0.199	-0.153	-0.162	0.566	0.386
	lotic	0.188	0.174	-0.219	-0.211	0.066	0.054
Dry season data	dbh 1	0.007	0.007	-0.007	0.070	-0.959	-0.960
	dbh 2	-0.696	-0.589	-0.384	-0.323	0.020	0.017
	dbh 3	0.085	0.036	0.130	0.095	-0.097	-0.069
	dbh 4	0.076	0.039	0.005	-0.006	-0.123	-0.126
	dbh 5	0.089	0.081	0.290	0.024	-0.046	-0.034
	lentic	-0.150	-0.087	0.673	0.445	0.163	0.161
	lotic	-0.182	-0.170	0.125	0.121	0.217	0.209
Wet season data	dbh 1	-0.853	-0.829	0.431	0.360	-0.074	-0.058
	dbh 2	0.159	0.140	0.337	0.236	0.704	0.569
	dbh 3	-0.070	-0.042	0.015	0.030	-0.256	-0.202
	dbh 4	-0.131	-0.125	0.097	0.100	-0.087	-0.029
	dbh 5	-0.111	-0.066	-0.066	0.059	-0.198	-0.176
	lentic	0.142	0.137	-0.662	-0.420	0.055	0.003
	lotic	0.223	0.209	-0.265	-0.231	0.078	0.062

Appendix 3 Quadratic regression of log-transformed (*log*+1) relative species abundance with ordination axes; only significant correlations are reproduced. For species abbreviations see Appendix 1.

	Species	Axis	r^2	*d.f.*	*F*	*p*
Entire study period	togo	2	0.029	224	3.39	0.035
	albo	1	0.062	224	7.45	< 0.001
		2	0.032	224	3.71	0.026
	aub	2	0.035	224	4.09	0.018
	aequ	2	0.057	224	6.73	0.001
	all	2	0.044	224	5.16	0.006
	tok	1	0.054	224	6.42	0.002
		2	0.120	224	15.30	< 0.001
		3	0.027	224	3.10	0.047
	gutt	2	0.048	224	5.70	0.004
	liber	1	0.072	224	8.72	< 0.001
		3	0.171	224	23.13	< 0.001
	phyl	1	0.031	224	3.54	0.031
		2	0.094	224	11.61	< 0.001
	plic	2	0.196	224	27.25	< 0.001
	villi	2	0.176	224	23.84	< 0.001
	ast	3	0.070	224	8.41	< 0.001
	arthcomp	1	0.035	224	4.04	0.019
Dry season data	albo	1	0.032	209	3.47	0.033
		3	0.036	209	3.88	0.022
	aequ	3	0.028	209	3.05	0.049
	all	3	0.192	209	24.90	< 0.001
	tok	1	0.031	209	3.34	0.037
		3	0.164	209	20.52	< 0.001
	liber	1	0.038	209	4.17	0.017
		2	0.174	209	21.95	< 0.001
	phyl	1	0.047	209	5.20	0.006
		3	0.046	209	5.03	0.007
	plic	3	0.073	209	8.29	< 0.001

	villi	3	0.109	209	12.84	< 0.001
	ast	2	0.095	209	11.00	< 0.001
Wet season data	tai	2	0.038	215	4.30	0.015
	albo	2	0.03	215	3.34	0.037
	aub	2	0.028	215	3.09	0.048
	all	1	0.202	215	27.27	< 0.001
		2	0.076	215	8.84	< 0.001
		3	0.056	215	6.42	0.002
	tok	1	0.071	215	8.17	< 0.001
		3	0.028	215	3.06	0.049
	guin	3	0.065	215	7.48	0.001
	gutt	2	0.092	215	10.95	< 0.001
	liber	2	0.216	215	29.67	< 0.001
	phyl	1	0.096	215	11.41	< 0.001
		2	0.128	215	15.73	< 0.001
		3	0.027	215	3.03	0.05
	plic	1	0.101	215	12.06	< 0.001
		2	0.048	215	5.42	0.005
	villi	1	0.09	215	10.65	< 0.001
	ast	1	0.029	215	3.19	0.043
	leuco	3	0.029	215	3.23	0.041
	arthcomp	1	0.033	215	3.63	0.028
		2	0.132	215	16.41	< 0.001
		2	0.032	215	3.59	0.029
		3	0.030	215	3.35	0.037

Anthropogenically induced changes of predictability in tropical anuran assemblages

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Timber lot near Taï-NP, Côte d'Ivoire

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ANTHROPOGENICALLY INDUCED CHANGES OF PREDICTABILITY IN TROPICAL ANURAN ASSEMBLAGES

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Abstract. Anthropogenic habitat alteration has long been neglected as a factor in the analysis of predictability patterns in biological communities. We tested this factor by investigating anuran leaf litter assemblages in primary and secondary forests of Taï National Park, Ivory Coast, during two years.

We measured predictability of assemblage composition by analyzing correlations between the off-diagonal elements of distance matrices based on (1) species distribution, (2) environmental characteristics, and (3) geographic distance. Pairwise correlations between matrices were significant in all cases when considering data pooled across time and habitats. A different pattern emerged when data were split according to season and disturbance level (i.e., primary vs. secondary habitats). Assemblage composition in primary habitats was correlated with geographic proximity of sites exclusively, indicating otherwise stochastic recruitment from a regional species pool at the local community level. In contrast, assemblage composition in secondary habitats was predictable based on environmental parameters, not geographical proximity. This can be inferred to be the result of a strong local site filter effect (i.e., physiologically more-restrictive conditions within secondary forest habitats, especially due to an altered microclimate). Results were consistent throughout seasons. The observed transition in predictability patterns indicates that anthropogenic disturbance not only affects system descriptors, such as species richness, abundance, and diversity, but may also alter the system's dynamics.

Key words: anthropogenic disturbance; habitat alteration; leaf litter anurans; predictability patterns; primary and secondary forests; rain forest; species assemblages; West Africa.

Introduction

There is an ongoing debate about the way in which communities are organized, and a controversy over which community parameters should be considered in order to provide insight into the structure of a given community (Armbruster 1995, Wilson 1995). Communities are seen either as integrated, repeatable, tightly structured species assemblages that have evolved as units (Diamond 1975, Roughgarden 1976), or as the result of species-specific responses to a set of physiological constraints imposed by particular features of the environment (Wiens and Rotenberry 1981, Holmes et al. 1986). The first theory should lead to a high degree of predictability, whereas the latter allows for strong stochastic elements in the assemblage of species, thus yielding low degrees of predictability. In any case, the general objective is to specify which traits and therefore which subset of species will occur in a particular environment based on a given species pool, and the respective measured traits for each species. Because the problem primarily involves traits and environments, a generalization of answers with regard to systems with very different taxonomic composition should always be possible (Keddy 1992). Neither concept specifically addresses the possible role of anthropogenic disturbances that may lead to alterations in structure and predictability of communities. Yet this is receiving growing attention as degradation, fragmentation, and destruction of natural ecosystems proceeds with alarming rapidity (Didham et al. 1996, Wardle 1999).

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, for example, 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

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composition (for plants see Clark [1990], Denslow [1995]; for insects see Lima et al. [2000], Basset et al. [2001], Floren et al. [2001]; for lizards see Goldingay et al. [1996]; for mammals see Laurence and Laurence [1996]). The potential effects on system dynamics are as yet poorly understood. However, this knowledge would be crucial for the understanding of biological systems in general and systems that are strongly altered by human activities in particular.

We chose leaf litter amphibians for our analyses as they are especially appropriate for investigations concerning factors that influence community structure (Gascon 1991). They comprise a significant proportion of the amphibian fauna at any given site (~25–30 %; Allmon 1991). Standardized methods exist for estimating amphibian species richness and abundance (Rödel and Ernst 2004), and they make up a significant portion of the vertebrate faunas of tropical forests, where they are important, both as predators and as prey (Duellman 1990). Authors who have studied the influence of habitat alteration on amphibians either have focused only on the responses of individual species (Demaynadier and Hunter 1998) or have found no evidence for a concordance between sites with similar species composition and environmental characteristics (Inger and Colwell 1977). The influence of disturbance gradients on the correlation patterns of species–habitat associations in anuran communities and community predictability has previously not been addressed.

In this study we assay predictability of leaf litter anuran community composition in primary vs. disturbed forest habitats. We tested the following hypotheses. (1) Sites with similar environmental characteristics are also similar with respect to species composition (environmental signal). This is based on the assumption that community composition is determined by species-specific responses to environmental gradients, following an individualistic concept of community assembly. (2) Sites in close proximity are similar with respect to species composition (spatial signal). This is based on the assumption that priority effects (Wilbur 1987) and lottery recruitment mechanisms (Chesson and Warner 1981, Munday et al. 2000) are more important in the assembly of communities than species-specific responses to an environmental gradient. We also tested for a possible variance of species occurrence due to seasonal changes (temporal signal) and disturbance of the system (disturbance signal).

MATERIAL AND METHODS

Study site.—Taï National Park (TNP), in southwestern Ivory Coast, is the largest remaining protected area of rain forest in West Africa. Our study sites (5°50′ N, 7°20′ W) comprised ~30 km^2 of primary and secondary rain forest. Anthropogenic disturbance (selective logging, coffee and cacao plantations) ceased ~25 years ago. However, 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).

Data acquisition.—The field data were acquired between February 1999 and September 2000. We collected wet-season data for a period of 11 months; dry-season data cover for 4 months. We established 10 transects, six in primary forest, four in secondary forest, each 600 m long. Transects were subdivided in 25-m subunits (SUs; 24 SUs per transect). Each SU was characterized using 14 parameters including vegetation density, substrate type, substrate moisture level, percentage of leaf cover, plant stem diameter at breast height, and the availability and type of potential aquatic breeding habitats. For a detailed description and discussion of transect design, definition of habitat variables, and data acquisition routine see Appendix A and Rödel and Ernst (2004). We registered a total of 3843 individuals of 24 leaf litter species during 382.5 h of visual transect sampling (765 transect walks). For species-related calculations we used relative abundance values (individuals per transect hour in each SU; Appendix A).

Analysis.—We first tested for differences in structural similarity and complexity between transects to ensure that the a priori definition of macrohabitats with regard to disturbance status (primary vs. secondary) could be retained. These analyses were based on all habitat parameters (abundance of habitat categories) recorded within all SUs of a particular transect. To compare structural complexity between transects we calculated the Shannon index of diversity (H') and its respective evenness measure (J').

We then tested whether SUs or transects should be considered the smallest independent data units. We tested for correlations between environmental variables and geographic distance, thus evaluating local spatial structure due to autocorrelated environmental variables or contiguous spatial processes. We chose two commonly used indices, Morans's I and Geary's C (see Legendre and Fortin 1989) and Mantel tests (PC-ORD for Windows, version 4.17, MjM Software Design, Gleneden Beach, Oregon, USA; see Appendix B). Units to be tested within transect comparisons using Morans's I and Geary's C indices of covariance were the Euclidean coordinates (in meters) of each SU and the axis residuals of a three-dimensional Non Metric Multidimensional Scaling (NMDS) habitat model based on the original habitat variables (R. Ernst and M.-O. Rödel, *unpublished data*). Mantel tests, on the other hand, allowed the evaluation of the entire set of habitat variables at the same time, rather than accounting for each parameter separately or reducing variance through ordination procedures. Cell entries for the Mantel tests

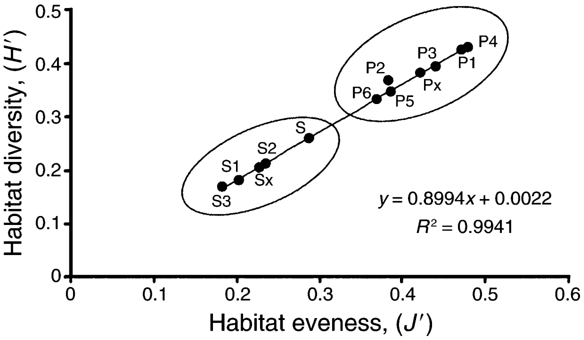

FIG. 1. Relationship between habitat structural diversity (Shannon's H'), and evenness (Shannon's J') based on 13 habitat parameters (substrate moisture levels not included). Abbreviations: Px: mean of pooled primary forest transects; Sx, mean of pooled secondary forest transects; P1–P6, primary forest transects; S1–S4, secondary forest transects.

were always the respective SU values. We compared pairs of matrices based on environmental vectors and geographic vectors (based on GPS data, Garmin 12 XL [Garmin International, Olathe, Kansas, USA], accuracy ± 10 m) for each transect (within-transect autocorrelation). To test for between-transect autocorrelation we compared pairs of matrices based on geographic and environmental characteristics of transects within a particular disturbance regime. We hence accounted for autocorrelation within a particular scale (geographic, disturbance), but did not control for a difference in magnitude of interscale interdependence. (e.g., higher environmental resemblance of SUs within transects as compared to between transects may be possible). The existence of these interscale differences cannot entirely be ruled out. Due to the nature of the matrix comparison tests, however, they are not a decisive factor in our analyses (see Appendix B). For this analysis it is more crucial to guarantee independence of SUs within a particular scale.

We compiled field data into three types of matrices (total of 17 distinct matrices, Appendix B). These were based on (1) species distribution vectors (SDM, species by SU matrix with relative species abundance as cell entry), (2) environmental characteristic vectors (ECM, habitat parameters by SU matrix with respective habitat parameter value as cell entry), and (3) geographic distance vectors (GDM, SU by SU matrix with true geographic distances between SU [in meters] as cell entry). Based on these original matrices we constructed distance matrices. For SDM we used the Sørensen quantitative (Bray-Curtis) index (Faith et al. 1987, Magurran 2004). For ECM we chose the relativized Euclidian distance (RED, Legendre and Legendre 1998). GDM was not transformed as it represents a distance matrix by definition.

The question of whether there was a correlation between the off-diagonal elements of these distance matrices was addressed by performing Mantel tests. The test evaluates the null hypothesis of no relationship between two dissimilarity (distance) or similarity matrices (see Appendix B). It is based on a simple cross-products term and is normalized so that it is equivalent to the familiar nonparametric Pearson product–moment correlation (Legendre and Fortin 1989). The magnitude of Mantel correlations is often small, even when highly significant statistically (Mantel–Pearson paradox, Dutilleul et al. 2000).

RESULTS

Spatial heterogeneity, structural diversity, and spatial autocorrelations

Analyses of habitat characteristics revealed structural differences between habitat complexes and verified the a priori distinction between primary and secondary forest habitats. Primary transects were structurally more diverse than secondary transects (Fig. 1). Within-transect comparisons indicated no spatial autocorrelation between respective subunits (SUs; 24 SUs/600-m transect) (Moran's I, Geary's C, Appendix B). Mantel tests corroborated these results and verified that transect SUs were not spatially autocorrelated (no correlation between geographic distance vectors [GDM] and environmental characteristic vectors [ECM]; $P < 0.001$ in all cases). Between-transect analyses of pairwise ECM comparisons likewise proved that transects were not spatially autocorrelated ($P < 0.001$ in all cases). This means that environmental characteristics within and between transects changed over very short distances. Hence, SUs can be considered independent.

Matrix comparison and community predictability

When we compared data from all transects covering the entire study period, pairwise correlations between SDM (species distribution vectors), ECM, and GDM were all significant (environmental and spatial signal). Thus SUs with similar environmental characteristics (species cf. environment: $r = 0.177$, $P = 0.0001$) or SUs in close proximity (species cf. geographic: $r = 0.415$, $P = 0.0001$) had similar species assemblages as well as similar sets of habitat parameters (geographic cf. environmental: $r = 0.266$, $P = 0.0001$). The latter finding is attributable to the fact that transects located within one disturbance regime are clearly distinct from those located within the other (see previous section) and are geographically closer to each other than to those located within the respective other regime. A different pattern emerged when we analyzed data from primary and secondary forest habitats separately. When

TABLE 1. Mantel test on comparison of three different distance matrices in primary and secondary forests of Taï National Park, Ivory Coast.

	Primary		Secondary	
Matrices compared	*r*	*P*	*r*	*P*
Entire study period				
Species/environmental	0.0551	0.1343	0.3470	0.0001
Species/geographic	0.1872	0.0001	0.0430	0.1389
Geographic/environmental	0.0277	0.1714	0.0387	0.2127
Dry season				
Species/environmental	0.0683	0.1029	0.3038	0.0001
Species/geographic	0.1538	0.0001	0.0233	0.2670
Geographic/environmental	0.0299	0.1310	0.0384	0.2096
Wet season				
Species/environmental	0.0321	0.2353	0.1938	0.0018
Species/geographic	0.1431	0.0001	0.0250	0.2400
Geographic/environmental	0.0227	0.2159	0.0766	0.0622

Notes: Randomization (Monte Carlo) test (10 000 permutations); *r* is the standardized Mantel statistic.

focusing on primary forest transects, only SDM and GDM were significantly correlated, indicating that SUs in close proximity have similar species assemblages (spatial signal but no environmental signal). In contrast, when considering secondary forest transects, a significant correlation existed between SDM and ECM exclusively. Thus, secondary forest sites with similar environmental characteristics had similar species assemblages (environmental signal but no spatial signal). The analyses thus revealed the existence of a disturbance-induced signal in the data (Table 1). These results were consistent throughout both seasons (no temporal signal; Table 1). Results hence indicated a general increase in community predictability with increasing proximity of SUs in primary forest, whereas predictability of communities was relatively indifferent to geographic distance between SUs in secondary forest, which per se exhibits high-level community predictability (Fig. 2).

DISCUSSION

Matrix comparison and community predictability

In the overall analysis, we found significant correlations between species composition matrices and environmental characteristics matrices, as well as between species composition and geographic distances, suggesting that there is a concordance between sites with similar species composition and environmental characteristics or geographic proximity, respectively. However, this pattern of species association did not prove to be uniform, indicating that the outcome of such analyses is not entirely independent of their scale. Scale dependence (either spatial or temporal, or both) has been emphasized in a number of previous studies (Ricklefs 1987, Fulton and Harcombe 2002). Complete scale independence would imply that patterns and processes observed on one spatial or temporal scale within a system are similar to those occurring on all larger and smaller scales (Aronson and Plotnick 1998), which evidently was not the case in this study.

However, effects attributed to comparatively small differences in scale may be largely outweighed by effects of habitat disturbance (Kerr et al. 2001). Whereas Gascon (1991) detected no pattern of species associations with respect to level of disturbance in tadpole communities of a homogenous area in Central Amazonia, our study revealed distinct patterns within habitat complexes exhibiting different levels of disturbance. Our results showed that primary forest sites in

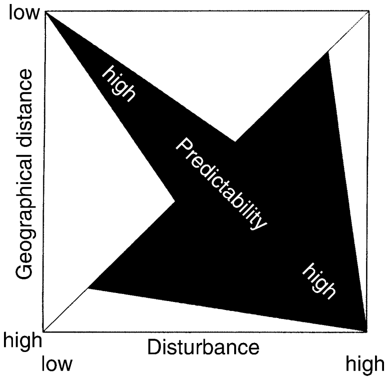

FIG. 2. Hypothetical relationship between geographic intersite distance, disturbance level, and predictability of community composition. The broad base of the downward-pointing arrow indicates relative indifference to geographic proximity in highly disturbed sites. Primary forest communities would rank in the upper left corner of the diagram. Secondary forest communities would rank in the lower right corner of the diagram.

PLATE 1. (Left) The frog *Phrynobatrachus tokba* is a direct developing species and most abundant in secondary forests. (Right) *Kassina lamottei* tadpoles exclusively develop in large stagnant ponds in primary forest. Photo credit: M.-O. Rödel.

geographic proximity to one another were similar with respect to species composition. It would seem obvious to conclude that sites in close proximity exhibit high habitat resemblance, and species composition would thus be predictable based upon habitat characteristics. However, there was no correlation between environmental parameters and geographic distance, nor between environmental parameters and species composition. Underlying random-walk dynamics, analogous to Hubbell's ecological drift (Hubbell 2001), provide the most parsimonious explanation for this compositional resemblance in geographically closer sites. These dynamics produce otherwise variable species assemblages across the entire range of the habitat complex. Similar species assemblages are hence the product of stochastic extinction and colonization events occurring in species with high turnover rates, recruited from a common regional species pool (Hecnar and M'Closkey 1997). The upper limit on the species composition of a new assemblage developing in a given place is set by the composition of the regional species pool. Membership in the regional species pool is constrained by, e.g., the geological history of respective regions, and the evolutionary processes of speciation within different taxonomic groups.

Membership in the local species pool, on the other hand, is more constrained by physiological tolerances related to factors such as temperature and humidity. This is especially the case in the presence of strong environmental filters and may hence explain the somewhat contradictory results of the analyses of secondary forest assemblages. Here correlations of species assemblages with environmental characteristics existed and geographic proximity did not seem to play a role. In the past, assemblages in these sites have been subject to habitat alteration, generally producing more restrictive environments, especially with respect to microclimate parameters. As species generally do not occur in areas that tax their physiological limits, the number of potential species that can successfully colonize is a priori being reduced (see also Hecnar and M'Closkey 1996). The existence of a strong site filter has a tremendous effect on the general processes governing recruitment from the regional species pool as outlined above. The remaining set of species thus consists of either highly adapted species, resulting in stronger species–habitat relations than would be detected in primary forest habitats, or it consists of species that exhibit a broad-scale physiological tolerance. Increases in abundance after disturbance regularly occur among those species with wide ecological tolerances and large geographical ranges (Hamer et al. 1997, Spitzer et al. 1997). In a study on small mammals and bats in a fragmented landscape in French Guiana, generalists were found to be the best survivors (Granjon et al. 1996). In the case of anuran leaf litter communities in Taï National Park (TNP), species exhibiting specialized reproductive modes (i.e., belonging to groups that are independent of open water, e.g., direct developers) had the highest abundance levels in disturbed forest sites (see Plate 1). These specializations enable species to cope with conditions, and to colonize habitats, not suitable for other species.

The failure to detect a spatial signal in secondary forest (i.e., the lack of correlation between species composition of geographically approximated sample units) supports the hypothesized general importance of random-walk dynamics and chance events in the assembly of communities in undisturbed habitats with respect to spatial patterns. Under these assumptions the direction of community change was not a priori determined. This was different in the case of environmental patterns under the influence of disturbance. Severe restrictions imposed by the comparatively harsher environmental conditions in disturbed sites (strong site filter) limit the number of potential species that could successfully colonize and hence seem to determine the predictability of communities in these habitats. It would, therefore, be interesting to examine if the species composition changes as the forest matures and becomes structurally and microclimatically more similar to old-growth primary forest, as has been supposed for other taxa (Johnston and Odum 1956). Our findings clearly indicate that, regardless of the actual underlying processes, the mechanisms that govern the assemblages' structure are largely subjected to anthropogenic disturbances.

The importance of anthropogenic disturbances for the mechanisms structuring anuran leaf litter assemblages and their influence on predictability patterns

The question of changes in correlation and thus predictability patterns of species habitat associations in anuran assemblages across disturbance gradients has previously not been addressed. It is, therefore, especially interesting that these changes do occur, and are consistently detectable throughout seasons. Our results suggest that the predictability of species assemblages at least partly depends on anthropogenic disturbance imposed on a particular habitat. Hence, human activities that lead to changes in the structure of a habitat, such as logging, not only alter the composition of organisms that form a particular assemblage but also alter the dynamics of the entire system. This has previously been shown to be the case in tropical ant communities (Floren et al. 2001), but to our knowledge has hitherto not been investigated in vertebrates. Recent studies, however, imply that this is probably a general pattern. Guilherme and Cintra (2001), for example, investigated the effects of intensity and time passed since selective logging occurred in a Central Amazonian terra firme forest. They revealed that the intensity of selective logging did not significantly affect species composition in an understory bird community. However, species richness, abundance, and frequency of use of particular habitats were strongly affected by the age of selectively logged forests. In the same context, Lima et al. (2000) showed that the density of a litter-feeding termite species decreased significantly with increasing logging intensity, thereby possibly reducing the rate of litter decomposition. This, in turn, is thought to reduce the rate of nutrient cycling in the forest, thus severely affecting the entire forest system. A change in climatic conditions, as is likely to occur in heavily altered habitats, has been shown to ultimately act as a limiting factor preventing certain assemblages of Mexican land birds from being saturated with regard to the representation of guilds or functional groups within these assemblages (Gómez de Silva and Medellín 2002). Neither of these studies addressed the change of predictability patterns and transitions from stochastic to deterministic systems, although it is likely that these changes can be observed. Floren et al. (2001) suggest that structural simplicity within disturbed forests, along with a reduction of the number of species occurring may be essential factors explaining the transition from stochastic to deterministic communities. This may, to a certain degree, also apply to the leaf litter anuran assemblages of TNP, as secondary habitats were less diverse with respect to the recorded habitat parameters. This was mainly due to a shift in the abundance of particular habitats that generally occur in both habitat complexes. However, a comparison of merely structural habitat features neglects qualitative differences, which can be severe. These may be more important to particular species than simply structural diversity itself. As an example, the number of sites with a broken or missing canopy increased in secondary forest habitats, resulting in higher temperatures on the forest floor. This, in turn, increases the probability of desiccation of aquatic breeding habitats, which occur in comparable numbers in secondary forest sites. It is thus not the lack of complex habitats that imposes restrictions, but rather temporal variations in the availability of such habitats.

We do not have an indication that the mere reduction of species accounts for the change in predictability, as potentially all species of the regional species pool could occur also in secondary forest habitats, as is indicated by occasional recordings of ''primary forest'' species in secondary forest habitats. It is more likely that the observed effects arise due to functional differences between species or differences in the number of species within a functional group, rather than number of species per se. This has previously been suggested for the relationship between biodiversity and ecosystem functioning in grassland ecosystems (Tilman et al. 1997, Hector 2001). However, it is difficult to completely separate the effects of species and functional-group richness in statistical analyses. Their particular contribution to changes in predictability patterns of biological systems is yet to be tested systematically. Linking the observed structure to causative agents remains a problematic task in the analyses of species assemblages, and the ultimate reasons along with the mechanisms that lead to these changes still remain uncertain. However, studies, such as the one presented here, in combination with field data based modeling approaches, may elucidate the underlying mechanisms of our findings. Regardless of the actual mechanism that leads to the changes in predictability patterns, our results suggest that the anthropogenic disturbance history of an area should always be considered when detecting deterministic patterns in the structuring of an assemblage, thus attenuating general applicability of deterministic explanations according to conventional niche theory.

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APPENDIX A

A description of the study period, selection of sites, design of sampling units, habitat characterization, data acquisition, and species recorded is available in ESA's Electronic Data Archive: *Ecological Archives* E086-171-A1.

APPENDIX B

A description of the statistical analyses and tests for spatial autocorrelation are available in ESA's Electronic Data Archive: *Ecological Archives* E086-171-A2.

Ecological Archives E086-171-A1

Raffael Ernst and Mark-Oliver Rödel. 2005. Anthropogenically induced changes of predictability in tropical anuran assemblages. *Ecology* 86:3111–3118.

Appendix A. A description (including two tables table and figures) of the study period, selection of sites, design of sampling units, habitat characterization, data acquisition, and species recorded.

The field data were acquired during February–May and September–December 1999, and May–September 2000. Wet-season data, months in which precipitation exceeds 100 mm, include data from February, April, May, September–November 1999, and March–June, September 2000. Dry-season data include data from March and December 1999, and July-August 2000. We chose sites within existing macrohabitats (primary / secondary forest) to establish a total of ten rectangular transects (six in primary forest, four in secondary forest). Each had a north–south extension of 200 m and an east–west extension of 100 m. For data acquisition the complete transect length was subdivided into 25-m subunits (SU; 24 SUs / transect). Transect paths were kept open so that walking at a constant speed was possible at all times. We avoided extensive cutting and thus manipulation of important habitat features. Transects were arranged in pairs, thus ensuring that all habitat types of a certain area within the inhomogeneous forest were covered. The rectangular transect design is a combination of two widely used standard techniques (see Heyer et al. 1994, Rödel and Ernst 2004). For a discussion of the advantages of rectangular sample units see Krebs (1989) and McCune and Grace (2002).

We characterized all 25-m SUs using several variables that were recorded at two defined points (beginning and midpoint of each SU). These variables included vegetation density in four strata (canopy: > 20 m, lower tree stratum: 3–10 m, bush and shrub stratum: 0.5–1.5 m, understory: < 0.5 m) divided into seven categories (Table A1). Soil was assigned to one of seven categories (compare Lieberoth 1982 and Table A1). Leaf-litter coverage was estimated according to Braun-Blanquet (1964). The vegetation of all 25-m SUs within a distance of about 100 cm left and right of the transect was recorded by counting the number of plants belonging to a certain category (plant stem diameter at breast height in centimeters, dbh1: 0–5 cm; dbh2: 6–10 cm; dbh3: 11–20 cm; dbh4: 21–50 cm; dbh5: > 50 cm). Definitions of habitat variables are summarized in Table A1. In order to quantify the availability of potential aquatic breeding sites, every aquatic habitat (lentic and lotic) located at a maximum distance of 25 m from either side of the transect was recorded with respect to type, surface, and depth. Substrate moisture was determined in four categories (from dry to saturated wet) during every transect walk. The habitat variables considered in the analyses were substrate type, substrate moisture, leaf-litter coverage, vegetation density in four strata, number of plants in the five respective dbh-categories, lotic habitats, and lentic habitats, thus summing up to a total of 14 variables.

Sampling was performed independent of prevailing weather conditions. Repeated controls of identical transects on consecutive days were avoided to ensure independence of samples. Transects were intensively patrolled at a constant speed (0.30–0.35 m/s), visually recording all amphibians within a distance of 100 cm from either side of the path. To avoid duplicate records, captured frogs were marked by toe clipping (Donnelly et al. 1994, Henle et al. 1997). Recaptures were excluded from the analyses. Individuals below nine mm SVL were not marked due to their small size. Probability of detection was not tested but seemed to be independent of frogs' sizes. Capture probability varied according to frog size and climatic conditions, but generally was higher than 90%. Frogs were more likely to escape after rain and larger frogs were more likely to escape than smaller ones. 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 Taï transect was walked independently at least 41 times. It is thus justified to assume that the local species assemblages have been almost completely recorded. Relative abundances of all leaf-litter frogs recorded during transect walks are summarized in Table A2.

TABLE A1. Three habitat variables measured on transects, and the categories to which their measurements were assigned.

	Vegetation†	Substrate types	Leaf cover (%)
Category	Absent	forest soil	0–20
	Transition	arenaceous forest soil	21–40
	Gaps predominating	loamy soil	41–60
	Transition		61–80
	Closed areas predominating	sabulose soil	81–100
	Transition	muddy soil	
	Swampy soil		

† Vegetation density was measured in four strata (see second paragraph, above), and assigned to one of seven categories.

TABLE A2. Abundance matrix of species recorded in primary and secondary forest habitats during the study in Taï National Park, Ivory Coast. Relative abundance, as considered in analyses, is given as individuals per transect hour (*i*/th).

Species	*i*/th primary	*i*/th secondary	*i*/th total	Total no. specimens
Bufonidae				
Bufo maculatus	-	0.0108	0.0026	1
Bufo taiensis	0.0035	-	0.0026	1
Bufo togoensis	0.2280	0.0968	0.1961	75
Ranidae				
Amnirana albolabris	0.1485	0.1075	0.1386	53
Amnirana occidentalis	0.0173	0.0108	0.0157	6
Aubria occidentalis	0.0207	-	0.0157	6
Ptychadena aequiplicata	0.3040	0.0215	0.2353	90
Ptychadena longirostris	-	0.0108	0.0026	1

Petropedetidae				
Phrynobatrachus accraensis	-	0.0108	0.0026	1
Phrynobatrachus alleni	5.0639	0.4624	3.9451	1,509
Phrynobatrachus annulatus	0.0069	-	0.0052	2
Phrynobatrachus fraterculus	0.0104	0.0108	0.0105	4
Phrynobatrachus guineensis	0.0484	0.0323	0.0444	17
Phrynobatrachus gutturosus	0.0967	-	0.0732	28
Phrynobatrachus liberiensis	1.0363	1.5591	1.1634	445
Phrynobatrachus phyllophilus	0.7081	0.0430	0.5464	209
Phrynobatrachus plicatus	1.0155	0.0538	0.7817	299
Phrynobatrachus tokba	0.0242	1.1613	0.3007	115
Phrynobatrachus villiersi	1.7098	0.2151	1.3464	515
Astylosternidae				
Astylosternus occidentalis	0.0035	0.0215	0.0078	3
Arthroleptidae				
Arthroleptis comb.	1.0328	1.3871	1.1190	428
Cardioglossa leucomystax	0.0242	0.0108	0.0209	8
Hyperoliidae				
Kassina lamottei	0.0933	-	0.0706	27
i/th total	11.5959	5.2258	10.0471	3,843

Notes: *Arthroleptis* species (two species known to occur, distinction possible by means of genetic and acoustic characters) could not be separated morphologically and thus were treated in the analysis as a single artificial taxon *Arthroleptis* comb.; *i*/th primary = no. of frogs per species per transect hour in primary forest transects; *i*/th secondary = no. of frogs per species per transect hour in secondary forest transects; *i*/th total = total number of individuals per species per transect hour in primary and secondary forest combined (rows) and total number of individuals per transect hour in primary forest, secondary forest, and both types of forest combined (columns); last column = absolute number of individuals recorded per species, column sum = absolute number of individuals recorded; - = absent; total number of transect walks = 765 (one transect walk lasted app. 30 min); nomenclature of amphibian species is according to Frost (2002). A dash in a species cell indicates the species could potentially be found (because it lives in the forest, but it was not recorded).

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Appendix B. A description of the statistical analyses and tests for spatial autocorrelation.

Statistical Analyses

Results of covariance comparisons.—Most statistics are based on the assumption that the values of observations in each sample are independent of one another. Positive spatial autocorrelation may violate this if the samples were taken from nearby areas. We thus tested the assumption of independence of sample units by means of covariance comparisons (Moran's *I* and Geary's *C*) using the Excel 97/2000 Visual Basic (VB) Add-in ROOKCASE (Sawada 1999) as well as Mantel-tests (see below). For a discussion of statistical analyses of spatial data in ecology see Liebhold and Gurevitch (2002).

The general method of describing autocorrelation in a variable is to compute some index of covariance for a series of lag distances from each point. The resulting correlogram illustrates autocorrelation at each lag distance. Membership in a given distance class is defined by assigning a weight to each pair of points in the analysis. Typically this weight is a simple indicator function. Moran's *I* compares the value of a variable at any one location with the value at all other locations. It is similar to the correlation coefficient and varies between –1.0 and + 1.0. When autocorrelation is high, the coefficient is high. A high *I* value indicates positive autocorrelation. Geary's *C* is inversely related to Moran's *I*. C values typically range between 0 and 2. If the values of any one zone are spatially unrelated to any other zone, the expected value of *C* will be 1. Geary's *C* does not provide identical inference because it emphasizes the differences in values between pairs of observations, rather than the covariation between pairs. Moran's I gives a more global indicator, whereas the Geary coefficient is more sensitive to differences in small neighborhoods. In ecological applications, Moran's *I* tends to perform better than Geary's *C*, capturing known patterns more cleanly and providing more interpretable results (Legendre and Fortin 1989).

Our analysis of covariance revealed that SUs (25-m subunits of each transect) were not spatially autocorrelated based on the assumptions outlined above. All values for Moran's *I* were slightly above or below 0, whereas all values for Geary's *C* were slightly above or below 1, indicating no significant spatial autocorrelation (Fig. B1).

Mantel test.—Mantel tests are widely used in ecological studies (Douglas and Endler 1982, Burgman 1987, Böhning-Gaese and Oberrath 1999), particularly when assessing the relationship between multivariate community structure and environmental variables (Gascon 1991, Diniz-Filho and Bini 1996, Parris and McCarthy 1999). The simple Mantel correlation addresses the basic ecological question of whether environmentally similar samples are also similar with respect to species composition. This is computed as the correlation between compositional and environmental dissimilarity matrices. Likewise, it is possible to correlate either compositional or environmental dissimilarity to geographic distance, and to test whether there is spatial structure (autocorrelation) in these data (Urban et al. 2002). This autocorrelation is averaged over all distances (Legendre and Fortin 1989).

The Mantel test evaluates the null hypothesis of no relationship between two dissimilarity (distance) or similarity matrices (Mantel 1967). It is an alternative to regressing distance matrices that circumvents the problem of partial dependence in these matrices. This dependence of pairwise elements does not allow for parametric testing of the correlation from matrix comparisons. Therefore Mantel tests are appropriate when more than one distance matrix is to be compared from the same set of sample units. The correlation can be tested by rearranging the rows and columns (simultaneously) of one of the matrices randomly and calculating a new correlation between one of the original matrices and the permuted one. After each permutation the Z statistic is calculated and the resulting values provide an empirical distribution that is used for the significance test. A randomization (Monte Carlo) test can be used for the calculation of the P value. In the case of this study we chose 10,000 permutations for the randomization test.

Original matrices.—Generally three types of "primary" matrices were constructed for each separate analysis (1) species by sample unit (SU) matrices with relative species abundance as cell entry; (2) habitat parameters by SU matrices with respective habitat parameter value as cell entry; and (3) SU by SU matrices with true geographic distances between SU in meters as cell entry. This means that a total of 17 distinct matrices (18 + 3 when counting those that are identical; note that geographic distance matrix (GDM) was identical across seasonal analyses within a respective disturbance regime) had to be constructed in order to perform 21 separate pairwise matrix-tests.

With the exception of GDMs which are distance matrices by definition, all "primary" matrices were transformed into distance matrices using the particular distance indices as outlined. The analyses were performed as follows: (A) using the entire data set disregarding season or disturbance status (3 distinct matrices, 3 pairwise tests; species distribution matrix (SDM) vs. environmental characteristic matrix (ECM); SDM vs. GDM; GDM vs. ECM); (B) using the entire data set disregarding season but considering disturbance status (2 × 3 distinct matrices = 2 × 3 pairwise tests; SDM vs. ECM; SDM vs. GDM; GDM vs. ECM for both primary and secondary forest). In B each matrix was distinct from the matrices used in previous analyses and "primary forest matrices" were distinct from "secondary forest matrices", i.e. they had different cell entries because relative species abundance values had to be calculated separately for each SDM, as the number of individuals and transect hours varied. ECMs represented a "subset" of the matrix used in previous analyses, i.e. split into primary vs. secondary forest. The same holds true for GDM, only distances between SUs within a habitat complex appeared in these matrices; (C) using dry-season data only, evaluating primary vs. secondary forest (2 × 2 distinct matrices; + 2 GDMs from previous analyses because GDM does not vary across seasons = 2 x 3 pairwise tests; SDM vs. ECM; SDM vs. GDM; GDM vs. ECM for both primary and secondary forest). SDM and ECM were distinct matrices, whereas GDMs were identical with GDMs from previous analyses since geographic distance does not vary seasonally; (D) using wet-season data only, evaluating primary vs. secondary forest (2 × 2 distinct matrices; + 2 GDMs from previous analyses because GDM does not vary across seasons = 2 × 3 pairwise tests; SDM vs. ECM; SDM vs. GDM; GDM vs. ECM for both primary and secondary forest). SDM and ECM again were distinct matrices, whereas GDMs remained identical.

SDMs and ECMs always differ between primary and secondary forest and between analysis complexes (A) and (D). GDM, however, only differs between primary forest and secondary forest and between analysis complex (A) and (B) but not between complexes (B) and (D), as geographic distances are fix and therefore not subject to seasonal change. Relative species abundances (individuals/transect hour), however, have to be calculated in every new case since the number of specimens and transect hours varies as do the recorded habitat parameters.

Distance measures.—Matrices of distance used in Mantel-tests were based on relative species abundance data and constructed using the Sørensen quantitative (Bray-Curtis) index.

It is most useful for ecological community data and appears to be a robust measure of the ecological distance between sites (Faith et al. 1987). As compared to Euclidean distance it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (Roberts 1986). For distances of environmental characteristics we used the relativized Euclidian distance (RED), since Euclidian distances are suitable for abiotic data (Legendre and Legendre 1998). RED is conceptually similar to Euclidean distance, except that the data are normalized, thus putting differently scaled variables on the same footing, eliminating any signal other than relative abundance. Geographic distance matrices were based on the actual distances (in meters) between single transect segments (SUs).

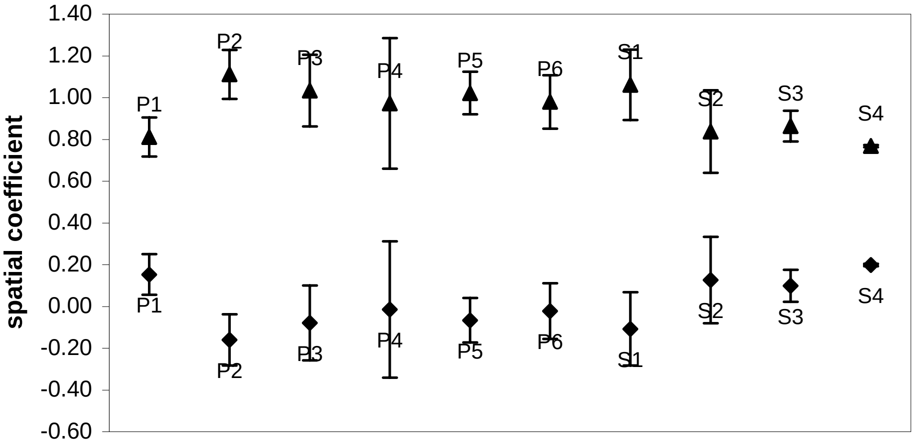

FIG. B1. Results of Moran's *I* (rhomb) and Geary's *C* (triangle) computation using Euclidean coordinates for each SU (coordinates in meters, lag distance 25 m) within single transects and axis residuals of a three-dimensional NMDS habitat model based on original habitat variables (three explanatory axes per transect). Coefficients were calculated for each dimension = axis residual separately, hence producing three values per coefficient per transect. Means and standard deviations (SD) thus represent the mean and SD of the calculated values for a given transect. P1-P6 = primary-forest transects, S1-S4 = secondary-forest transects.

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Disturbance related predictability patterns of community composition in two tropical treefrog assemblages

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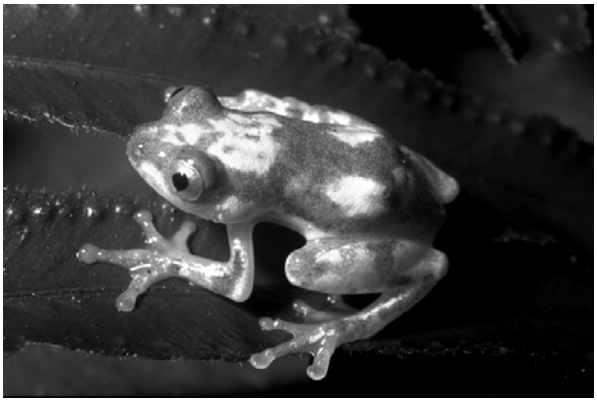

Afrixalus vibekensis, Taï-NP, Côte d'Ivoire

DISTURBANCE RELATED PREDICTABILITY PATTERNS OF COMMUNITY COMPOSITION IN TWO TROPICAL TREEFROG ASSEMBLAGES

Raffael Ernst and Mark-Oliver Rödel

Abstract

An ongoing controversy and major theme in community ecology involves the debate about the many factors that affect the assembly and species composition of a given community or assemblage and, therefore the predictability of community composition. Different patterns have been reported for many taxa in naturally or anthropogenically altered habitats. Theories suggest that these patterns are influenced by environmental gradients, or by contagious biotic processes, such as competition, predation, and dispersal. Functional group- or guild specific differences are most often neglected in the analyses of these patterns.

We analyzed predictability patterns of species composition in a specific group (arboreal frogs) of two tropical anuran assemblages in primary and exploited rainforests of two geographically distinct eco-regions: Guyana, northern South America and Côte d'Ivoire, West Africa.

Predictability patterns of species composition in treefrog assemblages differed between regions but were consistent within respective realms and disturbance regimes. All assemblages appeared to be spatially structured, i.e. sites in close proximity had similar species assemblages. However, spatially-structured environmental variation did not account for the spatial structure of species incidence. Environmental characteristic vectors proved to be significant predictors of species incidence in only one case (primary forest assemblages in Guyana). These results are in contrast to previously published results from a similar study on leaf litter anurans. Results indicate that it group-specific differences must not be neglected when analysing predictability patterns of species composition in anurans as they may drastically alter the outcome of the analysis.

Key words: anthropogenic disturbance; treefrog assemblages; predictability patterns; primary and exploited rainforests; northern South America; West Africa

Introduction

Despite the fact that general patterns in ecology have successfully been identified at the macroeclogical scale (Gaston and Blackburn 2000) or at species specific scales (e.g. habitat requirements, Beadle 1966) general rules of community assembly remain elusive. Even the very existence of any assembly rule has been debated (McIntosh 1995). Relationships between particular species' incidences and systematic (patch quality), temporal (seasonal / annual variation) and patch-specific (patch history) variables may often be idiosyncratic, rather than the majority of species responding to a few dominant factors in a similar way (e.g. Jeffries 2003).

Relationships between community structure and environmental conditions have been described as an adaptive process under constraints that can alter how the functional traits of species match up with the environmental conditions that they encounter. Strong correlations between community composition and environmental factors would indicate that this process is indeed influential (Leibold et al. 2005). In the absence of such a process, community composition would not correspond with environmental conditions.

The distribution and abundance of species, and thus the composition of entire communities are influenced by environmental parameters (individualistic concept or environmental control model, Gleason 1917, 1926, Whittaker 1956,Neave et al. 1996, Parris 2004) or biotic processes, such as competition, predation or dispersal (interactive concept or biotic control model, Clements 1916, Connell 1983, McCarthy 1997, McCarthy and Lindenmayer 2000). In the first case, sites with similar environmental characteristics would have similar species composition. In the second case communities would be spatially structured i.e. sites in close proximity would have similar species assemblages (Legendre and Fortin 1989). Spatial habitat heterogeneity may itself be correlated with the spatial distribution of species. This means that systematic spatially-structured environmental variation can result in a spatial structure of species incidence. Three factors may hence contribute to the variation of community composition. These factors are environmental variation, spatial variation and spatially-structured environmental variation (Bocard et al. 1992).

Environmental parameters, as well as biotic processes are not unaffected by either, natural or human-induced environmental changes. Environmental change and disturbance in local patches can strongly determine how closely tied the functional attributes of species in local communities are to environmental parameters and thus alters the pattern between community composition and environments.

In a recent study we examined the relationship between anthropogenic habitat alteration and predictability patterns of community composition in a tropical leaf litter anuran assemblage (Ernst and Rödel 2005). We showed that community composition in undisturbed primary forest habitats was exclusively correlated with geographic proximity of sites. In contrast, community composition in disturbed secondary habitats was predictable based on environmental parameters, not geographic proximity. This transition in predictability patterns hence appeared to be anthropogenically induced.

Few studies have investigated the effects of environmental variables and spatial or biotic processes on amphibian community composition (e.g. Skelly 1995, Hecnar and M'Closkey 1997, Hero et al. 1998, Azavedo-Ramos et al. 1999, Parris 2004) and even fewer studies have investigated the effects of anthropogenic disturbance in the same context (Ernst and Rödel 2005, Ernst and Rödel subm.)

Among all vertebrate groups, amphibians are the one with the highest proportion of species threatened with extinction (Stuart et al. 2004, Beebee and Griffiths 2005) and habitat loss and fragmentation have been identified as the most direct contributors to these threats (Carr and Fahrig 2001, Houlahan and Findlay 2003, Bowne and Bowers 2004). There is hence a clear need for studies that focus on the relationship between anthropogenic disturbance and amphibian community structure and composition.

Most of the studies on amphibian community assembly and composition have either focused on entire communities (i.e. no differentiation between different guilds or functional groups) or they have concentrated on easily assessable segments of the entire community (e.g. leaf litter anurans only). To our knowledge, this is the first study to specifically address questions concerning community structure and the impact of anthropogenic disturbance in arboreal anuran communities, a large segment of many amphibian communities, especially in the Neotropics with its highly divers hylid frog fauna (e.g. Duellman 1988, 1999). The underrepresentation of treefrog communities in amphibian studies is certainly due to difficulties in assessing a representative portion of the arboreal communities throughout all seasons.

Despite these difficulties group or guild specific approaches might be indispensable if compositional patterns are to be analyzed systematically. This is especially true with respect to patterns between community composition and environments as differences in life-history strategies and thus potential habitat associations, may strongly affect the analysis of correlation patterns. In other words it may be important, which segment of the entire community is being analyzed, as patterns may differ between different ecological guilds.

Because species-environment relationships may differ greatly among different groups across scales (Cushman and McGarigal 2004) it is even more important to perform analyses on a group-specific basis.

It has recently been pointed out that conservation strategies would benefit by moving from generalizations to process specific recommendations and by moving from site-specific actions to multiple scale and broad landscape-level implementations (Cushman, 2006). The objectives of this study are in direct concordance with this view as they address community processes and patterns of predictability in two amphibian communities in primary versus disturbed forest habitats in two geographically distinct eco-regions.

In this context we specifically tested whether: (1) sites with similar environmental characteristics are also similar with respect to species composition (environmental control model) and (2) sites in close proximity are similar with respect to species composition (biotic control model). We also tested for a possible variance of species occurrence due to seasonal changes (temporal signal) and disturbance of the system (disturbance signal). Because there may be large differences among amphibian species in terms of their habitat requirements and sensitivity to environmental changes, which in turn may be closely related to the geographic history of the respective site and the phylogenetic history of the respective species, we decided to take a large scale comparative approach. We therefore compared arboreal communities of two geographically distinct eco-regions, namely the Neotropic and the Afrotropic realm.

We finally relate our results to the patterns previously found in the terrestrial anuran community of the African forest site (Ernst and Rödel 2005) and discuss implications for proposed generalizations and conservation recommendations.

Methods

Study areas and disturbance history

Taï National Park (TNP), in south-western Côte d'Ivoire, is the largest remaining protected area of rain forest in West Africa. Our study sites (5°50' N, 7°20' W) comprised about 30 km² of primary and exploited rain forest. In TNP anthropogenic disturbance (selective logging, coffee cacao plantations) ceased approximately 25 years ago. Past human influence was still visible in this area and differences between primary and exploited forest sites were marked (Ernst and Rödel 2005). For a detailed description of TNP see Riezebos et al. (1994). The Mabura Hill Forest Reserve (MHFR) is situated in Central Guyana (5°13' N, 58°48' W). It comprises an area of approximately 20 km² of primary rain forest and is part of the Wappu compartment located within a 500 km² Timber Sales Agreement concession. Disturbed sites were located outside the reserve's core area, within the main logging concession. These sites have been logged with equal intensities (i.e. 19.5 trees or approximately 57 m^3 ha^{-1}). For a detailed description of MHFR and disturbance history of particular study sites see ter Steege et al. (1996) and Ernst et al. (2005).

Data Acquisition

The field data were acquired between February 1999 and September 2002 (TNP) and November 2002 and September 2004 (MHFR). We collected wet season data for a period of 11 months; dry season data cover four months in case of TNP. In case of MHFR, wet season data covers eight months and dry season data covers four months. We established ten transects, six in primary forest, four in exploited forest (TNP) and 11 transects, six in primary forest and five in exploited forest (MHFR), respectively (Rödel and Ernst 2004, Ernst et al. 2005). In both cases, sites included in the analyses are to be considered as classical chronosequences (sensu Plumptre 1996).

Each rectangular transect had a total length of 600 m. Transects were subdivided in 25 m subunits (SUs; 24 SUs / transect). Each SU was characterized using 14 parameters including vegetation density, substrate type, substrate moisture level, percentage of leaf cover, plant stem diameter at breast height, and the availability and type of potential aquatic breeding habitats. Only parameters recorded in both eco-regions were considered in the analysis. For species related calculations we used relative abundance values (individuals per transect hour in each SU). 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. 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 independence of sample units (test for spatial autocorrelation of environmental characteristics), and an evaluation of various methods have been published earlier (Rödel and Ernst 2004, Ernst and Rödel 2005). Descriptions given herein are hence restricted to relevant modifications and aspects specific to this study.

Statistical analysis

We compiled field data into three types of matrices. These were based on (1) species distribution vectors (SDM, species by SU matrix with relative species abundance as cell entry), (2) environmental characteristic vectors (ECM, habitat parameters by SU matrix with respective habitat parameter value as cell entry), and (3) geographic distance vectors (GDM, SU by SU matrix with true geographic distances between SU in [m] as cell entry). Based on these original matrices we constructed distance matrices. For SDM we used the Sørensen quantitative (Bray-Curtis) index (Faith et al. 1987, Magurran 2004). For ECM we chose the relativized Euclidian distance (RED, Legendre and Legendre 1998). GDM was not transformed as it represents a distance matrix by definition.

The question of whether there was a correlation between the off-diagonal elements of these distance matrices was addressed by performing Mantel-tests. The test evaluates the null hypothesis of no relationship between two dissimilarity (distance) or similarity matrices (see Appendix B). It is based on simple cross-products term and is normalized so that it is equivalent to the familiar non-parametric Pearson product-moment correlation (Legendre and Fortin 1989). The magnitude of Mantel correlations is often small even when highly significant statistically (Mantel-Pearson paradox, Dutilleul et al. 2000).

Results

Community composition

We registered a total of 3,431 individuals of 14 species belonging to two families during 382.5 hours of visual and acoustic transect sampling in TNP, and 4,227 individuals of 14 species belonging to three families during 393.5 hours of visual and acoustic transect sampling in MHFR, respectively.

Community composition was tremendously affected by disturbance in communities of both realms. Species richness and thus composition differed significantly between communities of primary and exploited forest sites in both realms. Yet, changes differed qualitatively between the African and the South American sites.. Whereas exploited forest communities of MHFR comprised an impoverished subset of primary forest communities with no species turnover (all species recorded in exploited forest sites occurred in primary forest), species thinning in exploited forest communities of TNP was less pronounced, however species-turnover occured (two species not recorded in primary forest, Table 1). The number of species recorded was subject to seasonal changes.

	TNP				***MHFR***		
Species	Complete	Primary	Exploited	Species	Complete	Primary	Exploited
Acanthixalus sonjae	x (x;-)	-	x (x;-)	*Dendropsophus brevifrons*	x (x;-)	x (x;-)	-
Afrixalus dorsalis	x (x;x)	-	x (x;x)	*Dendropsophus minusculus*	x (x;-)	x (x;-)	-
Afrixalus nigeriensis	x (x;x)	x (x;x)	x (x;-)	*Hypsiboas boans*	x (x;x)	x (x;x)	-
Afrixalus vibekensis	x (x;-)	X (x;-)	-	*Hypsiboas calcaratus*	x (x;x)	x (x;x)	-
Hyperolius chlorosteus	x (x;x)	x (x;x)	x (x;-)	*Hypsiboas geographicus*	x (x;x)	x (x;x)	-
Hyperolius concolor	x (-;x)	X (-;x)	-	*Hypsiboas granosus*	x (x;x)	x (x;x)	x (x;-)
Hyperolius fusciventris	x (x;-)	x (x;-)	-	*Osteocephalus leprieurii*	x (x;x)	x (x;x)	-
Hyperolius nienokouensis	x (x;-)	x (x;-)	-	*Osteocephalus oophagus*	x (x;x)	x (x;x)	x (x;x)
Hyperolius sylvaticus	x (x;x)	x (x;x)	x (x;-)	*Osteocephalus taurinus*	x (x;x)	x (x;x)	x (x;x)
Hyperolius zonatus	x (x;x)	x (x;-)	x (x;x)	*Phyllomedusa bicolor*	x (x;x)	x (x;x)	-
Leptopelis hyloides	x (x;x)	x (x;x)	x (x;x)	*Phyllomedusa vaillantii*	x (x;x)	x (x;x)	-
Leptopelis macrotis	x (x;x)	x (x;x)	x (x;-)	*Trachycephalus resinifictrix*	x (x;x)	x (x;x)	x (x;x)
Leptopelis occidentalis	x (x;x)	x (x;x)	x (x;x)	*Hyalinobatrachium* sp.1	x (x;x)	x (x;x)	-
Chiromantis rufescens	x (x;x)	x (x;x)	x (x;-)	*Eleutherodactylus marmoratus*	x (x;x)	x (x;x)	x (x;x)
Total	**14** (13;10)	**12** (11;8)	**10** (10;4)	**Total**	**14** (14;12)	**14** (14;12)	**5** (5;4)

Table 1 Species composition of arboreal frog communities in Taï National Park (TNP) and Mabura Hill Forest Reserve (MHFR). Complete = recorded in primary or exploited forest transects; primary = recorded in primary forest transects; exploited = recorded in exploited forest transects. x = recorded, - = not recorded. Entries in parentheses refer to respective seasons; first entry before semicolon = wet season, second entry after semicolon = dry season.

Of the 14 species recorded in the entire MHFR-community, only 12 species could be recorded during the dry season. All 14, however, were recorded during the wet season. Only five species have been proven to occur in exploited sites. All 14, however, were recorded in primary forest. Only four out of 12 species that were recorded during the dry season were registered in exploited forest sites. Primary forest records in the dry season included all 12 species recorded during that period (Table 1, MHFR).

The situation in TNP was similar with respect to seasonal differences in the number of species recorded in each of the habitat types. The actual pattern, however, deviated from the pattern found in MHFR. In case of TNP, only ten out of the 14 species recorded in the entire TNP-community were registered during the dry season and only 13 during the wet season. A total of 12 species was detected in primary forest and only ten were proven to occur in exploited forest. 11 out of 12 species that have been shown to occur in primary forest were detected during the wet season. Eight species were detected during the dry season, one of which (*H. concolor*), was recorded during the dry season exclusively. Dry season records incorporated only eight species. In exploited forest, differences between rainy and dry season records were even more pronounced. During the wet season, all species that have been proven to occur in exploited forest were recorded. However, number of species records in exploited forest was reduced to only four species in the dry season. None of the species was recorded during the dry season exclusively (Table 1, TNP).

Community predictability

Observed predictability patterns differed between treefrog communities of the two geographic regions but were consistent within respective realms and disturbance regimes (primary versus exploited). In all cases tested, species distribution vector matrices (SDM) and geographic distance vector matrices (GDM) were significantly correlated, indicating that SUs in close proximity have similar species assemblages (spatial signal, Tables 2 and 3). Hence, general correlative patterns were either completely (TNP, Table 3) or partly (MHFR, Table 2) determined by spatial dynamics.

In only one case (primary forest communities of MHFR) significant correlations existed between SDM and ECM (environmental distribution vector matrix). Thus, primary forest sites with similar environmental characteristics had similar species assemblages (environmental signal). This correlation was not retained in exploited forest sites. Here, community composition was exclusively determined by spatial factors (significant correlations between SDM and GDM).

		primary		exploited	
	Matrices compared	r	p	r	p
Entire study period	Species / environmental (entire)	0.1235	0.0240*	0.0623	0.1387
	Species / geographic (entire)	0.0924	0.0001*	0.1696	0.0009*
	Geographic / environmental (entire)	0.0064	0.3678	0.0830	0.0664
Data separated according to seasons	Species / environmental (dry)	0.1187	0.0373*	0.0309	0.2725
	Species / geographic (dry)	0.1458	0.0001*	0.2140	0.0293*
	Geographic / environmental (dry)	0.0141	0.3156	0.0871	0.0640
	Species / environmental (wet)	0.1575	0.0070*	0.0505	0.1883
	Species / geographic (wet)	0.0634	0.0030*	0.1579	0.0021*
	Geographic / environmental (wet)	0.0064	0.3652	0.0866	0.062

Table 2 Mantel-test on comparison of three different distance matrices MHFR. Entire study period, primary vs. exploited forest habitats; dry and wet season, primary vs. secondary forest habitats; randomization (Monte Carlo) test (10,000 permutations); r = standardized Mantel statistic

		primary		exploited	
	Matrices compared	r	p	r	p
Entire study period	Species / environmental (entire)	0.0110	0.3793	0.1010	0.2432
	Species / geographic (entire)	0.1384	0.0003^{*}	0.2120	0.0165^{*}
	Geographic / environmental (entire)	0.0537	0.1392	0.0420	0.3000
Data separated according to seasons	Species / environmental (dry)	0.0452	0.1848	0.0004	0.5411
	Species / geographic (dry)	0.1617	0.0001^{*}	0.3098	0.0031^{*}
	Geographic / environmental (dry)	0.0257	0.2657	0.0710	0.2697
	Species / environmental (wet)	0.0095	0.3966	0.1503	0.1352
	Species / geographic (wet)	0.1339	0.0004^{*}	0.2619	0.0084^{*}
	Geographic / environmental (wet)	0.0508	0.1535	0.0530	0.2932

Table 3 Mantel-test on comparison of three different distance matrices TNP. Entire study period, primary vs. exploited forest habitats; dry and wet season, primary vs. secondary forest habitats; randomization (Monte Carlo) test (10,000 permutations); r = standardized Mantel statistic

These results were consistent throughout both seasons (no temporal signal). In both geographic realms, results hence indicated a general increase in community predictability with increasing proximity of SUs in both forest types. However, species-habitat relationships appeared to be an important component in the pattern found in primary forest communities of MHFR but not in TNP (Table 2 and Fig. 1 b-c). We found no correlations between GDM and ECM in any of the 12 (MHFR and TNP, primary and exploited, wet season and dry season) pairwise matrix comparisons. Thus sites in close proximity of each other did not have similar environmental characteristics.

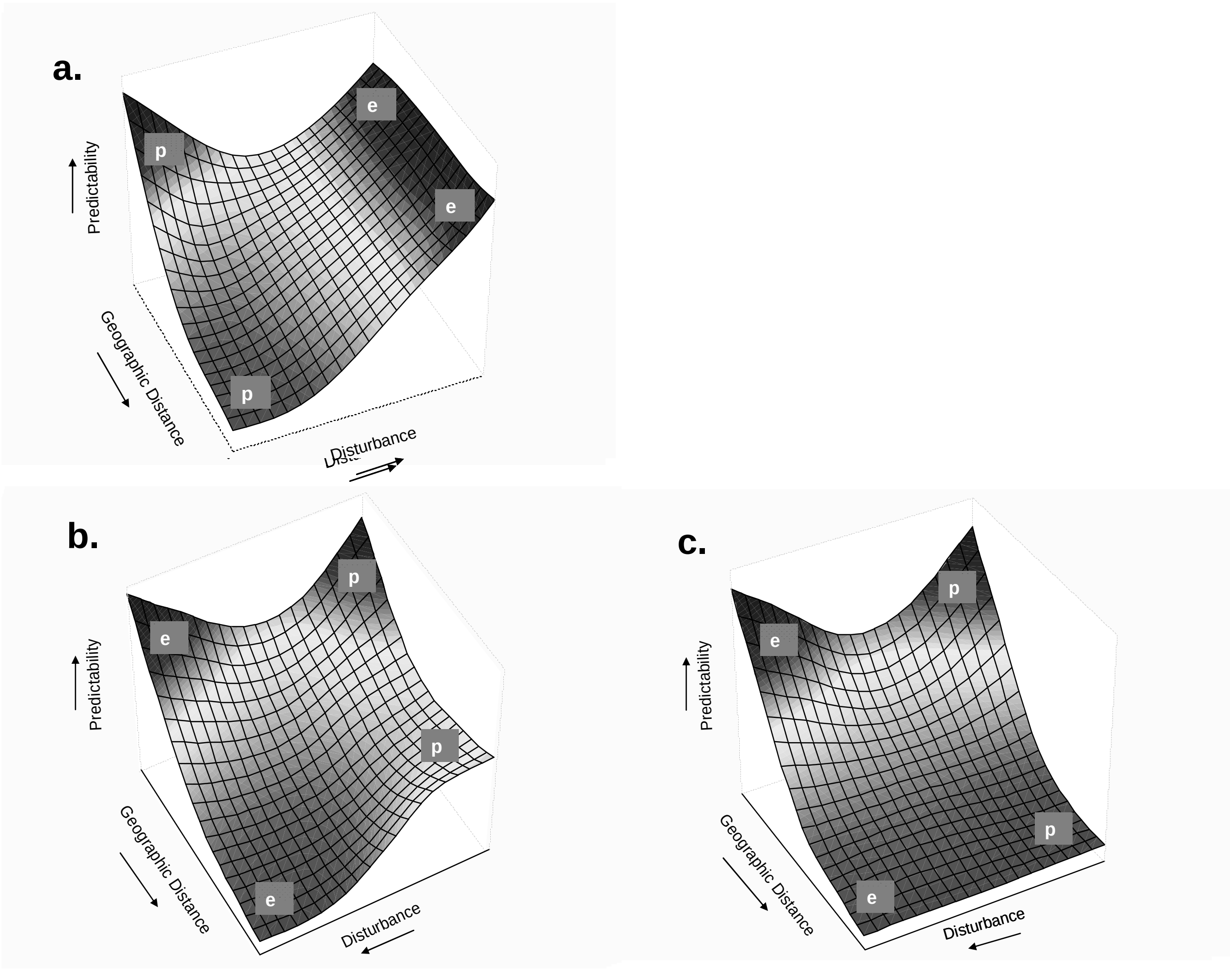

Figure 1 Hypothetical relationships between geographic inter-site distance, disturbance level, and predictability of community composition. P = primary forest communities; e = exploited forest communities. a. leaf litter anuran communities of TNP modified after Ernst and Rödel 2005; b. arboreal anuran communities of MHFR; c. arboreal anuran communities of TNP. Note reversed direction of disturbance arrow in b and c (chosen for better illustration of predictability surface).

Discussion

The predictability patterns of species composition in treefrog assemblages of two geographically distinct eco-regions differed between regions but were consistent within respective realms and disturbance regimes. All assemblages appeared to be spatially structured i.e. sites in close proximity had similar species assemblages. However, spatially-structured environmental variation did not account for the spatial structure of species incidence, as no correlations existed between environmental characteristic vector matrices (ECM) and geographic distance vector matrices (GDM). Thus sites in close proximity to each other did not share similar habitats. Environmental characteristic vectors proved to be significant predictors of species incidence in only one case (primary forest assemblages in Guyana). These results are in contrast to previously published results from a similar study on leaf litter anurans (Ernst and Rödel 2005) and need further explanation.

Species composition and turn over

Species composition varied considerably between habitat complexes in both realms. We noted a decrease in the total number of species, moving from primary forest to exploited forest. This was particularly marked in treefrog assemblages of MHFR where nine species were lost in disturbed forests. The species reduction in MHFR particularly concerned closed forest species, especially those associated with lotic habitats or those exhibiting reproductive strategies in which clutches are attached to vegetation above aquatic habitats and a large proportion of larval development takes place outside standing bodies of water (e.g. in MHFR: *Hyalinobatrachium* sp., *Phyllomedusa* spp., *Dendropsophus* spp.). Similar patterns have previously been reported for Amazonian frog communities (Tocher et al. 2001).The species reduction in TNP was less severe (four species lost) and concerned mainly small bodied hyperoliid frogs that attach clutches to vegetation above lentic aquatic habitats (*Afrixalus vibekensis*, *Hyperolius nienokouensis*, *Hyperolius fusciventris*). In case of TNP, no one habitat complex was found to have the full complement of species present in the TNP landscape. In MHFR on the other hand primary forest communities contained all species found in the MHFR landscape. Exploited forest communities were hence an impoverished subset of the entire MHFR community. However, even in MHFR we recorded three species (*Dendropsophus minutus*, *Hypsiboas crepitans*, and *Scinax ruber*, each with a single individual) associated with disturbed sites that were not recorded in primary forest communities. These species, however were not registered during transect walks and, hence not included in the analysis, as they cannot (yet ?) be considered part of the exploited forest community. They rather appeared to be invading the area from an outside source. They were most likely accessing the reserve area via the main access road (see Ernst et al. 2005). Species turn over in exploited forest communities of TNP also involves mainly species that are known to be comparatively efficient dispersers and invaders. In West Africa these species are commonly referred to as farmbush elements (sensu Schiøtz 1967), *Afrixalus dorsalis* being one prominent example. In case of TNP, previous invasions of this species have apparently been successful, as it appears to maintain stable populations in exploited forest and was hence frequently and regularly recorded during transect walks. Two species exclusively recorded in primary forest are generally considered farmbush (*Hyperolius concolor*) or disturbance (*Hyperolius fusciventris*) elements (e.g. Rödel 2000, Rödel and Ernst 2003, Rödel et al. 2005) and their absence in exploited forest needs further explanation. Whereas *Hyperolius fusciventris* is a true forest species that can cope considerably well with altered environmental conditions following human-induced disturbance, *Hyperolius concolor* has been reported to occur in the transitory zone between rainforest and savanna and even penetrates far into true savanna habitats (Rödel 2000). The record of this species in a single primary forest site may be comparable with the situation of the three invading hylid species in MHFR and represent a random invasion event (an old logging road connects to this particular primary forest site). We observed amplectant pairs of *H. concolor* but successful reproduction was not confirmed.

Community predictability

The composition of the arboreal frog communities in both geographic realms proved to be determined by spatial factors and environmental parameters. However, the relative contribution of each of these factors appeared to differ between communities of different disturbance regimes and geographic origin (primary vs. exploited sites and Afrotropics vs. Neotropics). Results thus support environmental, as well as biotic control model aspects, depending on the disturbance status of a given forest and the geographic realm. In all cases, sites that were geographically proximal tended to have similar communities. This is an indication that biotic processes, such as dispersal from particular species pools may influence the composition of communities at the cross regional level. This in turn is based on the assumption that priority effects (Wilbur 1987) and lottery recruitment mechanisms (Chesson and Warner 1981, Munday et al. 2000) are more important in the assembly of communities than species specific responses to an environmental gradient.

Yet, in case of the primary forest communities of MHFR, an environmental response signal was detected. Here, sites with similar habitat parameters tended to have similar frog communities. This is in contrast to the pattern previously found in anuran leaf litter assemblages of West Africa (Ernst and Rödel 2005). There, the composition of primary forest communities was exclusively determined by spatial proximity of sites. The deviation from this pattern may become clearer when looking at differences in species habitat associations between the two functional groups (arboreal anurans vs. leaf litter anurans). On average and in contrast to leaf litter anurans, adult arboreal anurans are more readily detected during their reproductive phase. Hence, incidence records are automatically more likely to reflect breeding habitat choice. A large proportion (> 70 %) of species that makes up the arboreal frog community of MHFR has very specific breeding habitat requirements, i.e. species depend on specific lotic or large large lentic aquatic habitats for reproduction. Species habitat associations may therefore appear tighter than e.g. among members of the leaf litter anuran community that can readily be detected throughout all life-history stages and regardless of their actual reproductive phase.

Lotic and large lentic sites are absent or become ephemeral in exploited forest sites of the MHFR. The community in these exploited sites is reduced to members that exhibit a rather broad scale habitat tolerance or show high levels of response diversity (sensu Elmqvist et al. 2003). Others possess special adaptations that enable them to cope with the harsher conditions in these disturbed forest patches, e.g. direct developers or phytotelmata breeders. However, these specific adaptations may not be reflected in the habitat parameters considered in our analysis. *Trachycephalus resinifictrix*, for example exclusively uses large water filled tree holes usually located in emergent trees (e.g. Zimmerman and Hödl 1983). The occurrence or abundance of these habitats however, could not be recorded in this study, as these canopy microhabitats are not easily accessible. This fact hence prevents the detection of habitat association in this species and at this scale, even though they might be comparatively tight. The majority (> 75 %) of species of the treefrog assemblages of TNP on the other hand depends on highly ephemeral lentic habitats for reproduction. Although the presence of these habitats is comparatively unpredictable, their occurrence is similar both in primary and in exploited forest. Only a small fraction of species in TNP, such as *Acanthixalus sonjae* (a species that, similar to *T. resinifictri* in the MHFR, uses large water filled tree holes, Rödel et al. 2003), appears to exhibit very tight habitat associations.

Therefore, a higher compositional predictability at the community level in exploited sites cannot be expected. This may be true for the treefrog assemblages in both regions. Species habitat correlations within a respective habitat type may rather be overlaid by spatial dynamics (strong spatial signal in all assemblages tested). The dispersal and colonization ability of a particular species, rather than its species specific habitat association thus appears to be more important in the assembly of a given community. In a study on patterns of nestedness and species associations in pond-dwelling amphibians, Hecnar and M'Closkey (1997) showed that species grouped as good dispersers were less nested than poor dispersers and species incidence was positively correlated with potential dispersal ability. It is obvious that this is likely to determine the species composition of a given assemblage considerably, especially if priority effects (Wilbur 1987) are an important factor shaping newly assembled communities.

In our case the assemblages in each of the habitat types may be dominated by species that can successfully colonize a given patch, which leads to a dominance of the spatial signal, perhaps even to a point at which an environmental response of a particular species is entirely covered or overlaid by the spatial response signal. This may explain the pattern found in the African communities, in which no environmental response signal was detected. However, this remains speculative as actual species-specific dispersal and colonization rates need to be investigated systematically. Nonetheless, the spatial pattern that was revealed in all cases deserves further attention. Even more so since patterns differ between different anuran groups.

In a study on the influence of spatial and environmental variables on the composition of frog assemblages in eastern Australia, Parris (2004) found the composition to be a product of environmental variables, as well as spatial position. However, this study did not distinguish between particular segments (i.e. functional groups) of the anuran community. The analysis included both arboreal and terrestrial anurans. Given the results of Ernst and Rödel (2005) and those of the study presented here, it seems likely that the pattern found in the Australian assemblages actually reflects the idiosyncratic influence of both functional response groups on general predictability patterns of the entire community. Treating distinct anuran groups as one coherent entity in the analysis of predictability patterns of species composition may actually obscure or confound patterns that are otherwise group specific. We therefore advocate studies that incorporate these group-specific differences, especially because important conservation strategies for this highly threatened vertebrate group may otherwise be based on the wrong assumptions.

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CHAPTER 4

PROCESSES

Explaining the transition – factors influencing pattern changes

The impacts of selective logging on three sympatric species of *Leptodactylus* in a Central Guyanan rainforest

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Leptodactylus knudseni foam nest

THE IMPACTS OF SELECTIVE LOGGING ON THREE SYMPATRIC SPECIES OF *LEPTODACTYLUS* IN A CENTRAL GUYANAN RAINFOREST

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Abstract

Selective logging has the potential to significantly alter environmental conditions experienced by both larval and adult amphibians and, therefore, may affect the population viability of particular species. In this study we evaluated the impacts of selective logging on the occurrence, larval development and survival of three sympatric foam nest constructing *Leptodactylus* species in a central Guyanan rainforest. The occurrence and abundance of adults differed among species and between habitat complexes. Species-habitat associations appeared to be linked to species-specific reproductive habitat requirements. The response of tadpoles to logging-related habitat alterations varied among species. Experiments in one of the focal species showed that tadpole development and growth depend on larval residence time within foam nests and environmental factors related to solar exposure and temperature of aquatic habitats. Tadpoles that were reared within foam nests over extended periods of time significantly decreased in body mass. Tadpoles reared under exposed conditions developed slower than those reared under shaded conditions. Likewise, larval growth decelerated in the former. Larval survival differed among species and between habitats. Species-specific responses to disturbance-related environmental changes highlight that simplified generalizations that do not take into account species-specific variation are problematic. We therefore argue that sound conservation strategies for this group of amphibians would benefit by moving from generalizations to species specific recommendations.

Introduction

Tropical forests cover 6 % of the planet. However, an estimated area of 142,000 km^2 is lost every year equalling 1 % of the total tropical forest area. Timber harvesting is currently the most common use of tropical forests (Johns, 1996) and logging has been identified as one of the major threats to global vertebrate diversity (e.g. Thiollay, 1992; Lauck, 2005). The effects of deforestation are most often considered in terms of habitat loss on a gross landscape scale. However, smaller habitat modifications, such as selective tree harvesting of particular commercially valuable species that alter environments on a local scale, have received less attention.

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). Selective logging usually causes an increase in canopy openness, and hence alters the microclimate of respective forest sites (Vitt et al., 1998). Due to their physiology and unique aspects of their biology amphibians are particularly sensitive with respect to habitat changes and altered microclimatic conditions. Although the mechanisms of individual responses are unclear in most cases, physiological constraints unarguably exist. Amphibians usually have biphasic life-cycles, very limited dispersal abilities and short reproductive cycles resulting in high population turnover rates. However, particular species certainly respond differently to forest fragmentation and disturbance and species-environment relationships may differ greatly among different amphibian groups across temporal and spatial scales (Cushman and McGarigal, 2004). Most of the trends that have been identified in previous studies on the impacts of logging on amphibians were highly variable and much of this variability was due to species-specific responses (DeMaynadier and Hunter, 1995).

Interspecific life history differences may also result in different predispositions towards sensitivity to habitat alterations. Most often it is a particular guild or functional group that exhibits higher susceptibility than others (Hero et al. 2005). Species that are able to maintain stable populations after habitat alteration usually possess preadaptations that make them more resistant to changes in, e.g. microclimate and aquatic breeding habitat availability, whereas others go extinct.

Members of the neotropical frog genus *Leptodactylus* are commonly grouped on grounds of their similar reproductive biology (Heyer, 1969; Prado et al., 2002). All known members of the genus construct foam nests but there is considerable variation in the genus (Lynch, 1971). Foam nests are generally seen as an adaptation to minimize the risk of predation (Heyer, 1969; Magnusson and Hero, 1991) and, which appears more important with respect to microclimatic alterations, desiccation (Heyer, 1969; Downie, 1988; Seymour and Loveridge, 1994). High proportions of species that deposit eggs in foam nests are commonly found in seasonal habitats with pronounced dry seasons (e.g. Prado et al. 2005). Foam nests also provide thermally advantageous conditions for larval development due to the white foam's heat-reflecting property (Gorzula, 1977; Dobkin and Gettinger, 1985; Downie, 1988). This is an important feature, especially under thermally extreme environmental conditions.

Based on these assumptions members of the genus *Leptodactylus* should thus be able to cope comparatively well with disturbance-related habitat alterations that lead to changes in microclimate and water regime. Drastic changes in their population structure should be less likely even in disturbed habitats. Yet, Ernst et al. (2005) recently showed that not all sympatric *Leptodactylus* species recorded in differently disturbed sites in a central Guyanan rainforest also occurred in syntopy, i.e. occurring in both primary and exploited forest. This raises the question of why species with apparently similar preadaptations to the alterations imposed by selective logging show different species-specific responses.

In the present study we specifically address the following questions relating to potential disturbance-related effects on occurrence, larval development and larval survival of three sympatric species of the genus *Leptodactylus*:

(1) What are the explanatory variables for the presence / absence of a particular species in a particular habitat? (2) Are particular species differentially affected by habitat alterations caused by selective logging, i.e. does their occurrence vary between habitats? (3) How important are variations in habitat quality between differently altered forests for larval development and survival of a particular species?

Material and methods

Study areas and disturbance history

The study was conducted in the Mabura Hill Forest Reserve (MHFR), situated approximately 20 km south-east of the township Mabura Hill, Central Guyana (5°13’ N, 58°48’ W). The reserve comprises an area of approximately 20 km² of primary rain forest. Disturbed sites were located outside the reserve’s core area. Disturbed sites included in the analyses have been logged in 1988 with an intensity of 19.5 trees or approximately 57 m^3 ha^{-1}. For a more detailed description of MHFR and particular study sites see ter Steege et al. (1996) and Ernst et al. (2005).

Data acquisition

The field data were acquired between April and August 2004. We established 14 quadratic plots, eight in primary forest and six in exploited forest. Starting co-ordinates for each 25 m x 25 m plot were chosen randomly within a particular macrohabitat. Each plot was subdivided in four 12.5 m x 12.5 m subplots, which form the basic sampling unit. The minimum distance between plots was 50 m. Habitat parameters within plots were characterized following routines established by Rödel and Ernst (2004). The plot design itself is a modification of the well established transect-based research design by the same authors. In addition we recorded three parameters related to the hydro regime of the site on a weekly basis: 1) mean total plot area covered by water in eight 12.5 % categories from 0 to 100 %; 2) mean depth of aquatic habitats measured at five defined positions within plots in five 10 cm categories from 0 to > 40 cm; 3) a coefficient of water cover variation, which reflects the ratio of the number of water cover category transitions within the study period and the total number of records.

The coefficient of water cover variation (W_v) can be calculated using the following formula:

$$W_v = \frac{\sum \Delta c_t}{n} \qquad \text{eq.} \quad (4.1)$$

Where: Δc_t = transition from one of eight particular water cover categories (see above) to another water cover category at recorded point in time t and n= total number of records in recording period.

This ratio allows estimating predictability of water availability in a habitat. Temperature was recorded on an hourly basis at eleven randomly chosen sites (six in primary forest, five in secondary forest) using thermobutton data loggers (i-Button-TMEX, Version 3.12 ± 0.1°C). Data loggers were placed 150 cm above ground within the vegetation.

Mean densities (individuals/dip-netting draw) of known aquatic predators of tadpoles were registered by systematically dip-netting aquatic sites within respective plots using a fine meshed colander (diameter 18.0 cm). Each aquatic site was sampled by performing five separate draws, whereby the colander describes an "eight-shape". We restricted sampling to particular groups of predators. These included Zygoptera and Anisoptera (only larvae), Heteroptera, Coleoptera (in two categories, imago and larva), fish, the aquatic frog genus *Pipa*, and fresh water crabs (Pseudothelphusidae). Because the latter frequently forage on land, mean densities (individuals/plot hour) were additionally monitored visually during plot sampling. A single sampling run included one hour of day and night visual and acoustic encounter surveys (VES / AES) within each plot. All plots were sampled in six-day cycles. Incidence and abundance data of adult frogs as acquired through plot sampling were supplemented by data acquired between November 2002 and September 2004 and derived from standardized visual and acoustic transect sampling (SVTS / SATS) routines that have been established for amphibian community studies at the same site (see Rödel and Ernst, 2004 and Ernst et al., 2005). In the present study these data were only used to confirm the presence or absence of a particular species within a particular habitat complex and to identify broad scale habitat preferences. Only data derived from plot sampling enter subsequent analyses.

Experimental design

We designed four types of experiments focusing on larval development, mortality, and survival of three sympatric *Leptodactylus* species.

First we tested the role of foam nests in early larval development of *Leptodactylus knudseni* to assess whether or not this reproductive mode poses particular advantages or disadvantages with respect to disturbance related factors. For this type of experiment we used three entire foam nests (A-C) of *L. knudseni* that were collected in primary forest sites. Tadpoles of each nest were separated from the foam and counted. Equal numbers of tadpoles (30, stage 24, Gosner, 1960) were transferred into two types of treatments consisting of 1,000 ml Zip-lock ® bags equipped with either 500 ml rainwater or 500 ml foam of the original nest. Each nest was used to set up two times two treatments, i.e. two bags containing water and two bags containing foam that contained a total of 120 tadpoles originating from the same nest (mean initial weight of tadpoles from respective nests A: 5.2 mg ± 0.2 mg, *n*= 120; B: 3.3 mg ± 0.3 mg, *n*= 120; C: 3.1 mg ± 0.1 mg, *n*= 120). This results in a total number of six treatments or twelve bags and 360 tadpoles used in the experiment. Bags were arranged free hanging and covered with mosquito mesh to exclude predation and parasitism. The setup was installed on an open porch of the field station. The roof prevented the bags from being exposed to direct sunlight and rain. Concurrent experiments were run for 28 days. Tadpoles were fed with 65 mg of commercial fish food (Flumon®) twice weekly. On weekly controls we recorded mortality and additionally preserved one tadpole from each bag (total of five tadpoles / bag, including first sample) in 70 % ethanol for subsequent analyses in the laboratory. After determining Gosner (1960) stages, sampled tadpoles were left to dry for 52 hours at a temperature of 50 °C in a cabinet desiccator in order to determine their dry weight using a fine-scale balance (Ohaus Navigator accuracy 2 mg). Data from two corresponding sets (bags) of each treatment were pooled and only means enter subsequent analyses.

The second type of experiment was aimed at revealing the role of the thermal environment and solar radiation in development and growth of tadpoles of the same species. The experiment comprised two treatments. Each treatment consisted of five plastic boxes (10 cm x 10 cm x 6 cm) containing 500 ml pond water. We placed five stage 27 (Gosner, 1960) *L. knudseni* tadpoles (each total length = 28.0 mm) originating from the same clutch in each of the boxes (total of 25 tadpoles / treatment). An additional plastic box in each treatment was equipped with a thermo-button data logger (see above), set at 30 min recording intervals. Treatment one (exposed) was set up at the southern edge of a large forest clearing. The treatment received an average of ten hours of direct sunlight depending on weather conditions (overcast vs. unclouded). Treatment two (shade) was set up in the primary forest interior underneath a closed canopy. We covered all boxes with mosquito mesh to exclude predation and parasitism as factors in our analyses. We kept water levels constant throughout the experiment. For this purpose we equipped boxes with small holes at the defined filling level (500 ml) that acted as overflow devices in case of rainfall. During dry periods we replaced evaporated water in containers. To keep densities constant, we replaced missing tadpoles with conspecifics from the same clutch that were reared in separate containers under similar conditions. Tadpoles were fed with 25 mg Flumon® twice weekly. On weekly controls we recorded total length [mm], measured to the nearest 0.05 mm using calipers and respective Gosner stage of each individual throughout a total period of 12 weeks. Only median values of the respective box and week enter the analyses to account for deviations that result from replacements of missing tadpoles.

Finally we set up two types of concurrent *in situ* experiments to test for differences in tadpole survival as a function of artificial pool location (primary forest vs. exploited forest) and habitat-specific predation. Here we followed an interspecific and intersite comparison approach. Each experiment consisted of three sets of artificial pools with two treatments each. A set comprised two artificial pools (transparent plastic bowls, max. volume = 5,000 ml, diameter: 26 cm), one of which (control treatment) was tightly covered with white mosquito mesh to exclude predation. We buried bowls level with the ground maintaining a distance of 30 cm between pools. Sets were set out randomly within randomly chosen plots in respective habitat complexes (six pools per experiment, 12 pools total). To keep starting conditions equal, each bowl was filled with 2,000 ml rain water and equipped with three leaves of equal size and color, mainly for cover against optically hunting predators, as well as with thermo-buttons (see above). Tadpoles were initially fed with commercial dried soy cubes (2.5 g per bowl). No food was added subsequently. Tadpoles of all species have successfully been raised using this food source in previous experiments. Its comparatively slow disintegration in water is an advantage in experiments in which additional food is not to be added frequently. It was hence given preference over commercial fish food, which dissolves very rapidly and would result in the turnover of the water if given in larger quantities. Experiments were run concurrently to control for phenological effects. We tested tadpoles of three different species (*L. knudseni, L. petersii, L. rhodomystax)* in five different runs (two with *L. knudseni* and *L. petersii* tadpoles, one with *L. rhodomystax* tadpoles). At the beginning of each run, we placed ten stage 27 (Gosner, 1960) tadpoles of equal size (total length *L. knudseni*: 18 mm, *L. petersii*: 12 mm, *L. rhodomystax*: 22 mm) in each of the bowls (exception: *L. rhodomystax*, seven). Every run lasted 28 days. Surviving tadpoles were counted once a week throughout the entire period. For analyses we regarded treatments as independent. Likewise experiments in different habitats were regarded as independent.

Statistical analyses

To test for the importance of habitat parameters with regard to species occurrence and abundance we constructed habitat models for each species. We only used habitat parameters that proved to have the best explanatory power in a previously performed three-dimensional Non-Metric-Multidimensional Scaling (NMDS) analysis that was based on the original habitat variables, recorded in each plot and relative abundance values (individuals per plot hour) of particular species as time based density measures (R. Ernst et al. unpubl. data). For a detailed description of the algorithm and procedure see Kruskal (1964) and McCune and Grace (2002). Mean stress values of the NMDS-analysis were below 5.0 and Monte-Carlo randomisation tests showed differences between mean stress values of real data and those of randomised data, significant at the conventional $P < 0.05$ level. This corroborates the goodness of the analysis (Clarke, 1993). Parameters that proved to be most influential according to the NMDS were tested for correlation with species abundance using multiple backward regression analyses (MBR). These included six of originally nine habitat variables (mean depth of aquatic habitat, mean total plot area covered by water, mean water cover variation, vegetation density of canopy, lower tree stratum, and understorey). The three parameters describing the water regime within habitats proved to have the highest explanatory power in NMDS, i.e. axes including water regime parameters explained 80 % of total variance. These parameters reflect different aspects related to either physical features (depth and surface area) or temporal dynamics of respective aquatic habitats (water cover variation) and were hence additionally tested in a separate regression analysis. This analysis was aimed at further assessing the importance of each of these factors.

Experimental treatments were tested using non-parametric tests if not indicated otherwise. Comparisons between habitats and / or treatments were done using Mann-Whitney-*U*-tests. NMDS analyses were performed using the software package PC-ORD$^{©}$ for Windows Version 4 (MjM Software Design). All remaining tests, including regression analyses, were performed using the software package SPSS for Windows 12.0, SPSS$^{©}$ Inc.

Results

Species abundance and distribution across habitat complexes

Generally, the occurrence of the three focal species differed between primary and exploited habitats. *Leptodactylus knudseni* was recorded in both primary and exploited forest sites. However, reproduction could only be confirmed in primary forest. *Leptodactylus rhodomystax* was recorded and reproduced in both primary and exploited forest sites. *Leptodactylus petersii*, finally, was recorded and reproduction could be confirmed in primary forest sites exclusively.

We registered a total of 437 adult individuals of the three focal species during 42.0 hours of visual and acoustic plot sampling, equaling 10.41 individuals / plot hour (ind / ph). Overall abundance was highest in *L. petersii* (6.86 ind / ph), followed by *L. rhodomystax* (3.41 ind / ph), and *L. knudseni* (0.14 ind / ph). Individuals were not equally distributed across habitat complexes (primary vs. exploited forest plots). Records of *L. petersii* and *L. knudseni* were restricted to primary forest exclusively, whereas the majority of individuals of *L. rhodomystax* were recorded in exploited forest plots (0.21 ind / ph in primary forest vs. 7.67 ind / ph in exploited forest).

Transect sampling data largely corroborated these results. However, *L. knudseni* was additionally shown to occur in exploited forest and *L. rhodomystax* proved to be generally more abundant than *L. petersii*. We registered a total of 261 adult individuals of the three *Leptodactylus* species during 393.5 hours of SVTS and SATS, equaling 0.66 individuals / transect hour (ind / th). Overall abundance was highest in *L. rhodomystax* (0.32 ind / th), followed by *L. petersii* (0.19 ind / th), and *L. knudseni* (0.16 ind / th). Again, individuals were not equally distributed across habitat complexes (primary vs. exploited forest plots). Records of *L. petersii* were restricted to primary forest exclusively, whereas the majority of individuals of *L. rhodomystax* were recorded in exploited forest plots (0.26 ind / th in primary forest vs. 0.39 ind / th in exploited forest). The majority of individuals of *L. knudseni* on the other hand were recorded in primary forest (0.26 ind / th in primary forest vs. 0.05 ind / th in exploited forest). *L. knudseni* and *L. rhodomystax* were hence equally abundant in primary forest but their abundance differed considerably in exploited forest.

Species habitat relationships

Regression analyses yielded significant habitat models for only two species (*L. petersii* and *L. rhodomystax*). The first model for *L. petersii* included two out of five variables tested (table 1) that accounted for 60.0 % of the variance (ANOVA: $F = 10.764, P < 0.01$). Understorey vegetation density appeared to be the most influential factor (negative value = low vegetation density) followed by mean water cover of total plot area (positive value = high levels of water cover) The second model based on water regime parameters only included one parameter, i.e. water cover variation (table 1) that accounted for 43.1 % of the variance (ANOVA: $F = 10.858$, $P < 0.01$). In the case of *L. rhodomystax*, only one variable (canopy density; negative value = low vegetation density in canopy) remained in the first model (table 1) that accounted for 37.4 % of the variance (ANOVA: $F = 8.764$, $P < 0.01$). The second model, again based on water regime parameters only, included all variables tested, accounting for 42.4 % of the variance (ANOVA: $F = 4.198$, $P < 0.05$). Variables contributed to the model with varying degrees (table 1), mean water cover variation (negative value = low variability) being most important followed by mean water cover of total plot area (positive value = high levels of water cover) and mean depth of aquatic sites (negative value = shallow aquatic sites).

Species and Model	Factor	*B*	Standard error	Standardized coefficients Beta	*T*-value	*P*-value
L. petersii Model 1	constant	32.164	8.704		3.695	0.004
	water cover	4.963	1.962	0.444	2.529	0.028
	understorey density	-40.095	10.033	-0.701	-3.996	0.002
L. petersii Model 2	constant	-6.147	4.667		-1.317	0.212
	water variation	29.877	9.067	0.689	3.295	0.006
L. rhodomystax Model 1	constant	2.327	0.548		4.244	0.001
	canopy density	-2.007	0.678	-0.65	-2.96	0.012
L. rhodomystax Model 2	constant	2.928	0.703		4.167	0.002
	water cover	0.93	0.703	0.771	2.037	0.069
	water variation	-4.383	1.754	-0.937	-2.499	0.032
	depth	-0.593	0.224	-0.568	-2.65	0.024

Table 1 Regression coefficients of significant multiple backward regression models for two *Leptodactylus* species based on relative species abundance and habitat variables derived from NMDS-analyses.

Influence of growth medium on larval development and mortality

Leptodactylus knudseni tadpoles that were raised in foam were significantly (Mann-Whitney-*U* test: $Z = 1.964$, $n = 6$, $P < 0.05$) heavier than those raised in rainwater (fig. 1). This effect was already pronounced after the first week. However, throughout the following weeks, mean body mass decreased constantly in tadpoles raised in foam, whereas it remained constant in tadpoles raised in water. Development did not differ between treatments. Final Gosner stages were identical in both treatments (Gosner stage 28, starting stage 24). Mortality increased in foam treatments and reached 100 % at the end of the experiment, whereas mortality was zero in water treatments.

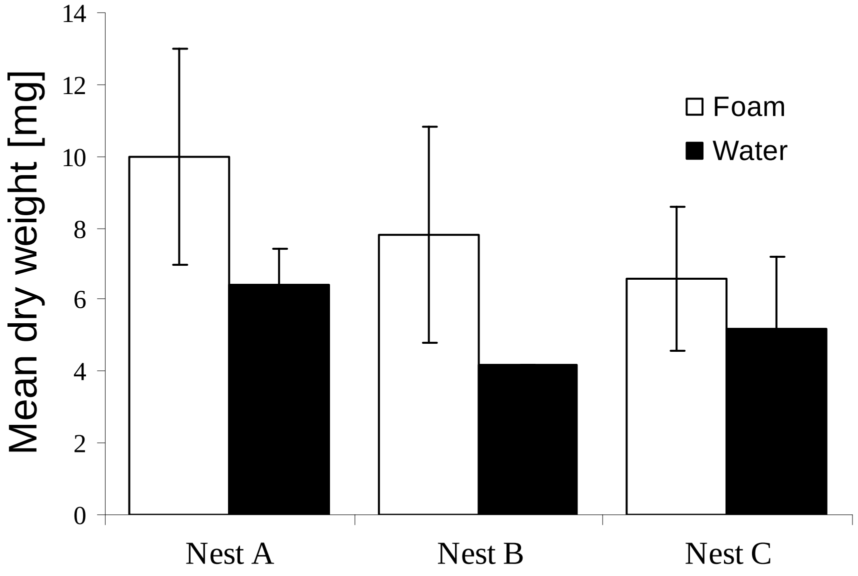

Figure 1 Dry weight in[mg] of *Leptodactylus knudseni* larvae raised in foam vs. water. Given are means ± SD of pooled sets (= bags of identical treatment) from each of three nests (A-C). Differences are significant at the conventional $P < 0.05$ level.

Impacts of solar exposure and temperature on larval development and mortality

Mean daily temperatures varied significantly between the two treatments in experiment two. Weekly mean temperatures in the exposed treatment (mean: 25.9 ± 0.30 °C) were constantly 1.5 °C above those measured in shade treatments (mean: 24.4 ± 0.29 °C; *t*-test, $t = 11.36$, $n = 24$, $P < 0.01$). Growth and development of *L. knudseni* tadpoles differed significantly between treatments. Tadpoles in the exposed treatment were generally smaller and developed slower (indicated by differences in Gosner stages) than their shade treatment counterparts (pairwise comparisons with

Mann-Whitney *U* tests based on weekly controls all significant at the conventional *P* < 0.05 level, fig. 2).

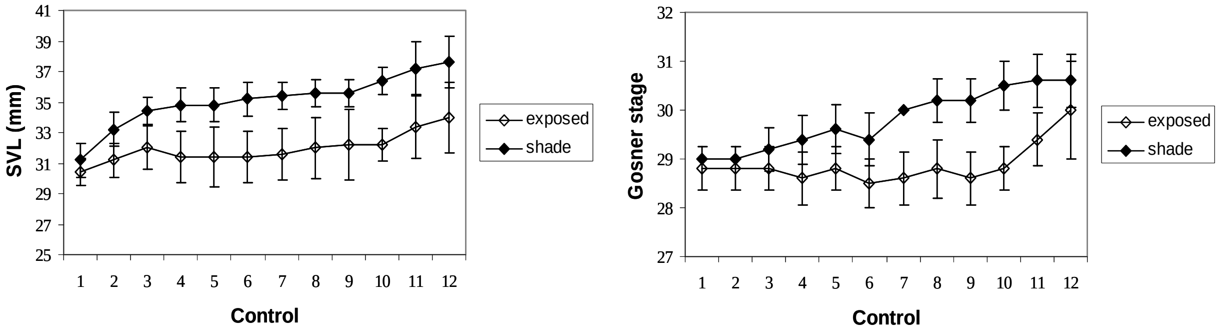

Figure 2 Growth (a) and development (b) of *Leptodactylus knudseni* larvae under exposed and shaded conditions. Given are means ± SD of weekly controls based on median values of particular boxes. Growth is given as snout-vent length (SVL) in [mm]; development is represented by respective Gosner stages of larvae.

Total mortality and hence the number of tadpoles that were replaced also differed between treatments. Mortality in exposed treatments was twice as high (total of six tadpoles = 24 %) as mortality in shaded treatments (total of three tadpoles = 12 %).

Survival and mortality of larvae in situ

Generally mortality of tadpoles of all three *Leptodactylus* species was significantly higher in treatments that were not covered with mosquito mesh (all exact Mann-Whitney-*U*-tests significant at the conventional *P* < 0.05 level). Hence, predation appeared to be a major factor causing mortality in both habitats. Direct observations in open treatments (in two cases) indicate that fresh water crabs (Pseudothelphusidae) are responsible for the majority of predation events. Crabs have frequently been observed in open treatments in both primary and exploited forest. The ability of these crabs to prey on tadpoles of *L. rhodomystax* and *L. knudseni* has been tested in *ad libitum* experiments in bowls of the same size as used in *in situ* experiments. Members of this family have also frequently been observed feeding on foam nests of *L. rhodomystax* and *L. knudseni* where they caused 100 % mortality. Mean densities of fresh water crabs (individuals/plot hour) derived from visual sampling were higher in primary (0.44; ± 0.24 ind./ph; *n* = 8) as compared to exploited forest (0.28 ± 0.17 ind./ph; *n* = 6). However, these differences were statistically not significant.

The only aquatic predator that showed significant (Mann-Whitney-*U* test: $Z= -2.982$, $n = 14$, $P < 0.05$) differences in mean density between primary and exploited forest sites were dragonfly larvae infraorder Anisoptera, with higher densities (individuals/dip-netting draw) in primary forest (0.81 ± 0.47 ind./dd; $n = 8$) as compared to exploited forest (0.28 ± 0.17 ind./dd; $n = 6$). However, we never observed odonate larvae (neither Anisoptera nor Zygoptera) in any of the experimental treatments.

Despite the congruence in mortality of open treatments, differences in mortality existed both between species and between habitats (primary *vs.* exploited sites).

L. knudseni: Results for *L. knudseni* were inconsistent between runs. However, in both runs, predation was the most important factor in primary forest. There was mortality due to predation in exploited forest, however, at least in the first run habitat factors appeared to be more influential (high mortality in controls; Mann-Whitney-*U*-tests, $Z = 1.993$, $n = 6$, $P < 0.05$; fig. 3 b-c).

L. rhodomystax: Mortality in *L. rhodomystax* tadpoles was similar across habitats. Predation appeared to be the single most important factor for mortality in nearly all cases (no mortality in controls; fig. 3 a).

L. petersii: Mortality in *L. petersii* tadpoles was high in all treatments, regardless of habitat (fig. 3 d-e). We detected a correlation between an increase in temperature and mortality in tadpoles of this species. Mortality was highest when mean temperatures rose by 0.5 °C, from 24.0°C to 24.5°C in primary and 24.1°C to 24.6°C in exploited forest, respectively. These temperature differences were significant in all treatments (all exact Mann-Whitney-*U*-tests significant at the conventional $P < 0.05$ level).

There was no hint towards temperature related mortality in tadpoles of *L. knudseni* and *L. rhodomystax*. Highest temperatures (26.5°C) were recorded in both, primary and exploited forest treatments. However, mortality in respective treatments was not affected (no additional mortality recorded). Temperature differences between habitat complexes were inconsistent and were more dependent on microhabitat setting.

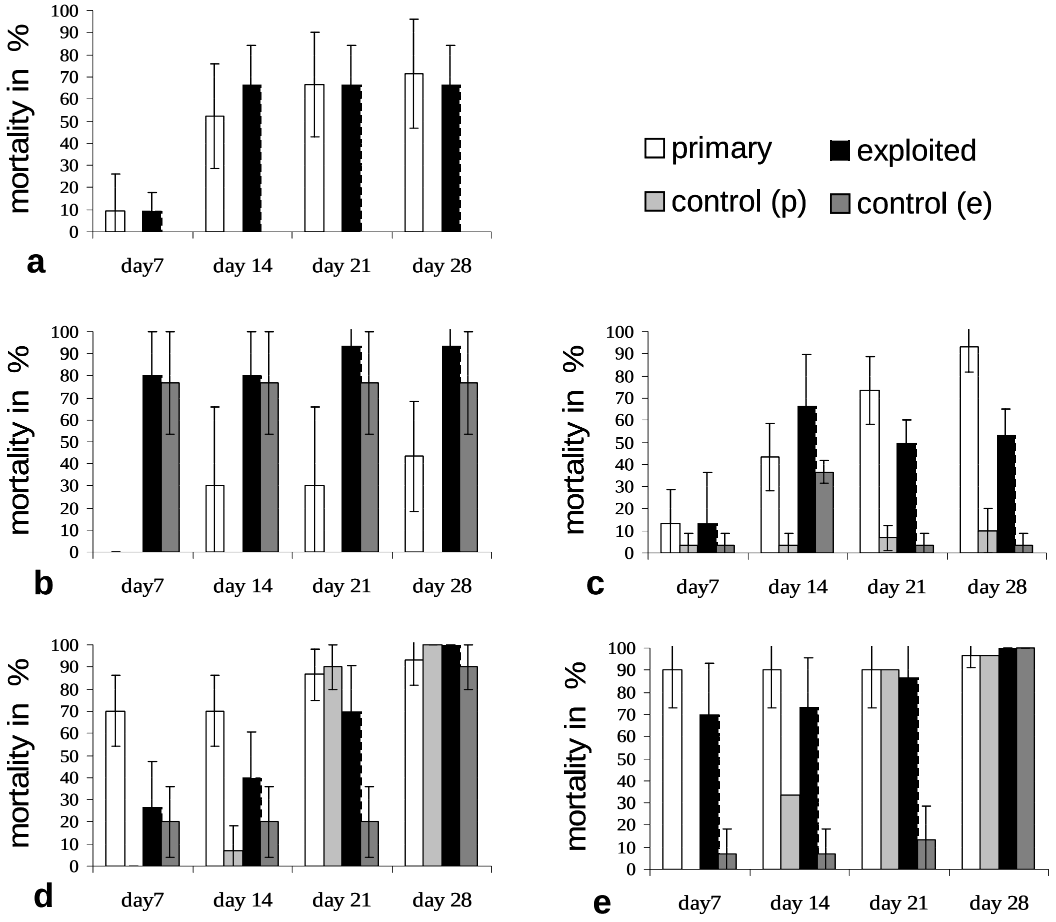

Figure 3. Accumulative larval mortality [%, mean ± SD] of three *Leptodactylus* species in primary and exploited forest sites of MHFR. Given are pooled mortalities for sets (primary, *n* = 3 vs. exploited, *n* = 3) and treatments (open, *n* = 6 vs. closed control, *n* = 6) for each of the runs. a: *Leptodactylus rhodomystax* (only one run); b-c: *Leptodactylus knudseni* (run 1 and 2); d-e: *Leptodactylus petersii* (run 1 and 2). Days on x-axis represent respective control days. Ideally, each set is represented by two bars (open treatment and closed control) in case of recorded mortalities. p= primary, e= exploited.

Discussion

Species habitat relationships

Species habitat relations in amphibians are almost always based on some kind of moisture gradient and thus, intrinsically, breeding habitat requirements (e.g. Hödl, 1990; Gascon, 1993; Zimmerman and Simberloff, 1996). The spatial and temporal availability of open bodies of water therefore decisively influences the structure of an anuran assemblage as well as the reproductive success of single species (Semlitsch et al., 1996). Choice of breeding sites by amphibians can be influenced by the quality of the surrounding terrestrial habitat as well as by characteristics of the water body (Alford, 1999; Semlitsch and Bodie, 2003). Availability of aquatic habitats and the quality of these aquatic sites, as well as the surrounding habitat matrix are likely to be altered by drastic habitat disturbances, such as selective logging and thus directly affect species that depend on these habitats for reproduction. Habitat quality and pond availability have recently been shown to be a key factor in the maintenance of a tropical hylid species in fragmented forests of the Brazilian Amazon (Neckel-Oliveira and Gascon, 2006). In our analysis on species habitat associations we found local conditions for reproduction equally important for the distribution of a particular species and their occurrence in primary or exploited forest sites.

Coarse-scale species habitat associations as revealed in our species-specific habitat models appeared to be strongly linked to the reproductive modes of particular species and therefore depended on species-specific reproductive habitat requirements at least in two cases, *Leptodactylus petersii* and *L. rhodomystax*. *L. petersii* preferred habitats that were characterized by open, scarcely vegetated understorey and the presence of large, highly dynamic aquatic sites. This corresponds to temporarily inundated streamside habitats commonly found along larger lotic habitats (streams and large creeks) within primary forest but mostly absent in exploited forest. *L. rhodomystax* preferred habitats that were characterized by an open canopy and the presence of small and shallow but comparatively persistent aquatic habitats, frequently occurring in disturbed habitats and to a lesser degree within primary forest. Habitat model results for *L. knudseni* were not unambiguous. However, based on the reproductive activity and abundance data of the species, *L. knudseni* appeared to prefer habitats that contain large and deep lentic sites exhibiting comparatively high dynamics due to frequent flooding and draining events (e.g. large streamside ponds). Yet, habitat associations appeared to be less pronounced in this species, potentially reflecting the particular reproductive strategy (reproduction at onset of rainy season, eggs and early larval stages in foam nest in water filled depressions close to water, subsequent to flooding, exotrophic tadpoles in lentic water) that enable the species to cope with unpredictable environmental conditions rather than ubiquitous habitat preferences. This is supported by the failure to confirm reproduction of *L. knudseni* in exploited forest sites that lack large aquatic habitats. Both *L. petersii* and *L. knudseni* appeared to prefer high-dynamic and thus unpredictable reproductive habitats. However, they seem to cope with these conditions with different strategies. *L. knudseni* reproduces early in the season, even before the respective aquatic sites have filled up completely and constructs large foam nests that are less prone to desiccation as a direct result of their lower surface area to volume ratio. This has previously been suggested as and explanation for the construction of communal nests in *Physalaemus pustulosus* (Ryan, 1985) and has recently experimentally been proven to be the case in the same species (Zina, 2005). Due to this head start, tadpoles of this species potentially are strong competitors and may use available resources more successfully than larvae of subsequently reproducing species. Another advantage of this strategy, which may be even more important is the possibility to exploit a (nearly) predator free space as most aquatic predators colonize the reproductive habitats at later successional stages. By this time, tadpoles may have reached sizes that exclude them as prey for some of these potential predators. The shortened aquatic phase of their larvae also reduces the risk of mortality due to desiccation. *L. petersii* on the other hand responds to the unpredictable environment by producing small nests with high numbers of eggs and tadpoles with fast developmental times. Foam nests are usually located in areas that are frequently flooded, at least in the peak and late rainy season. Tadpoles are hence likely to be dispersed and their residence time in stagnant, truly lentic habitats would thus be reduced although this has not been confirmed by systematic dip netting in lotic habitats and thus remains speculative.

L. rhodomystax chooses different reproductive habitats that are less dynamic with respect to the hydroregime. Additionally reproduction in this species is concentrated on the peak rainy season, when water availability is more predictable.

Larval development under the influence of disturbance related factors

Foam nests of leptodacylids are commonly regarded as post-hatching refuges (e.g. Downie, 1993) that allow their larvae to outlast less favourable environmental conditions. In most cases this means prolonged droughts and decreased water availability due to increased temperatures and solar radiation. Tadpoles of *Leptodactylus fuscus* and *L. mystaceus* have even been reported to autonomously generate foam and undergo developmental arrest within the nest (e.g. Caldwell and Lopez, 1989; Downie, 1994 a, b). This enables them to endure and survive until conditions improve (Downie and Smith, 2003). However, this strategy may be very costly, when unfavourable conditions extend over long periods of time, which is very often the case in exploited forest habitats. Despite their head start and faster growth, larvae that remain inside foam nest may undergo a developmental arrest and their body mass may even decrease once yolk reserves have been exhausted, as was the case in the *L. knudseni* tadpoles tested here. The severe reduction in body mass may hence negatively impact the survival of tadpoles to metamorphosis (Downie, 1994 a, b; Downie and Weir, 1997). High mortality rates of larvae have likewise been observed in our study. This may have tremendous effects on the population structure of the species. A strategy that is highly adaptive in case of unpredictable environmental changes at small temporal scales (case primary forest) may turn out to be a population level dead end under prolonged unfavourable conditions (case exploited forest).

Complete development of larvae within the foam nest and therefore complete independence of water has previously been reported for *L. fallax* (Gibson and Buley, 2004). However, in this species, nests were routinely supplied with unfertilized eggs by the attending female. Larvae of the species are obligatory oophagous. In other species with oophagous tadpoles, such as *L. labyrinthicus*, extended developmental and growth periods within the nest have been reported (Shepard and Caldwell, 2005). After depletion of eggs, larval growth ceased and tadpoles did not develop beyond stage 31. The ingestion of trophic eggs has previously been interpreted as an adaptation of tadpoles to environments with unpredictable rainfall and hence water availability (Prado et al., 2005). Like the closely related *L. pentadactylus*, *L. knudseni* is known to feed on eggs of other species and conspecifics (Heyer et al., 1975; Muedeking and Heyer, 1976; Hero and Galatti, 1990), yet maternal brood care and the deposition of trophic eggs have not been observed. The ideal scenario for the species is hence, for rains to fill a larger aquatic habitat, flood the nest, and wash the tadpoles into the water, once resources are depleted. However, due to the short persistence or complete absence of these habitats in exploited forest, this does not happen and tadpoles cannot complete their development.

An increase in temperature and solar radiation may not only result in a decrease of aquatic habitat availability, it also directly affects the thermal conditions within the aquatic environment. The development and growth of poikilothermal organisms, such as anurans, largely depend on the surrounding temperatures (Álvarez and Nicieza, 2002). Changes in the thermal environment may therefore drastically alter the development and growth of tadpoles, as has been observed in the tadpoles of *L. knudseni*. Low temperatures have previously been shown to decelerate development more drastically than growth, thereby increasing stage-specific growth (Smith-Gill and Berven, 1979) and temperature has been considered to be the fundamental mechanistic influence of canopy cover (shading conditions) on amphibian growth rates (Skelly et al., 2002). A recent study on the impacts of shading on larval traits of a hylid frog in a Tasmanian commercial forest (Lauck et al., 2005) showed that increased shading of ephemeral ponds resulted in decreased developmental rates and a higher coefficient of variation for size at metamorphosis (larval growth and development did not respond significantly to shading in permanent ponds). Results of our experiments, however, revealed opposite effects. Tadpoles raised under higher temperatures developed slower and their growth was decelerated, likewise. One possible explanation may be the existence of a temperature threshold, beyond which development and growth are inhibited due to physiological constraints. It is more likely however, that an increase in UV-B radiation is ultimately responsible for the developmental arrest in tadpoles of exposed treatments. This has previously been reported in temperate zone amphibians (Belden et al., 2000; Pahkala et al., 2000; Blaustein et al., 2003; but compare Pahkala et al. 2003) but has not yet been tested systematically in the tropics. In the specific case of *L. knudseni* results corroborated the assumptions of Zimmerman and Simberloff (1996) who characterize *L knudseni* as being a species adapted to closed forest conditions.

Interspecific comparisons of tadpole survival in differently disturbed forest sites yielded species-specific patterns that have the potential of explaining the presence or absence of particular species at the local scale. Among the three species compared, *L. rhodomystax* appeared to be the most successful species in exploited forest, exhibiting the highest tolerance to temperature changes and altered environmental conditions. In our experiments that did not address intraspecific competition tadpole mortality in this species was exclusively linked to predation. Since mortality rates were similar in both habitat complexes (primary vs. exploited) and because we do not have evidence for strictly environmentally caused mortality, it seems reasonable to conclude that the species is comparatively indifferent to habitat alterations, at least at the comparatively small spatial scale that has been investigated. This is likely due to relatively broad reproductive habitat requirements and broad-scale physiological tolerance of its larvae. Larvae of *L. knudseni* on the other hand responded to changes in environmental factors, as indicated by higher mortalities in exploited forest controls in one of two runs. However, predation was the most important factor causing mortality in both habitat complexes. The influence of habitat alteration on larval survival can hence not finally and unambiguously be resolved for this species. Yet, results from the exposure experiments indicate that under severe conditions (high temperatures and increased solar radiation), development and survival of the species may be affected considerably.

Mortality patterns observed in *L. petersii* finally underscore the results from our habitat models. The tolerance of tadpoles to changes in the thermal environment appeared to be very low and the nature of the reproductive habitat seems to be the crucial factor for the population viability. Due to this lack of physiological plasticity and narrow thermal tolerance, the species seems to be unable to colonize habitats that are still suitable for *L. rhodomystax*. This may explain the complete absence of the species in exploited forest.

Conclusions and implications

Various studies on the influence of timber harvesting on wildlife in tropical forest have provided evidence for both positive and negative effects of logging on populations of different groups of organisms (e.g. insect herbivores: Basset et al., 2001; lizards: Lima 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, 1995 and Ernst et al., in press). Whereas some species were unable to survive, a great number of species maintained stable and viable populations or even benefited from the disturbance. The tendencies observed clearly depended on the specific group of organisms that were exposed to the disturbance. Even closely related species, such as the frogs investigated in this study, may face very different challenges and problems if being exposed to environmental alterations following anthropogenic disturbance. They are hence to be regarded on a species-specific basis, rather than treating them as a group with identical limitations and adaptations. In addition, human-induced habitat alterations, such as logging, affect these anurans both at the larval (development and survival) and the adult (habitat selection) stage. Assessments of the impacts of these alterations should thus not exclusively focus on adult frogs. This is especially true because severe impacts on tadpoles may ultimately result in critical changes of the population structure of adult frogs. The presence of a species in exploited forest habitats will ultimately depend on the reproductive success of the species in these habitats.

Different responses to disturbance related environmental changes in different yet closely related species also highlight that simplified generalizations are problematic. Conservation strategies will be based on wrong or only insufficient assumptions if more fine-grained differences between species are a priori being neglected. Statements, such as (semi-) terrestrial reproduction means increased independence of aquatic sites, and hence lower susceptibility towards habitat alterations, appear in a different light when considering these species-specific differences. In the specific case of the anurans investigated here, a sound conservation strategy would aim at preserving a wide spectrum of different habitats of both larvae and adults, including those that have already been altered in order to safeguard the long-term population viability of all species involved.

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

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Colostethus sp. Mabura Hill, Guyana

DIVERSITY EROSION BEYOND THE SPECIES LEVEL: DRAMATIC LOSS OF FUNCTIONAL DIVERSITY AFTER SELECTIVE LOGGING IN TWO TROPICAL AMPHIBIAN COMMUNITIES

Raffael Ernst, K. Eduard Linsenmair and Mark-Oliver Rödel

Abstract

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.

Key Words: Selective logging; communities; Amphibia; Anura; functional diversity; West Africa; northern South America

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 (Laurence and Laurence, 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, 1995).

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; Diaz and Capido, 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.

Methods

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 km² 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 km² of primary rain forest and is part of the Wappu compartment located within a 500 km² 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 app. 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).

Data Acquisition

The field data were acquired between February 1999 and September 2002 (TNP) and November 2002 and September 2004 (MHFR). We established ten 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 hours of visual and acoustic transect sampling in TNP, and 7,799 individuals of 30 different anuran species belonging to six families during 393.5 hours 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.

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 (2000) 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.

Results

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 reversed 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 in1988), 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 app. 25 yrs. 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.

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(exp)92 /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(exp)92 /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(exp)92 /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.**

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. 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.

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 1). 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).

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 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.

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 1.

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.

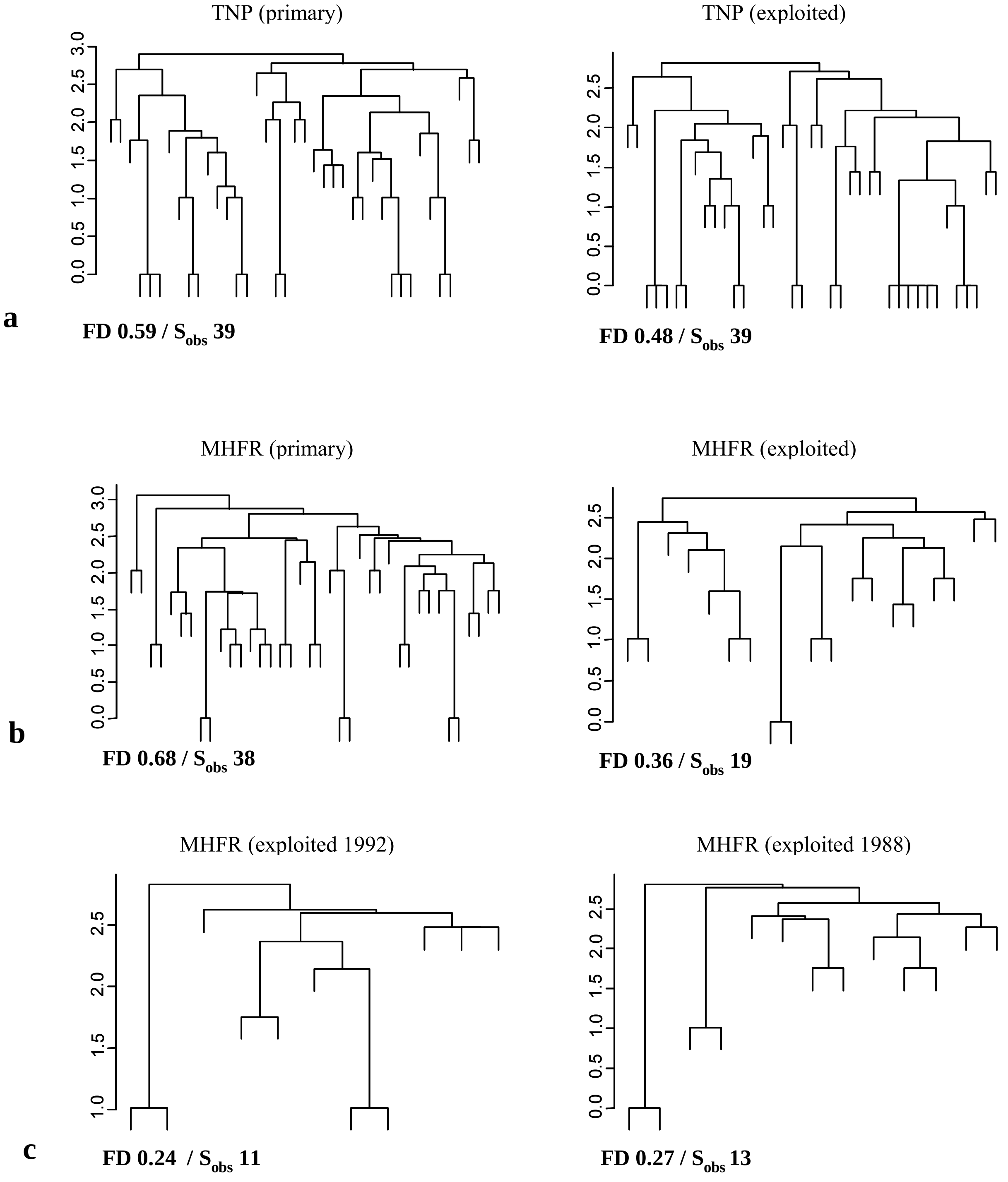

Figure 1 UPGMA-dendrograms (Euclidean distance) based on species trait matrices (each matrix based on all records within a particular habitat complex). Given are FD standardized to vary between 1.0 and 0.0 and S_{obs} = number of observed species for respective communities. Note different scales on distance 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).

Discussion

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 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.

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.

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Appendix 1 Species composition and functional group (FG) – allocation of anuran communities in TNP. 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.

	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

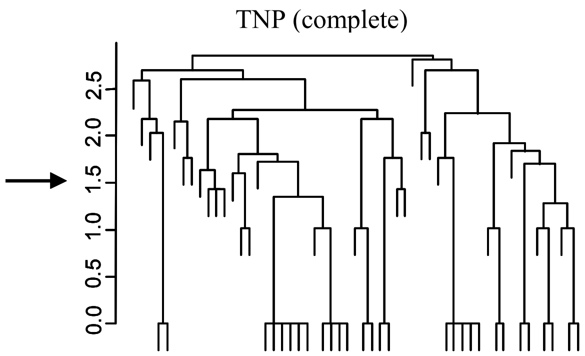

Figure 1 UPGMA-dendrogram (Euclidean distance) based on complete community. Arrow indicates cut-off value.

Table 2 Species composition and functional group (FG) – allocation of anuran communities in MHFR. 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.

	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		

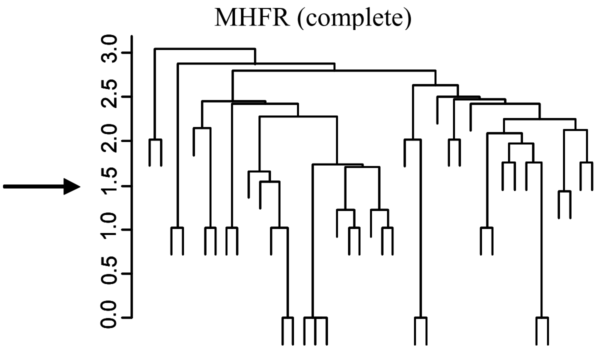

Figure 2 UPGMA-dendrogram (Euclidean distance) based on complete community. Arrow indicates cut-off value.

CHAPTER 5

EXTENDED SUMMARY AND SYNTHESIS

Amphibian communities in disturbed forests: lessons from the Neo- and Afrotropics

R. Ernst, K. E. Linsenmair, R. Thomas & M.-O. Rödel

Hyperolius concolor, Taï NP, Côte dÌvoire

AMPHIBIAN COMMUNITIES IN DISTURBED FORESTS: LESSONS FROM THE NEO- AND AFROTROPICS

Raffael Ernst, K. Eduard Linsenmair, Raquel Thomas and Mark-Oliver Rödel

Summary

Timber harvesting is currently the most common commercial utilisation activity in tropical forests. Assessing the effects of logging on different aspects of biodiversity and general ecosystem properties is hence of prime importance if the few remaining areas of intact tropical forest are to be protected effectively and efficiently.

As we will point out in this chapter, tropical amphibian communities are an appropriate model system for studies on the impacts of human-induced environmental changes on the dynamics of complex biological systems. Here, we elaborate on patterns of diversity changes in tropical forest amphibian communities facing habitat alterations associated with selective logging in two globally important eco-regions (Côte d'Ivoire, Upper Guinea, West Africa and Guyana, the Guiana Shield, northern South America), and discuss findings from other previously conducted studies with similar focus.

A key statement that we stress on in this chapter is the fact that common measures of diversity, such as species richness and α-diversity only inadequately reflect processes of diversity change following anthropogenic disturbance. They also fail to describe actual impacts on the dynamics of complex biological systems. We argue that commonly used measures produce an incoherent and insufficient picture of diversity patterns and the underlying processes that shape these patterns. Thus, an understanding of higher levels of diversity, such as β-diversity and functional diversity (and hence compositional patterns) appears to be the key to effectively mitigating the impacts of human-induced disturbance on amphibian communities.

We show that the predictability of amphibian community composition depends on the respective level of anthropogenic disturbance imposed on a particular habitat. Hence, human activities that lead to changes in the structure of a forest, such as logging, not only alter simple system descriptors, such as the number of species in a given community, but rather alter the dynamics of the entire system. In this context, functional diversity is shown to be an important aspect underlying the actual mechanism that leads to the observed change of predictability patterns. Functional

differences between species, rather than number of species per se appear to be the decisive factor in sustaining desirable ecosystem states and thus in maintaining important ecosystem services.

Because biological diversity appears to play a substantial role in ecosystem resilience required to safeguard essential ecosystem functions in the face of environmental change, we call for a critical revision of common diversity assessments approaches. We advocate the reconsideration of the uncritical use of widespread measures and descriptors of biodiversity on grounds of inconsistent patterns found throughout numerous studies, including those presented herein.

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 and spatial scales. When investigating the impacts of human-induced environmental changes on diverse vertebrate communities in the tropics, we should hence address compositional changes, as well as β-, and functional aspects of biodiversity. Special attention should also be drawn to the particular disturbance history of a given site and large scale cross-regional comparisons should be given priority. The consideration of these approaches in future studies would likely provide deeper insight in ecosystem processes at large scales and improve the effectiveness of current ecosystem management strategies.

Key words: Anthropogenic disturbance; habitat alteration; logging; communities; Amphibia; diversity; predictability patterns; community dynamics; conservation; West Africa; northern South America

Introduction

Tropical forests cover 6 % of the planet. However, as early as the late 1980s an area of 142,000 km^2 was estimated to be lost every year equalling 1 % of the total tropical forest area (Myers 1989). Deforestation rates have been increasing ever since (Lambin et al. 2003). The major threats to tropical rain forests are clearance and fragmentation of the forest, and the overexploitation of organisms in the remaining area (Laurance et al. 2001, Primack 2002).

Tropical amphibians are a diverse vertebrate group that is threatened by multiple factors. Since their first appearance approximately 299-251 million years ago, this group has evolved into what could be the most diverse group of tetrapod vertebrates (Köhler et al. 2005). Currently, 5,743 amphibian species are recognized and given the rate of new descriptions and species estimates, amphibians could possibly outnumber bird and reptile species within the next years (white papers of Amphibian Conservation Summit, Conservation International and IUCN 2005). Despite this alleged evolutionary success story, many amphibian species throughout the world are facing severe population declines or even extinction. The Global Amphibian Assessment (http://www.globalamphibians.org) revealed that almost one third (32%) of all amphibian species are threatened and around 120 species have gone extinct in recent times. This percentage is far higher than in all other known groups of organisms (Stuart et al. 2004, Young et al. 2004). These facts have prompted many amphibian population and community studies acknowledging an alarming phenomenon known as the Global Amphibian Decline (Lips et al. 2005), which has affected amphibian populations in various areas throughout the world. Although many factors, such as increased ultraviolet-B radiation, climatic change associated with global warming, and environmental contaminations adversely affect amphibians (e.g. Blaustein et al 1994, 1996, Pechman and Wilbur 1994, Pounds et al. 1999), habitat loss and alteration are probably the most serious causes of amphibian population declines, currently affecting almost 70 % of the species (http://www.globalamphibians.org). Many amphibian species whose populations have previously been weakened or experienced declines due to habitat degradation and destruction ultimately appear to fall victim to a previously unknown disease, the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*). This pathogen seems to be responsible for the loss of entire populations previously facing environmental stress (e.g. Weldon and du Preez 2004). New evidence supports the possibility that the fungus rapidly spreads and wipes out amphibian population in connection with global warming (Cary and Alexander 2003, Pounds and Puschendorf 2004, Pounds et al. 2006), which in turn is substantially promoted by rapidly increasing deforestation. Given the current rate of deforestation and habitat destruction, it cannot be overstated that habitat loss is the principle factor determining the uncertain future of many amphibian populations and furthermore the general level of species extinctions in tropical forests.

Due to their physiology, mostly short generation times, and predominantly biphasic lifecycle, amphibians are particularly sensible with respect to habitat changes and altered microclimatic conditions that accompany these changes. There is a common misperception concerning amphibian habitat requirements (Dodd and Smith 2003). They are usually thought to be exclusively associated with large wetland habitats and it is assumed that preventing the net loss of wetland habitats is an adequate measure to protect entire amphibian communities. However, amphibian habitat requirements, especially in the tropics, are very diverse and far more complex, not only among different species, but also with regard to different life history stages of a particular species. So far little is known about differences between sexes or among size classes.

Most amphibians have much shorter reproductive cycles than, for example large mammals or trees, resulting in faster detectable alterations in population size and structure with changing environmental conditions. Many species reflect landscape differences and exhibit a high sensitivity to habitat modification (Pineda et al. 2005, Ernst and Rödel 2005, Ernst et al. subm.). Amphibians in general also comprise a significant portion of the vertebrate fauna of tropical forests throughout the world, where they are important, both as predators and as prey (Inger 1980a, b, Duellman 1990). Standardized quantitative methods exist for estimating their species richness and abundance (Heyer et al. 1994, Rödel and Ernst 2004, Veith et al. 2004). For these reasons amphibian communities are an appropriate model system for studies on the impacts of human-induced environmental changes on the dynamics of complex biological systems.

This chapter focuses on the effects of forest disturbance due to timber harvesting on amphibian communities. Timber harvesting is currently the most common and lucrative utilisation of tropical forest resources (Johns 1997), and it has been identified as one of the major threats to global vertebrate diversity (e.g. Thiollay 1992, Lauck 2005).

Rain forests and their fauna are not identical and just as the forests in the major rain forest regions differ, so does the percentage of forest remaining and the nature of threats to its continued survival (Primack and Corlett 2005). Despite the urgent need for comparable studies on actual effects of logging on diverse vertebrate communities, across various regions, there is still a lack of knowledge and generalizable results. In an attempt to further narrow this gap we summarize some of our work on amphibian communities in two geographically distinct eco-regions, Côte d'Ivoire (Upper Guinea, West Africa) and Guyana (Guiana Shield, northern South America); see Fig. 1; for detailed study site descriptions see ter Steege et al. 1996, Riezebos et al. 1994). We discuss our findings in relation to other previously conducted studies with a similar focus. In the following sections we specifically elaborate on patterns of diversity changes in tropical forest amphibian communities facing human-induced environmental changes. We examine observed pattern changes at different levels of diversity (α-, β-, functional diversity) and discuss their respective significance and suitability in the context of the study of ecosystem dynamics and functioning. We address problems arising from the uncritical use of common diversity descriptors and finish with a discussion of the management implications.

Figure 1 Location of field studies (arrows). From west to east: i) Mabura Hill Forest Reserve (MHFR), central Guyana - 05° 09.322' N, 058° 41.983' W -; ii) Taï National Park (TNP), south-western Côte d'Ivoire - 05° 50.003' N, 007° 20.536' W.

Forest disturbance and logging methods – From single tree harvesting to clear felling

The creation of forest margins, which is the leading theme of this book, is intrinsically linked with commercial timber harvesting. This is because most medium and large scale logging operations move into pristine forest areas from a surrounding matrix, which in most cases is already highly anthropogenically altered. Logging operations thereby increase edge area and create margin situations in the remaining forest stand. Even small scale logging creates margins that are often big enough to foster negative effects. This may be especially true with regard to very sensitive and relatively immobile organisms, such as amphibians.

Most extant tropical rain forests have been logged or will be logged in the near future and huge areas are damaged through commercial logging every year (Whitmore 1997).

The most common form of timber extraction from tropical forest is selective logging. This kind of logging aims at the extraction of a limited number of tree species with high commercial value, which generally comprise only a small proportion of the trees present in a given area. Technological advances and an increasing demand for wood products, however, have resulted in a substantial increase in the number and intensity of logging operations world-wide (Dawkins and Philip 1998). A recent study revealed that selective logging, which in the past has often been neglected in deforestation studies, doubles previous estimates of anthropogenically induced forest degradation (Asner et al. 2005). The term 'selective logging' has hence become misleading, because, even though only a small percentage of the trees are felled for timber today still, a much larger percentage is killed or damaged during logging operations (e.g. Jonsson and Lindgren 1990). Logging damage may appear random, mimicking natural disturbance by creating canopy openings and debris piles comparable to those found in natural Chablis of mature rainforests. Yet, the scale, level of selectivity, and intensity of the disturbance caused by logging operations often differs. Estimated annual rates of gap formation in natural forests range between 1-2 % (Hartshorn 1990, van der Meer and Bongers 1996). Low-dynamical forests, such as the tropical rain forest of Guyana (ter Steege and Hammond 2001), fall well below these rates (0.4 %, van Dam and Rose 1997). Gaps created by logging are frequently larger than natural gaps and usually more gaps per area are being created (van der Hout 1999). In addition, large parts of forest landscapes are affected at the same time (due to e.g. road construction), even if logging operations are restricted to small patches, while natural disturbance, with the exception of large scale disturbances, such as extensive fires or hurricanes, will only affect smaller parts at a time.

Logging also has direct impacts on the biotic and abiotic conditions of the forest (Uhl and Vieira 1989, Johns 1997, Vitt et al. 1998). As mentioned above, the direct impacts of selective logging include the removal of harvested trees and associated damage to the residual stand but it also leads to significant disturbance of the soil and catchment's hydrology caused by the use of heavy machinery. Unlike most forms of natural disturbance, logging creates new habitats through soil compaction that in combination with increasing solar radiation, a direct result of the newly opened canopy, leads to alterations in the hydro-regime. Forest understoreys are characterized by strong vertical and horizontal gradients in light availability (Poorter and Arets 2003) with irradiance levels of 1-2 % of full sunlight under closed canopy. In tree fall gaps, however, irradiance levels can reach up to 25 % (Chazdon and Fetcher 1984). Although gap formation will locally change a multitude of parameters, increased light availability and hence intensified solar radiation with respective changes in temperature and humidity, is the most obvious change (van Dam 2001).

The sustainable management of tropical forests has been discussed very controversially (e.g. Bowles et al. 1998, Chazdon 1998, Gascon et al.1998) and the potential of forest and forest fauna recovery after logging applying various selective logging systems has been debated (e.g. Dawkins and Philip 1998, Clarke et al. 2005a). Forest recovery after logging depends highly on the severity of the impact. High logging intensities may have a disastrous effect on forest recovery (e.g. Chai and Udarbe 1997) and intensive exploitation may simply cause devastation (Nepstad et al. 1999). Selectivity is yet another problem as the selective removal of large reproductive trees may have severe consequences for regeneration (van Ulft 2004) and hence population development (Tilman et al. 1994). The overall impact on biodiversity and the forest ecosystem is difficult to quantify. Even though the conservation value of secondary and logged forests is recently obtaining more and more recognition (Chazdon 1998, Peña-Claros 2001), the long-term capacity to support biodiversity is still insufficiently known for tropical forests that are managed for timber (Arets 2005). As timber harvesting is currently the most common use of tropical forests (Johns 1997) and since the quality of forest management will be one of the major determinants of global biodiversity in the next 50 years, assessing the effects of logging activities on biodiversity and general ecosystem functions is of primary importance to conservation (compare Fimbel et al. 2001).

Potential processes determining amphibian diversity in disturbed forests

The long-term effects of logging on amphibian diversity are only poorly understood. Generally, logging leads to habitat alterations, which in turn may result in species alterations. The effects and the actual impact strongly depend on the scale and type of logging. Extensive logging (e.g. clear-cutting) can lead to drastic climatic changes and loss of forest microhabitats. As a consequence, true forest species may go extinct, whereas open habitat species can invade newly opened areas. Even lower intensity logging (e.g. patchy or selective logging) has the potential of dramatically impacting habitats and associated species. Effects may be effective on smaller scales. However, the actual impacts may be just as drastic, i.e. loss of particular species or even entire functional groups due to microclimatic changes and changes in the hydro regime, as a direct consequence of an increased canopy openness (compare Fig. 2).

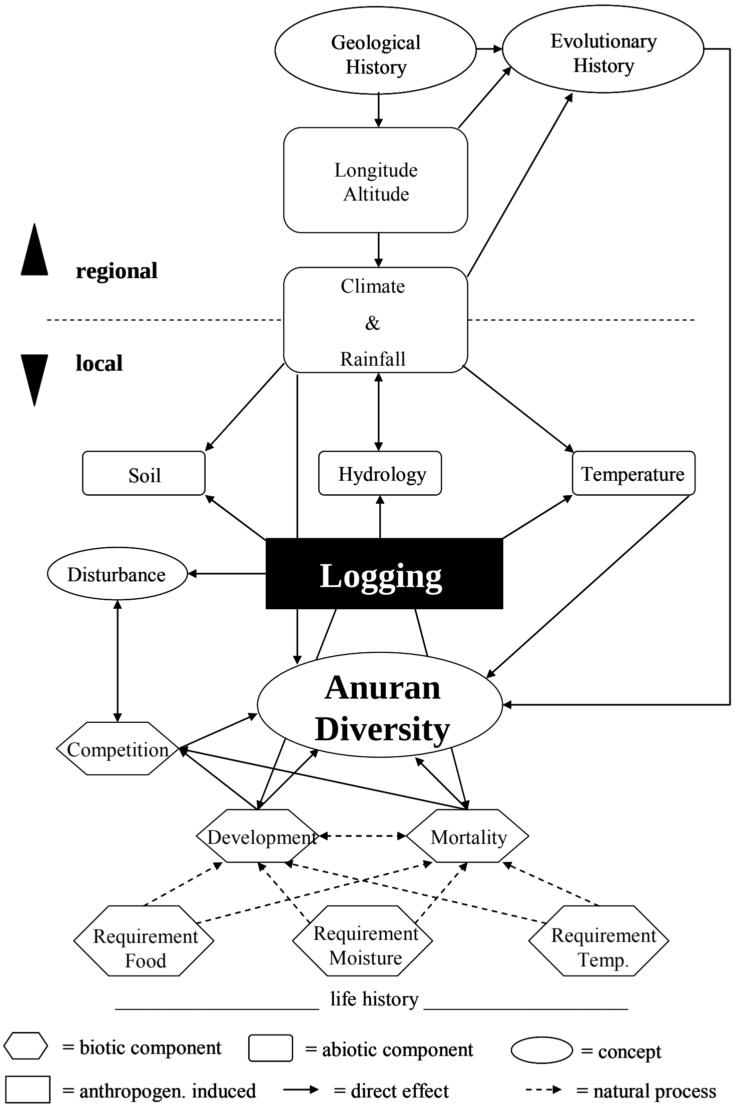

Figure 2 Simplified diagram of potential direct, and indirect influences of logging on anuran diversity. Note that life history traits and individual responses may vary between different groups or species and across scales. The direction of the respective effects (positive or negative) may thus be species- / group-specific,

Direct effects of disturbance on simple system descriptors

Changes in the natural disturbance regime, e.g. due to logging, can induce changes in species richness, α-diversity 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 (Laurence and Laurence 1996, Clarke et al. 2005b). The direction of the effects of logging on basic system descriptors such as species richness and diversity in forest communities is not consistent among different forests and different species groups. Both increased and decreased diversity after selective logging, as well as no changes in diversity have been reported. Even trends identifiable within particular taxa are highly variable, both within and between studies. (Table 1). Another major concern relates to the fact that only few studies indicate the intensity of logging or even consider it as a factor in the analyses. Most often they are not systematic with regard to temporal disturbance patterns (i.e. considering different forest recovery states or the time that has passed since logging occurred). In many studies, sites with very different disturbance histories are combined and analyzed without distinguishing between differing time spans elapsed since logging occurred.

Focal taxa	**Time since logging**	**Logging intensity $m^3 ha^{-1}$**	**Factor**	**Variables monitored and effect**	**Location**	**Source**
Amphibia	?	?	logging	richness (I)	Peninsular Malaysia	Heang et al. 1996
Amphibia	?	?	logging	abundance (D)	Kalimantan, Borneo	Lang 2000
Anurans	>20	?	logging to shade coffee plantations	richness (D), abundance (I and D according to species)	Highlands of La Antigua River, Mexico	Pineda et al. 2005
Amphibia	5-25		logging to cacao plantatin	abundance (from 5 to 25 yrs.D), biomass (D), richness (I), species diversity (I), evenness (I)	Costa Rica	Heinen 1992
Amphibia	5-20	?	logging to pasture	richness (NC) and composition (C) of hylid species (I) and *Eleutherodactylus* species (D)	Amazonia, Ecuador	Pearman 1997
Amphibia	3	25	logging techniques	richness (NC), composition (NC)	eastern Amazonia, Brazil	Azevedo-Ramos et al. unpubl.
Anurans	5-12	clearcut	logging to pasture	richness (I), composition (C), abundance (NC) *Phyllomedusa tarsius*	BDFFP-Project, Amazonia, Brazil	Tocher et al. 2001
Amphibia	12-16	57	logging	richness (Côte d'Ivoire: NC, Guyana: D) species diversity (Côte d'Ivoire: D, Guyana: D, NC from 12 to 16 yrs.), functional diversity (Côte d'Ivoire: D, Guyana: D)	Côte d'Ivoire, Guyana	Ernst et al. subm.

Table 1 Response of amphibians to logging. Only results related to logged areas are listed, even if studies addressed additional disturbance gradients (? = not data; D = decrease; I = increase; C = change; NC = no change). Modified after Alzevedo-Ramos et al. 2003.

In our studies on the effects of logging on the diversity of two tropical anuran communities in West Africa and the Guiana Shield we were able to demonstrate that the comparison of commonly used indices and simple system descriptors produces only idiosyncratic and inconsistent patterns with regard to the different geographic sites and disturbance regimes being compared. In case of the West African anuran communities, we found that species richness was identical in both, primary and exploited forest communities, while species richness of the Guyanan anuran communities decreased in exploited sites. We also demonstrated that there were no significant differences in diversity at the α-level in different recovery states. These results show that, given their conceptual basis, the search for general community patterns using traditional α-diversity measures, appears questionable. Common measures of biodiversity do not account for qualitative or compositional differences between assemblages. They may thus not adequately reflect actual changes and may hence be unsuitable and inappropriate indicators of forest disturbance as has previously been pointed out by Nummelin and Kaitala (2004).

The impacts of disturbance on community dynamics

As has been pointed out in the previous section, there is a substantial number of studies focusing on the direct effects of logging and habitat fragmentation and degradation on common system descriptors, such as species richness, relative abundance, and α-diversity, without providing a coherent and consistent picture of the underlying ecological processes and effects on the systems studied. Higher level diversity aspects and general system properties relating to ecosystem processes and functioning (e.g. compositional predictability patterns, functional diversity) are hardly ever addressed in most studies, even though they may be more likely to yield general patterns essential for drawing generalized conclusions with regard to entire systems. Anthropogenic habitat alteration has long been neglected as a factor in the analysis of system dynamics and compositional predictability patterns in biological communities. Yet, this issue is receiving growing attention as degradation, fragmentation, and destruction of natural ecosystems proceeds with alarming rapidity (Didham et al. 1996, Wardle 1999, Floren and Linsenmair 2001, 2005, Floren et al. 2001). The potential effects of human-induced environmental changes on system dynamics are yet poorly understood.

Results from our studies on anuran leaf litter communities in West Africa (Ernst and Rödel 2005) suggest that the predictability of community composition at least partly depends on anthropogenic disturbance imposed on a particular habitat. We were able to detect a transition from generally unpredictable systems in undisturbed primary forests to predictable systems in highly altered secondary forests, as has previously also been shown for canopy arthropod communities (Floren and Linsenmair 2001, 2005, Floren et al. 2001). Primary forest sites in geographic proximity to one another turned out to be similar with respect to species composition despite differences in habitat parameters. As tests for spatial autocorrelations clearly showed (Ernst and Rödel 2005), simple spatial auto-correlative patterns do not provide a sufficient explanation. The compositional resemblance in geographically closer sites can be understood as the result of underlying random walk dynamics, analogous to Hubbell's ecological drift (Hubbell 2001). These dynamics produce otherwise variable species assemblages across the entire range of the habitat complex. Similar communities are hence the product of stochastic extinction and colonization events occurring in species with high turnover rates, recruited from a common regional species pool (Hecnar and M'Closkey 1996). The upper limit on the species composition of a new community developing in a given place is set by the composition of the regional species pool. Membership in the regional species pool is constrained by, e.g., geological history of respective regions, and the evolutionary processes of speciation within different taxonomic groups. Random walk dynamics may also result in high turnover rates, i.e. high β-diversity among sites, which indeed was the case in the primary forest communities compared. Communities in exploited forests on the other hand have been shown to be largely subjected to the influence of strong environmental site filters. This factor mainly controls membership in the local species pool, the latter hence being constrained by physiological tolerances related to factors such as temperature and humidity. In exploited forests we uncovered correlations of community composition with environmental characteristics, whereas geographic proximity did not seem to play a role. In the past, communities in these sites have been subject to habitat alteration, generally producing more restrictive environments, especially with respect to microclimatic parameters. The existence of a strong site filter has a tremendous effect on the general processes governing recruitment from the regional species pool as outlined above. The remaining set of species thus consists of either highly adapted species, resulting in stronger species-habitat relations than would be detected in primary forest habitats, or it consists of species that exhibit a broad-scale physiological tolerance. As a direct result, turnover rates, i.e. high β-diversity, are lower in these exploited sites, even though, as has been pointed out in the previous section, α-diversity and other simple system descriptors may not differ between communities of differently disturbed habitats. We found the same patterns in leaf litter anuran communities of primary and exploited forest habitats in central Guyana (Ernst et al. 2005, R. Ernst unpubl. data), a site with a very different evolutionary and geographic history. Figure 3 illustrates the hypothetical relationship between geographic inter-site distance, disturbance level, and predictability of community composition based on the results of our studies. Similar patterns have likewise been reported from tropical moth communities in Borneo, Ecuador, and Tanzania (see Fiedler et al. previous chapter) as well as tropical ant communities in Borneo (Floren et al. 2001, Floren and Linsenmair 2005).

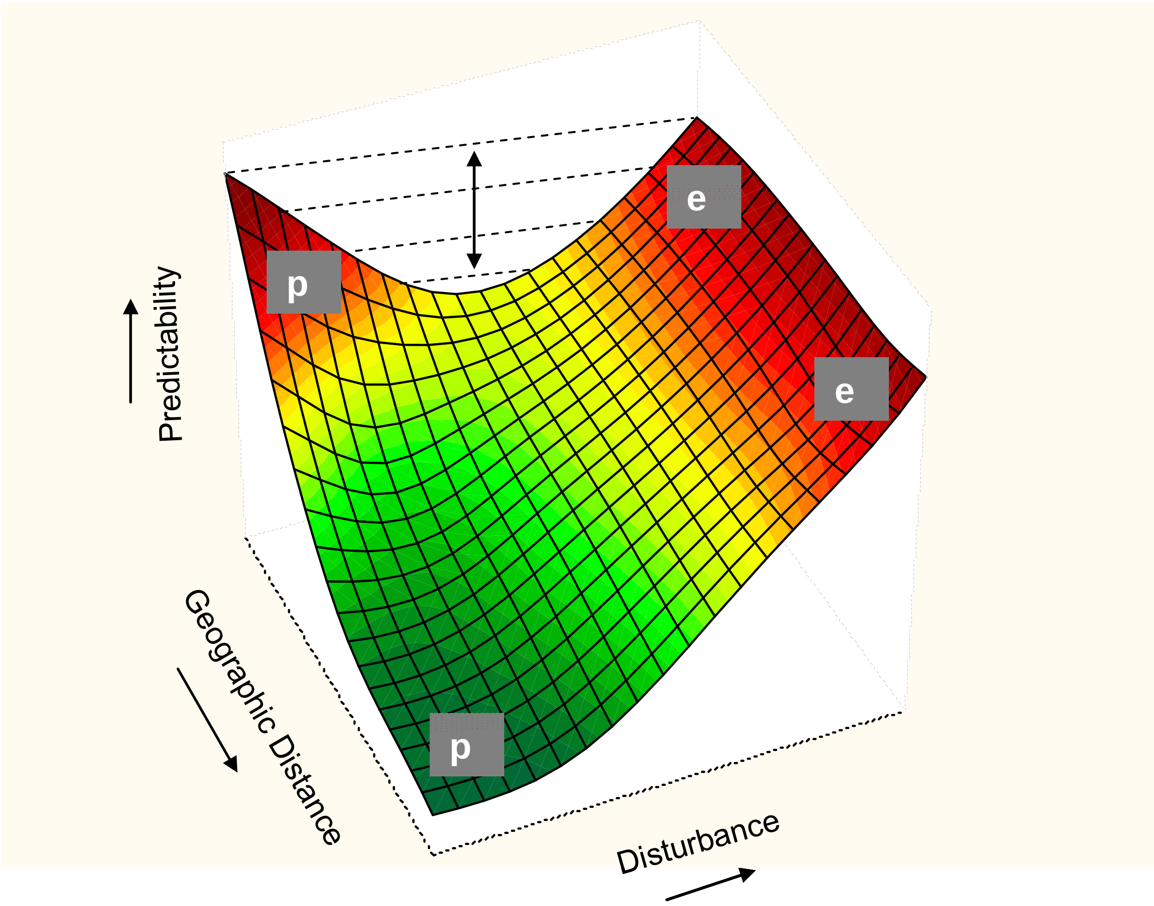

Figure 3 Hypothetical relationship between geographic inter-site distance, disturbance level, and predictability of community composition. P = primary forest communities; e = exploited forest communities. Note relative indifference to geographic proximity in highly disturbed sites, whereas predictability in undisturbed sites depends strongly on geographic proximity. As a result, β-diversity is generally higher in primary forest than in exploited forest. It remains unsolved whether predictability changes gradually from high to low levels of disturbance, or if the pattern change is the result of a transitional threshold. At small geographic distances the pattern may remain constant. However the underlying process may be different, as indicated by the bend at intermediate disturbance levels. In low disturbance systems geographic proximity may be the key factor, whereas in high disturbance systems species-habitat associations and hence environmental restrictions may be more important. Red areas indicate high levels of predictability. Green indicates low levels of predictability. Modified after Ernst and Rödel (2005).

As more studies, explicitly focusing on the impacts of anthropogenic disturbance on complex biological communities, are being conducted, it becomes even more evident that human activities that lead to changes in the structure of a habitat, such as logging, not only alter the composition of organisms that form a particular community but also have the potential of altering the dynamics of the entire system. The anthropogenic disturbance history of an area should hence always be considered when detecting deterministic patterns in the structuring of a community, as general applicability of deterministic explanations according to conventional niche theory may be attenuated. In their seminal work on response diversity, ecosystem change, and resilience, Elmqvist et al. (2003) pointed out that ecosystems can be strikingly conservative in their organization and function, despite differing histories and species compositions (Forys and Allen 2002, Brown et al. 2001). The same may hold true for predictability pattern changes after human-induced disturbance in complex biological communities. Even though evidence for direct impacts on system dynamics has generally been scarce because anthropogenic disturbance has largely been neglected as an important factor in previous works, the studies presented in this book, as well as a number of recent studies indicate that amphibian communities are not simply a unique case but that we are very likely dealing with a general pattern. The observed pattern changes illustrate strikingly that anthropogenic disturbance affects the underlying processes that shape diversity patterns at large scales.

In search of key factors

It seems tempting to argue that structural simplicity within disturbed forests and therefore a reduction of system parameters per se (the number of occurring species and/or habitats and therefore the degrees of freedom of the entire system) may be essential factors explaining the transition from rather stochastically organized to deterministically organized communities. However, a comparison of merely structural habitat features and simple species numbers neglects qualitative differences, which can be severe. As has repeatedly stressed upon, simple system descriptor changes may not be representative, as patterns are incoherent and vary among different forests and different species groups, as well as between studies (compare Fig. 4).

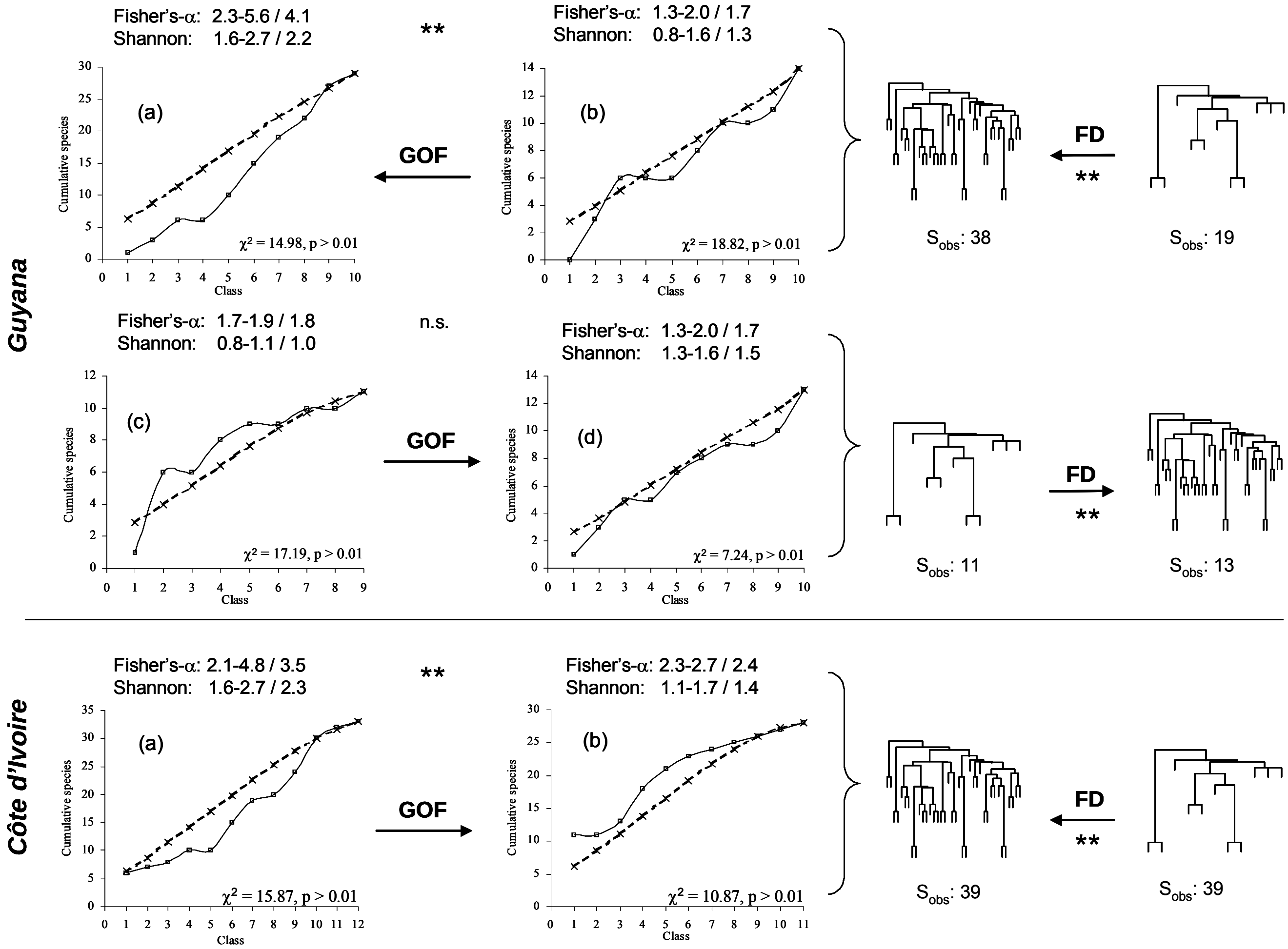

Figure 4 Comparison of species richness (S_{obs}= species richness given as species observed), α-diversity (represented by the parametric Fisher's α and non-parametric Shannon index, given are range and mean) and functional diversity (FD sensu Petchey and Gaston 2002) between anuran communities of differently disturbed forests in Côte d'Ivoire and Guyana (a) primary forest community, (b) exploited forest community, (c) exploited forest (1992) community, (d) exploited forest (1988) community. ** = statistically significant, n.s. non significant difference in α-diversity and functional diversity, respectively. Goodness-of-fit (GOF) to log-series distribution illustrated as cumulative observed (solid line) and expected (broken line) number of species in relation to abundance class. Direction of arrows indicates increase. Complexity of functional dendrograms symbolizes high/low functional diversity in communities of respective habitats. Data from (Ernst et al. subm.).

Even if a reduction in species richness or α-diversity after anthropogenic disturbance is recorded, it is important to note that a reduction of species numbers is not necessarily an unbiased reduction of functional trait diversity. 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 as has been pointed out in the previous section. At the α-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. This has previously been suggested for the relationship between biodiversity and ecosystem functioning in grassland ecosystems (Tilman et al. 1997, Hector 2001). As evidence of links between functional diversity and ecosystem processes is constantly growing (Chapin et al. 2000, Diaz and Capido 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. However, it is difficult to completely separate the effects of species and functional group richness in statistical analyses. Their particular contribution to changes in predictability patterns of biological systems is yet to be tested systematically.

In a recent study we approached this problem by assaying the impact of selective logging on different levels of diversity in two tropical anuran communities.The results of this study illustrated that simple measures of diversity, such as species richness may not adequately reflect the actual extent of biodiversity loss (e.g. loss of functional trait diversity) after anthropogenic disturbance (Ernst et al. subm.). Whereas species richness in the amphibian communities that where studied remained unchanged or only little affected, functional diversity (FD) differed significantly. We found extinctions after disturbance to follow a non-random pattern. They appeared to be trait dependent as has previously been shown to be the case in four natural communities, one being an animal assemblage (Petchey and Gaston 2002). Lea et al. (2005) likewise 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 case of the African and South American amphibian communities studied, we found a clear trend with regard to group membership and loss of particular species in exploited sites. Functional groups most affected by habitat alteration associated with logging contained species that depend on lotic or large lentic habitats for reproduction (e.g.: *Aubria subsigillata*, *Leptopelis macrotis,* and *Kassina lamottei* in Côte d'Ivoire; *Hyalinobatrachium* spp., *Atelopus spumarius,* and *Phyllomedusa bicolor* in Guyana; Plate 1). These habitat features are most often disappearing in disturbed forests due to an altered microclimate. High intensity logging may drastically alter hydrological cycles and enhance erosion and siltation (ter Steege et al. 1996). Very often, previously permanent aquatic habitats become ephemeral and lotic habitats become stagnant or disappear entirely. On the other hand, groups that persisted contained species that have reproductive modes making them less dependent or entirely independent of large aquatic habitats for reproduction as is the case in many direct developing or tree hole breeding species (e.g.: *Arthroleptis* spp., *Phrynobatrachus tokba,* and *Acanthixalus sonjae* in Côte d'Ivoire; *Eleutherodactylus marmoratus* and *Osteocephalus oophagus* in Guyana; Plate 1). These species were able to maintain stable populations or even increased in abundance. Despite the different evolutionary history of the communities in the two geographically separated regions, functional groups that were most affected or least affected showed a high resemblance.

In case of high levels of functional redundancy (sensu Loreau 2004) the loss of a particular species may seem 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. Symptomatically, systems that lose entire functional groups as a result of environmental change are characterized by low response diversity (sensu Elmqvist et al. 2003) across scales (Jackson et al. 2001). The removal of species within the same functional group may also have dramatic consequence for evolutionary characteristics (Pauly et al 2002) with additional negative cascading effects (Carr et al. 2002). This kind of diversity erosion beyond the species level may hence potentially affect the stability of ecosystem structure and function tremendously (McCann 2000, Jackson et al. 2001).

Patterns found in different recovery states deviated in terms of differences between changes in α-diversity versus functional diversity, which is alarming from a conservation or management point of view. Whereas no significant differences in diversity of communities in different recovery states were detected at the α-level, significant differences in functional diversity were observed. Anuran communities showed a tendency towards recovery i.e., communities of old recovery states were functionally more diverse than those of young recovery states (Fig. 4), yet this recovery potential would have remained concealed if looking at α-diversity exclusively. However, it has to be said that the difference in recovery time (only 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, differences were significant and it seems promising to tests whether this pattern proves to be consistent in systems in which differences in recovery time are more distinguished. This would be especially important as the role of disturbed systems in conserving the remaining biodiversity will most likely increase in the near future.

What has previously been pointed out could have a tremendous influence on the planning of ecosystem management and restoration. Overall, patterns at the α-level appeared to be very inconsistent, whereas patterns at higher levels β- or functional diversity were more coherent (compare also Fig. 4). Given that these very differences, i.e. species' identity not number per se, seem to influence ecosystem functioning tremendously (see O'Connor and Crowe 2005) it seems necessary to rethink common approaches of diversity assessments aimed at the protection of entire communities or even ecosystems, even more so if essential ecosystem services are to be secured in the long run.

Plate 1 Representatives of functional groups most (left) / least (right) affected by logging (a-d: West Africa, e-h: South America). a. *Leptopelis macrotis;* b. *Phrynobatrachus tokba*, inlet: froglets undergoing semi-direct development in jelly layer; c. *Kassina lamottei*, inlet: large lentic-nektonic tadpole; d. *Arthroleptis* sp.1; e. *Phyllomedusa bicolor*, inlet: clutch of *P. vaillantii*, a syntopic species, wrapped in leaf; f. *Osteocephalus oophagus* in front of water filled tree hole; g. *Hyalinobatrachium nouraguensis*; h. *Eleutherodactylus marmoratus*.

Many of the chapters in this book and the studies and publications associated with them leave little doubt as to the tremendous negative effects of habitat loss and fragmentation on numerous rainforest species, entire communities and the principles that govern their functioning. These factors will ultimately also affect the human population, locally as well as globally that depends on a vast number of forest resources and the ecosystem services that these forests provide. It has widely been acknowledged that, although forests have been altered by humans for millennia, recent changes have occurred at an unprecedented pace and scale. However, necessary steps towards an effective protection of the remaining tracts of intact tropical forest and the biodiversity contained therein have up to now not been taken. Another common theme of many chapters in this book is the call for a revision of "traditional" diversity perspectives and measurement approaches, which all too often addressed simple α-diversity changes exclusively and neglected sometimes more important and informative patterns, such as changes in β-diversity, functional diversity or changes in predictability patterns of entire communities. Concepts for management and conservation planning were hence very often based on incorrect or at least incomplete assumptions.

IN A NUTSHELL

There are three major conclusions that can be drawn from our results and that have direct implications for management and conservation even beyond issues innate to amphibian conservation.

1. Scale matters: It is important to monitor different levels of biodiversity (α-, β-, functional diversity) in order to reveal important patterns that influence system dynamics and to be able to assess the actual loss after anthropogenic disturbance. Differential responses of different taxa, functional groups within particular taxa, and hence, particular species to habitat alterations induced by anthropogenic disturbance, complicate generalizations and require a good knowledge of the organism groups studied. Taxonomic and autecological studies are therefore not simply a luxurious addition but rather a prerequisite for the development of integrative coherent concepts.

2. Time matters: The disturbance history of a site is important to estimate its role in the structuring of a given biological community and to assess its impact on the system's dynamics. The analysis of e.g. different chronosequences and hence recovery states is important to detect potential recovery patterns. This implies that there is an urgent need for long-term studies and studies addressing pre- and post-harvesting phenomena, as these provide the only real opportunity for uncovering patterns in time, which are central to long-term conservation planning. The resulting information can then be used to establish sound and ecologically sustainable management concepts not only for the remaining primary forest that is protected in national parks and nature reserves, but also for areas set aside for sustainable use of tropical forests. This is especially true as these areas will very likely constitute the majority of forest habitats in the decades to come and because in reality, only a small fraction of tropical forests is adequately protected in reserved areas.

3. Geographic history matters at the local scale: 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. It is important to differentiate between common (in many cases regional or even global) and specific (in many cases site specific or local) phenomena. This again is of course intrinsically a matter of scale. Despite different geographic and evolutionary histories, general patterns at a particular level (here e.g. β-diversity, functional diversity or predictability) are similar in otherwise distinct geographic realms. On the other hand, slight differences may exist, hence possibly limiting assertions and general predictive power. Differences are mainly differences by order of magnitude in factors, such as variations in species composition and functional diversity.

Both aspects, general and specific are, however, important when it comes to sound ecosystem management plans and conservation strategies. Congruence in general patterns determines the overall management agenda, whereas site-specific differences have to be considered in the implementation of the agenda at the local scale.

Some specific recommendations with regard to the conservation of amphibians in altered tropical forest

Habitat diversity and habitat size: Although this has not specifically been addressed in this chapter, there is multiple evidence that habitat diversity is a crucial factor in the conservation of amphibian diversity. Even though amphibians may generally require less area than, e.g., large mammals or birds of prey, to maintain stable populations, habitat diversity is likely to increase with habitat size. A minimum habitat size is also essential to maintain ecosystem functions that determine e.g. climatic conditions and thereby directly affect amphibians. An important implication of our findings directly involves habitat size. Amphibian diversity in primary habitats has been shown to be determined by the dynamics of compositionally unpredictable local communities. Local community composition varies across the spatial range as a result of stochastic patterns of extinction and colonization events. Species turnover is hence comparatively high. Conserving overall amphibian diversity and thereby a large proportion of the functional traits of members (species) of a particular community requires conserving a large proportion of all species that make up the community. However, within these highly dynamic systems 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. With respect to the protection of diverse habitat features simple measures can be taken when logging operations are being carried out. These are partly addressed and implemented in already existing national legislation (e.g. Guyana Forestry Commission's code of practice for timber harvesting, GFC 2002). The exclusion of diverse and representative parts of the concession from logging activities should be considered. A special focus should be given to the presence of diverse aquatic habitats, such as permanent forest ponds, swamp areas, streams and small creeks. Old emergent trees provide a number of unique microhabitats and should thus be spared from felling. Some species, e.g. the large neotropical hylid *Phrynohyas resinifictrix,* are almost exclusively recorded calling from the crown level of the largest emergent trees, they hardly ever descend to the ground. These old trees usually provide large water filled tree holes on which this species depends for reproduction and should hence be given special consideration for protection as habitat trees.

Protection of interior forest conditions and hence microclimatic and hydrological factors: As has repeatedly been pointed out, logging may drastically alter hydrological cycles and microclimate. Hydrological cycles within exploited sites have been reported to change dramatically, i.e. previously permanent creeks were becoming ephemeral, only being lotic during the peak rainy season. Large lentic ponds were reportedly more prone to desiccation. These changes especially affect species that depend on these habitats for reproduction, e.g. members of the neotropical genera *Atelopus* and *Hyalinobatrachium* or the afrotropical genera *Aubria* and *Kassina.* A significant proportion of any given tropical amphibian community is composed of small, leaf litter inhabiting species (app. 25-30 %; Allmon 1991). These may especially be prone to decreases in abundance or even extinction, as they rely on dens and moist litter for cover and nutrition (small leaf litter arthropods). However, leaf litter quantities frequently decrease as a result of forest stand thinning and formerly moist and shaded patches are opened up and hence prone to desiccation.

Continued logging and hence intensified disturbance along with a tremendous decrease in primary habitat size may thus put the survival of populations of these high priority conservation species at stake. Silvicultural techniques that minimize negative effects on canopy structure and openness and that prevent extensive soil compaction and collateral damage of the remaining stand may represent effective measures in safeguarding local amphibian communities. Among these practices are so called “Reduced Impact Logging” (RIL) methods that incorporate the clipping of lianas before felling to prevent incidental damage on surrounding trees, applying log hauling methods that do not make use of heavy machinery and restricting logging operations to dry periods, thus avoiding excessive soil compaction.

Avoiding access, fragmentation, and the formation of large margin areas: Historically, anthropogenic pressure in areas such as the Guiana Shield has been limited due to the very low population density and minimal access to the area in general. However, road construction accompanying logging operations has facilitated the access to previously uninhabited areas. Locally operating logging companies additionally facilitate access through skid trails and roads linking concessions. New areas are thus frequently opened and the size of forest margins and edges is being increased. Restricting road formation and, thus access to previously intact areas may therefore be essential for the maintenance of forest connectivity. The establishment of large buffer zones may here be and efficient additional tool, guaranteeing the protection of interior-forest habitats. Maintaining connectivity through protection of adequate corridors between primary and exploited forest patches is yet another important step to be taken in order to guarantee the persistence of colonization and recolonization dynamics.

Guaranteeing adequate recovery periods: Higher functional diversity in old forest recovery states can be seen as an indication that amphibian communities may have some potential of recovery, given that 1: original logging was conducted in a sustainable manner 2:,remaining forest stands maintain sufficient connectivity among each other to allow recolonization of true forest species, and 3: adequate recovery periods are provided. One important implementation of this finding could be the extension of harvesting cycles i.e. long rotation periods, in combination with reduced impact logging methods and low intensity harvest in order to guarantee recovery of the system in the long run. However, systematic long-term studies are needed in order to specify and concretize recommendations with regard to harvesting cycles and recovery potential of the forest communities affected by the disturbance.

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CHAPTER 6

ALLGEMEINE ZUSAMMENFASSUNG

Gemeinschaftsökologie – die Suche nach Mustern und Prozessen zur Beschreibung von Lebensgemeinschafen

Gegenstand der Arbeit - Anurengemeinschaften auf Messers Schneide. Bereits dieser Teil des Titels ist eine Paraphrasierung des Inhalts und Untersuchungsgegenstandes. Ziel der hier präsentierten Arbeit ist folglich die Beschreibung von biologischen Gemeinschafen und darüber hinaus des Einflusses von Störungen auf diese Gemeinschaften. Zentrales Thema der wissenschaftlichen Beschreibung von biologischen Gemeinschaften, also der Gemeinschafts-, oder Synökologie ist die Suche nach Mustern und die Beschreibung von Prozessen, die diese Muster verursachen. So wie die Basisdisziplinen der organismischen Biologie ineinander greifen (Abb.1), so ist auch die von Ökologen herkömmlich verwendete Trennung von Mustern und Prozessen (nach Watt, 1947) nicht absolut. Vielmehr besteht zwischen ihnen eine direkte Verbindung, die sich z.B. sehr deutlich in Nischenaufteilungsmodellen (z.B. Tokeshi, 1999) oder Nullmodellen zur Erklärung empirischer Artenabundanzmuster (z.B. Hubbell, 2001) manifestiert. Die vorliegende Arbeit ist hier keine Ausnahme.

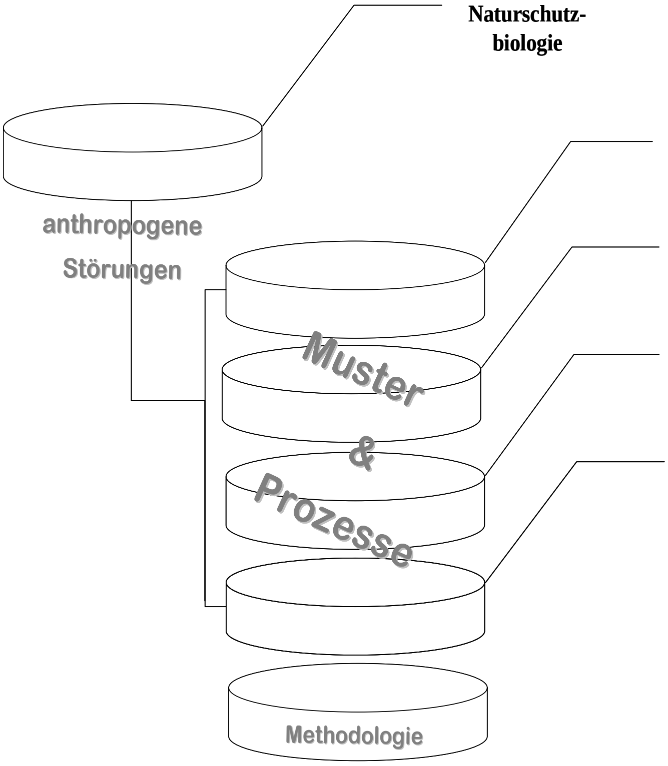

Abb. 1. Thematischer Aufbau und Struktur der Arbeit

Nach einer Einführung (**Kapitel 2**) in die verwendete Methodologie und die taxonomische Zusammensetzung der betrachteten Modelsysteme (Anurengemeinschaften der Afro- und Neotropis), also den unteren Ebenen in Abb. 1, beschäftigt sie sich auf Art-, Populations- und Gemeinschaftsebene (den höheren Ebenen in Abb.1) zunächst primär mit Mustern im Allgemeinen und mit den Veränderungen dieser Muster unter dem Einfluss anthropogener Störungen im Besonderen (**Kapitel 3**). Die Aufklärung von Prozessen die zu diesen Mustern oder deren Veränderung führen ist Gegenstand von **Kapitel 4**. Auch hier ist die Trennung nicht absolut, vielmehr bestehen diverse Querverbindungen zwischen den ansonsten unabhängigen und eigenständigen Kapiteln.

Muster und Prozesse stellen also einen Schwerpunkt der Arbeit dar. Ein weiterer, nämlich die Bedeutung von anthropogenen Störungen, im speziellen Fall (selektiver) Holzeinschlag, verbindet theoretisch-ökologische Konzepte mit angewandten Aspekten der Naturschutzbiologie (insbesondere **Kapitel 5**).

Allgemeine Muster der Bildung und Struktur tropischer Anurengemeinschaften (**Kapitel 3**)

Eine der fortwährenden Debatten innerhalb der synökologischen Forschung hat die multiplen Faktoren, die Bildung und Zusammensetzung einer gegebenen biologischen Gemeinschaft und somit deren Vorhersagbarkeit bestimmen, zum Inhalt. Traditionell werden zwei gegensätzliche Ansätze diskutiert.

a. das <u>individualistische Kontinuumskonzept</u> nach Gleason (1926) und
b. das <u>interaktive Konzept</u> nach Clements (1916).

In der vorliegenden Arbeit wurden in diesem Kontext exemplarisch die <u>Laubstreuanurengemeinschaften</u> primärer und sekundärer Waldhabitate des Taï Nationalparks (TNP) im Südwesten der Elfenbeinküste untersucht. Eine Analyse der Laubstreuanurengemeinschaft mittels Nischenüberlappungsmodellen und anschließende Überprüfung der empirischen Muster mittels geeigneter Nullmodelle, zeigte, dass die beobachtete multivariate Struktur nur in geringem Maße von biotischen Interaktionen beeinflusst wird und somit nicht das alleinige Ergebnis vergangener oder aktueller interspezifischer Interaktionen ist. Die Anurengemeinschaften der Laubstreu des TNP lassen sich am besten als Ansammlung locker interagierender Individuen beschreiben, die auf eine Reihe spezifischer physiologischer Zwänge reagieren, welche ihnen durch die Umwelt auferlegt werden. Es handelt sich hierbei also nicht um fest integrierte und in hohem Maße interagierende Artenansammlungen, die als Einheit evolvierten. Die Gemeinschaften zeigten vielmehr Eigenschaften, die weitgehend mit den Annahmen des individualistischen

Kontinuumkonzeptes übereinstimmen. Gleichwohl legen die Ergebnisse nahe, dass die empirischen Muster nur unter Berücksichtigung der unterschiedlichen Lebenslaufstrategien (*life-histories*) einzelner Arten erklärt werden können.

Eine weitergehende Analyse der Vorhersagbarkeit der Artenzusammensetzung lokaler Gemeinschaften zeigte, dass sowohl im Primär-, als auch im Sekundärwald distinkte Artengemeinschaften existieren. Allerdings unterschieden sich die Vorhersagbarkeitsmuster zwischen beiden Habitaten grundlegend. Im Primärwald konnten diese durch die geographische Nähe einzelner Untersuchungsabschnitte zueinander erklärt werden.

Die Vorhersagbarkeit der Sekundärwaldgemeinschaften hingegen beruhte auf der Ähnlichkeit spezifischer Umweltparameter. Dies ist höchstwahrscheinlich das Ergebnis physiologisch restriktiverer Bedingungen (lokale Filter) innerhalb sekundärer Waldhabitate, basierend auf einem extremeren, stark veränderten Mikroklima. Ausschließlich angepasste und tolerante Arten können unter derartigen Bedingungen überlebensfähige Populationen aufrechterhalten.

Bei der Überprüfung dieser Muster innerhalb eines anderen Segmentes des Modellsystems, den arborikolen Anurengemeinschaften in zwei geographisch getrennten Ökoregionen, dem Guiana Schild im nördlichen Südamerika und des Oberguineischen Raumes in West Afrika, zeigte sich, dass diese Muster gruppen- und regionsabhängig variieren. Im Gegensatz zu den untersuchten Laubstreuanurengemeinschaften zeigte sich, dass die arborikolen Gemeinschaften fast ausschließlich räumlich strukturiert waren. Mit einer Ausnahme ließ sich Artenzusammensetzung der Gemeinschaften sowohl primärer als auch sekundärer Waldhabitate in beiden Ökoregionen ausschließlich basierend auf der geographischen Distanz zwischen Untersuchungseinheiten vorhersagen. Eine signifikante Habitatkomponente konnte nur in den Gemeinschaften primärer Wälder in Guyana nachgewiesen werden. Unterschiede zwischen verschiedenen funktionalen Gruppen sollten bei der Analyse der Vorhersagbarkeit von Artengemeinschaften also unbedingt berücksichtigt werden.

Schlüsselfaktoren und Prozesse der Vorhersagbarkeitsmustervariabilität tropischer Anurengemeinschaften unter dem Einfluss anthropogener Störungen (**Kapitel 4**)

Für die Interpretation der empirisch gefundenen Muster und Übergänge zwischen tendenziell stochastisch organisierten Gemeinschaften in primären, ungestörten Wäldern einerseits und tendenziell deterministisch organisierten Gemeinschaften in anthropogen gestörten Wäldern andererseits, kommen prinzipiell zwei Prozesse in Frage.

Zum einen die einfache Reduktion der Systemparameter (Arten und Habitate) in gestörten Wäldern, die zu einer Simplifizierung des Gesamtsystems führt. Diese Simplifizierung, d.h. die Reduzierung auf wenige interagierende Parameter, könnte wiederum in einer erhöhten Vorhersagbarkeit resultieren. Die verminderte Artenzahl per se wäre somit verantwortlich für den Übergang von stochastischen zu deterministischen Systemen. Die Untersuchung der arborikolen Gemeinschaften legte allerdings nahe, dass die Zugehörigkeit einer Art zu einer definierten funktionalen Gruppe, also ihre Identität, beziehungsweise ihre artspezifischen Eigenschaften, das beobachtete Muster maßgeblich beeinflusst. Dies mag im Besonderen zutreffen, wenn einzelne, durchaus nahe verwandte Arten, unterschiedlich auf Störungen reagieren. In diesem Fall würde eine Analyse auf Artenreichtums- und Artendiversitätsebene gefundene Muster nur unzureichend erklären.

Die Untersuchungen an drei sympatrischen Vertretern der Gattung *Leptodactylus* in primären und selektiv eingeschlagenen Waldhabitaten in Zentralguyana zeigte, dass nahe verwandte Arten, die überdies ähnliche Adaptationen an Prädation, Austrocknungsrisiko und generelle Variabilität der thermischen Umwelt besitzen, artspezifisch unterschiedlich auf Störungen reagieren. Von den drei untersuchten Arten, *L. knudseni*, *L. petersii* und *L. rhodomystax* reproduzierte sich lediglich letztere erfolgreich in gestörten wie in ungestörten Waldhabitaten. *L. knudseni* wurde zwar in beiden Habitatkomplexen nachgewiesen, Reproduktion konnte aber nur im Primärwald bestätigt werden. *L. petersii* schließlich fehlte in gestörten Waldhabitaten gänzlich. Die Untersuchung der Larvalentwicklung und –mortalität in Abhängigkeit von störungsrelevanten Parametern wie Sonnenexposition und Temperatur zeigte, dass die durch selektiven Holzeinschlag veränderten Habitate und die darin herrschenden mikroklimatischen Bedingungen durchaus drastische Auswirkungen auf das Überleben von Populationen einzelner Arten haben können. So konnten gezeigt werden, dass das Larvalwachstum und die larvale Entwicklung durch erhöhte Sonnenexposition und damit ebenfalls einhergehenden Temperaturerhöhungen signifikant gehemmt werden. In einigen Fällen zeigte sich auch eine erhöhte Mortalität der Quappen unter Realbedingungen in gestörten Habitaten. In allen Fällen wurde jedoch deutlich, dass artspezifische Eigenschaften maßgeblich für das Aufrechterhalten oder Verschwinden stabiler Populationen in anthropogen gestörten Lebensräumen verantwortlich sind.

Diese Befunde legen den Schluss nahe, dass herkömmliche Systemdeskriptoren, wie Artenreichtum und Artendiversität, die Veränderungen von Gemeinschaften nach anthropogenen Störungen nur unzureichend wiedergeben. Die systematische Analyse von herkömmlich verwendeten α-Diversitätsmaßen, wie Artenreichtum und unterschiedlichen Heterogenitätsmaßen unterstützten diese Vermutung.

In einem Vergleich zwischen Anurengemeinschaften primärer und gestörter Waldhabitate in West Afrika und Zentralguyana zeigte sich, dass diese Deskriptoren ein äußerst inkoherentes Bild wiedergeben und zwischen den untersuchten Systemen variieren. Vielversprechender erwiesen sich hier Modelle, die funktionale Komponenten in der Analyse berücksichtigen. Im spezifischen Fall zeigten die Analysen auf höheren Diversitätsebenen, (hier funktionale Diversität), dass anthropogene Störungen, wie selektiver Holzeinschlag, einen immensen Einfluss auf die Funktionalität biologischer Systeme haben können, die mit herkömmlichen Analysen auf unteren Diversitätsebenen (Artenreichtum und Artendiversität) unentdeckt blieben. So konnte z.B. gezeigt werden, dass die funktionale Diversität in tropischen Anurengemeinschaften unter dem Einfluss anthropogener Störungen signifikant abnimmt, während Artenreichtum und Artendiversität unverändert bleiben. Auch hier zeigte sich ein gewisses Maß an Variabilität zwischen den untersuchten Systemen und Regionen. Das generelle Muster erwies sich jedoch als robust.

Synthese und Naturschutzbiologischer Kontext (**Kapitel 5**)

Die in den vorangegangen Abschnitten erläuterten Befunde sind besonders beunruhigend, da ein Verlust an Reaktionsdiversität (Response Diversity *sensu* Elmqvist et al. 2003) einen Verlust an adaptiver Kapazität bedeutet. Diese adaptive Kapazität oder Vielfalt ist jedoch unabdingbar für die Erneuerung und Reorganisation biologischer Systeme nach einschneidenden, nachhaltig verändernden Störungen. In einer zunehmend vom Menschen dominierten Umwelt ist dieser Aspekt von besonderer Bedeutung.

Zukünftige Naturschutzbemühungen werden sich zunehmend mit bereits gestörten Habitaten und dem Erhalt der darin befindlichen „Restbiodiversität“ auseinandersetzen müssen. Es ist daher umso wichtiger, genaue Kenntnis über Muster und Prozesse der Organisation biologischer Gemeinschaften unter Störungseinfluss zu haben, um die nötigen langfristigen Maßnahmen für eine sinnvolle Naturschutzkonzeption ableiten zu können.

Daher sollten besonders bei Untersuchungen der Struktur und Zusammensetzung biologischer Gemeinschaften, die in direktem Zusammenhang mit Naturschutzkonzeptionen und Naturschutzmanagementfragen stehen, funktionale Aspekte und höhere Ebenen der Biodiversität (z.B. auch β-Diversitätsmuster) berücksichtigt werden. Dies ist umso bedeutsamer, wenn z.B. der Verlust funktionaler Attribute einer Gemeinschaft zum Verlust von Ökosystemleistungen (*ecosystem services*) führt, die von essentieller Bedeutung für diese Systeme und somit von außerordentlicher Bedeutung für unser eigenes Überleben und Wohlbefinden sind.

Die Kernpunkte der Arbeit im Überblick

1. Die beobachtete multivariate Struktur der untersuchten tropischen Anurengemeinschaften wird nur im geringen Maße von biotischen Faktoren (hier direkte Konkurrenz) beeinflusst und ist somit nicht das alleinige Ergebnis vergangener oder aktueller interspezifischer Interaktionen. Die gefundenen Muster entsprechen vielmehr den Erwartungen des individualistischen Kontinuum Konzeptes, nachdem sich einzelne Arten entsprechend ihrer individuellen Bedürfnisse (*life-history*) unabhängig voneinander entlang eines Umwelgradienten gruppieren. Die so entstandenen Gemeinschaften stellen daher lediglich eine Ansammlung von Organismen dar, die zufällig den gleichen Lebensraum bewohnen. Starke stochastische Elemente in der Rekrutierung der die Gemeinschaften bildenden Arten und unvorhersagbare Umweltfluktuationen führen zu erhöhter Variabilität in der Zusammensetzung einer gegebenen Gemeinschaft.
2. Die Vorhersagbarkeitsmuster der Artenzusammensetzung der untersuchten Gemeinschaften unterscheiden sich in Abhängigkeit vom Störungsgrad des Habitats. Gemeinschaften primärer Waldhabitate sind ausschließlich aufgrund der geographischen Nähe einzelner Untersuchungsabschnitte zueinander vorhersagbar, folgen ansonsten aber eher stochastischen Organisationsprinzipien, in denen Prioritäts- und Lotterierekrutierungseffekte von großer Bedeutung sein können. Die Zusammensetzung von Gemeinschaften gestörter Waldhabitate lässt sich basierend auf der Ähnlichkeit spezifischer Habitatparameter vorhersagen. Diese Gemeinschaften folgen offensichtlich eher deterministischen Organisationsprinzipien. Starke lokale Filter ermöglichen es lediglich wenigen angepassten oder ubiquistischen Arten, stabile Populationen aufrechtzuerhalten.

3. Empirische Vorhersagbarkeitsmuster variieren sowohl gruppen-, als auch regionsspezifisch. Andere Segmente (funktionale Gruppen) der untersuchten Anurengemeinschaften (arborikole Anuren) folgten fast ausschließlich räumlichen Strukturierungsmustern. Diese Muster erwiesen sich als stabil und unabhängig vom Störungsgrad des untersuchten Habitats. Arten-Habitat-Assoziationen waren lediglich im Fall der südamerikanischen Primärwaldgemeinschaften für die Vorhersagbarkeit der Gemeinschaftszusammensetzung von Bedeutung.
4. Einzelne phylogenetisch durchaus verwandte Arten, zeigten artspezifische Reaktionen auf anthropogene Störungen, wie etwa selektiven Holzeinschlag. Die durch diese Störungen resultierenden strukturellen und mikroklimatischen Veränderungen des Habitats vermögen es, Larvalentwicklung und -mortalität einzelner Arten negativ zu beeinflussen. Dies hat natürlich weitreichende Folgen für das Überleben oder Aussterben lokaler Populationen.
5. Funktionale Komponenten der Biodiversität in den untersuchten Systemen erwiesen sich als bedeutsame Faktoren für die der Gemeinschaftsbildung zugrunde liegenden Prozesse. Die Zugehörigkeit einzelner Arten einer lokalen Gemeinschaft zu einer spezifischen funktionalen Gruppe, also ihre Identität, nicht jedoch die reine Anzahl von Arten (Systemfaktoren) scheint ausschlaggebend für die Vorhersagbarkeitsmuster der Gemeinschaftszusammensetzung zu sein.
6. Herkömmliche Biodiversitätsmaße, wie etwa Artenreichtum und – diversität, erwiesen sich als unzureichende Systemdeskriptoren und Indikatoren für anthropogene Habitatstörungen. Diese Maße lieferten inkoherente Muster und erwiesen sich als wenig sensitiv für funktionale Änderungen in biologischen Systemen. Vielversprechender waren in diesem Zusammenhang Maße, die funktionale Komponenten in der Analyse der Struktur von Gemeinschaften und ökosystemarer Prozesse berücksichtigen (Anzahl funktionaler Gruppen und funktionale Diversität). Diese Maße zeichneten ein realistischeres und stabileres Bild der tatsächlichen Veränderungen von Gemeinschaften unter Störungseinfluss.

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(Raffael Ernst)

Ehrenwörtliche Erklärung

gemäß §4 Abs. 3 Ziff. 3, 5 und 8
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Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt habe und keine anderen als die angegebenen Quellen und Hilfsmittel verwendet habe. Die Dissertation wurde bisher weder vollständig noch teilweise an einer anderen Hochschule mit dem Ziel, einen akademischen Grad zu erwerben, vorgelegt. Am 25.02.2002 wurde mir von der Universität Würzburg der akademisch Grad „Diplom-Biologe Univ.“ verliehen. Weitere akademische Grade habe ich weder erworben noch versucht zu erwerben.

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