Facing Complexity in Tropical Conservation: How Reduced Impact Logging and Climatic Extremes Affect Beta Diversity in Tropical Amphibian Assemblages

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Short Title: Beta diversity shifts in frog assemblages

ABSTRACT

Biodiversity in pristine forest biomes is increasingly disturbed by human activity. Drivers such as logging and climate extremes are thought to collectively erode diversity, but their interactions are not well understood. However, ignoring such complexities may result in poor conservation management decisions. Here, we present the first study dealing with the complexity arising from the effects of interactions of two increasingly important disturbance factors (selective logging and climatic extreme events) on beta diversity patterns at different scales. Specifically, we examined extensive amphibian assemblage datasets obtained within a quasi-experimental pre-/postharvesting scheme in the lowland rainforests of Central Guyana. Changes in small-scale patterns of beta diversity were not detectable at the higher landscape level, indicating that local-scale dynamics are more informative for evaluating disturbance impacts. The results also underscore the importance of including abundance data when investigating homogenization or heterogenization effects, which should be considered when designing post-logging impact assessments and selecting impact indicators. Moreover, logging should be regarded as a multifaceted driver that contributes to changes in biodiversity patterns in different ways, depending on interactions with other drivers. The effects of extreme climate events were significantly more pronounced in unlogged forest, while logged forest assemblages appeared buffered due to the presence of novel habitats. Imprudent post-logging renaturation measures may thus counteract conservation targets. These findings highlight the fact that indicator bias and unaccounted interactions between multiple drivers can lead to misguided management strategies.

Key words: forest certification; frogs; Guiana Shield; Guyana; indicator bias; interaction effects; novel habitats.

INTRODUCTION

TROPICAL FORESTS ARE PROBABLY AMONG THE MOST AFFECTED TERRESTRIAL ecosystems on our planet, and deforestation rates have reached unprecedented levels (Hansen et al. 2010, 2013). As primary habitats are dwindling at alarming rates, both ecologists and conservation practitioners have shifted their attention to humanmodified habitats (Putz et al. 2012, Laufer et al. 2013). For example, selectively logged forests retain substantial biodiversity, making them important targets for future conservation efforts (Barlow et al. 2007, Burivalova et al. 2014, Edwards et al. 2014). However, it is difficult to quantify their actual biodiversity values due to inherent difficulties associated with selecting appropriate measures and indicators and a lack of comparability across studies (Barlow et al. 2007, Gardner et al. 2009, Laufer et al. 2013). There is increasing consensus that the mere analysis of alpha (within-habitat) diversity is not sufficient for fully grasping the mechanisms and processes that drive local communities and ultimately shape diversity patterns at different scales (Su et al. 2004, Kessler et al. 2009, Imai et al. 2012). As a consequence, the analysis of beta diversity (the variation in species composition among sites) has become a key topic in ecology, biogeography, and evolution (Baselga et al. 2012, Beck et al. 2012, Al-Shami et al. 2013, Baselga 2013). This approach has been hailed as one of the most promising methods for quantifying the biodiversity of anthropogenic landscapes, aiding the efficient design of nature conservation areas (Barlow et al. 2007, Gardner et al. 2009, Anderson et al. 2011).

Human activities influence central processes in the assembly of biological communities and thus, beta diversity patterns. Resident species are often replaced by a small set of degradation-tolerant native and/or invasive non-native species (McKinney & Lockwood 1999, Lôbo et al. 2011, Baeten et al. 2012, Tabarelli et al. 2012). This process may ultimately lead to biotic homogenization (Olden & Poff 2003), which is considered the most dominant process shaping the future global biosphere (Lockwood & McKinney 2001). Yet, this process is likely driven by an eclectic set of factors.

Complexity introduced through multiple interacting drivers is often regarded as a nuisance that needs to be eliminated or controlled. However, community assembly is almost always affected by a combination of multiple environmental drivers that may interact to produce synergistic or opposing effects (Parmesan et al. 2011, Fox et al. 2014). It is not clear how this affects the frequently reported process of homogenization resulting from logging (e.g., Hamer et al. 2003, Gunawardene et al. 2010, Klimes et al. 2012, Kitching et al. 2013).

In our study, unlike other studies that were restricted to the analysis of a single environmental driver for practical and conceptual reasons (compare Laufer et al. 2013, Burivalova et al. 2014 and references cited therein), we approached this complexity by analyzing the impacts of two potentially synergistically interacting disturbance factors (selective logging and climatic extreme events) on beta diversity patterns of tropical anuran amphibian assemblages.

Climatic extremes are recognized as important drivers of ecological dynamics, which has increased interest in phenomena such as severe drought and extensive flooding (Hill et al. 2003, Slik 2004, Smith 2011). The effects of extreme climatic events are more pronounced in logged forests (Curran et al. 1999), implying that both factors interact positively and thus aggravate the negative impact on forest biota. To determine if beta diversity is an appropriate indicator of the effects of logging and extreme climatic events and their potential interactions on biodiversity, we analyzed amphibians, a suitable, sensitive organismal model system for analyzing the impacts of environmental change on community structure, composition, and diversity at different levels (e.g., Ernst et al. 2006, Ernst & Rodel 2008). Due to their peculiar biology (Wells 2007), amphibians should be particularly prone to the effects of both disturbance factors.

Within the scope of a rigorously standardized analytical framework, we investigated two related hypotheses: (1) Logging reduces beta diversity (increases homogenization) within logged sites (1st level beta diversity), which increases beta diversity (heterogenization) between logged and unlogged sites (2nd level beta diversity); both processes ultimately influence beta diversity at the landscape level (3rd level beta diversity). (2) Seasonal climatic extremes act synergistically by enhancing the effects of logging disturbance.

METHODS

STUDY AREA AND STUDY DESIGN.

We conducted the study within a strictly regulated polycyclic reduced impact logging (RIL) scheme in the Iwokrama Forest, Central Guyana (4°400 12″ N, 58°410 24″ W, Fig. S1; for exact locality map, see Figs. S2–S4). Harvesting follows a 60-yr felling cycle, with an annual allowable cut of 20,000 m3 and a maximum annual harvesting area of 1140 ha (unpubl. report Iwokrama Intl. Centre). From 2008– 2011, all harvesting activities were under the auspices of Forest Stewardship Council (FSC).

In total, we established 24 independent rectangular transects in three different localities (eight transects per site) across the forest landscape. Sites were pre-selected according to the Iwokrama forest zonation and harvesting plan (stratified random sampling design). Eight transects were in a site harvested in 2007, 2 yr prior to the start of our study (logged forest = LF, mean extraction volume 15.73 m3 /ha). The second set of eight transects was established within a site that was harvested in late 2010 (mean extraction volume 9.69 m3 /ha), 2 yr after the beginning of data acquisition. This site served as a pre-post harvesting impact assessment site (pre-/post-logged forest = PLF). The eight remaining transects were located within a non-impacted primary forest site excluded from any logging activities and served as a non-impact control site (unlogged forest = UF). While LF and PLF were of the same general forest type (Mixed Greenheart, Black Kakaralli, Wamara Forest), UF was in a different forest formation (Mora, Manicole, Crabwood, and Trysil, typical riparian forest).

We used a general standardized transect design modified after Rodel and Ernst (2004). To account for small-scale habitat heterogeneity, we adjusted the original design by reducing transect size and increasing transect number. We therefore reduced each rectangular transect to a north–south extension of 100 m and an east–west extension of 50 m, with 25 m subunits (SU) as the smallest sample unit (12 SUs/transect = 96 SUs per site = 288 SUs total). The minimum distance between transects was 112 m and the maximum distance was 17.2 km, with a mean distance of 1037 m between transects within sites.

The study area experienced an anomalously dry wet-season in 2009 and an unusually prolonged wet season in 2010, clearly demonstrated by comparison with previous years' precipitation data (Fig. S5).

DATA ACQUISITION AND PREPARATION.

We performed fieldwork between June 2009 and September 2011, during the main wet seasons. We generated species abundance data through standardized visual and acoustic transect sampling, following Rödel and Ernst (2004). We used relative abundances expressed as a timebased density measure (individuals per transect hour) for all species-related calculations.

We characterized each SU by recording a total of ten different environmental variables, again following the established protocol of Rödel and Ernst (2004) with modifications (see Table S1). Prior to analysis, we tested all originally recorded environmental variables for collinearity using Variance Inflation Factors (VIF) with a threshold of 3.0 as exclusion criterion. We thus reduced the original set of 10 variables to eight variables for 2009 and 2011 and six variables for 2010, respectively (Table S1).

We tested spatially structured environmental autocorrelation using Mantel test routines. Results indicated that transects should be chosen to represent the smallest sample unit in our species and environmental matrices to guarantee independence between samples (compare Ernst & Rodel 2005). Cell entries therefore represent pooled data from all SUs (12) per transect.

STATISTICAL ANALYSES.

Statistical analysis followed the general framework outlined in Fig. 1, with all analytical steps organized along the two overarching hypotheses. We addressed both hypothesis I (logging impacts) and hypothesis II (synergistic climate extreme impact) using identical statistical procedures. We assessed beta diversity using CqN multiple-assemblage overlap measure (Chao et al. 2008, 2012). This measure is a transformation of "true" beta diversity and therefore shares its mathematical properties, such as the independence from alpha diversity (Jost 2007, Chao et al. 2008, 2012). Furthermore, the measure is unaffected by the number of sampled communities (N) (Chao et al. 2008). Following these authors, we used the complement of CqN (1 CqN), which measures the relative differentiation between communities (0 = identical; 1 = distinct). The parameter q determines relative weights of rare versus abundant species, where increasing q corresponds to increasing weight assigned to abundant species. The cases q = 0, q = 1, and q = 2 are multiple-assemblage generalizations of the classical Sørensen, Horn, and Morisita-Horn measures. We validated all measures of CqN using bootstrapping routines (10,000 replicates) that yield standard errors.

We performed calculations of beta diversity at three different levels (Fig. 1B): between transects within each particular site (1st level beta diversity), pairwise between study sites using pooled transect data for each site (2nd level beta diversity), and between all transects across study sites (3rd level beta diversity). We illustrated differences in species composition between transects using non-metric multidimensional scaling (NMDS) ordinations. For NMDS calculations, we used distance matrices based on the complement of Horn's index, calculated using the vegetarian package in R (Charney & Record 2010) to guarantee comparability with Horn's CqN. Scree plot analyses indicated three dimensions as the optimal explanatory setting. We used a similarity profile permutation test (SIMPROF, Clarke et al. 2008) based on the complement of Horn's index to identify significant site groupings by superimposing significant SIMPROF clusters on NMDS plots. We ran the analysis with 10,000 generated similarity profiles and 9999 permutations to test the null hypothesis of no meaningful group structure.

To identify environmental factors that ultimately drive patterns of variation in assemblage composition, we applied Per(mutational) MANOVA (Anderson 2001, McArdle & Anderson 2001) on covariance-controlled environmental factors (Table S1). We allowed interactions among factors and calculated distance matrices based on the complement of Horn’s index. To compute P-values for Pseudo-F test statistics, we ran 9999 permutations. This approach is superior to related techniques, such as ANOSIM, because it uses actual dissimilarity coefficients rather than ranked dissimilarities, and the variation in response data can be explicitly partitioned according to complex designs, including interactions among factors (Martin et al. 2012).

We performed all statistical analyses using the packages vegan (Oksanen et al. 2012), vegetarian (Charney & Record 2010), clustsig (Whitaker & Christman 2010), and AED (Zuur et al. 2009) with R statistical software, v. 2.14.2, R Development Core Team (2012).

RESULTS

A total of 2628 frogs (2009: 545, 2010: 1024, 2011: 1059) belonging to 39 species and 11 families were recorded during 232.25 h of transect sampling (929 transect walks) across all study sites (see Tables S2 and S3).

LOGGING-INDUCED BETA DIVERSITY SHIFTS.

Shortly after logging, 1st level beta diversity showed a marked decrease (homogenization) in 2011, using the presence/absence-based dissimilarity of order $q = 0$ (PLF profile Fig. 2A.a). However, this trend was dramatically reversed (heterogenization) when increasing weight was given to abundant species ($q \geq 1$; PLF profiles Fig. 2A.b–d). Generally, 1st level beta diversity in the older logged site LF was above levels reached in PLF (both before and directly after logging). Only at order $q = 3$ (emphasis on superabundant species) did PLF (after logging) and LF approach identical dissimilarity levels (Fig. 2A.d). With the notable exception of the wet year 2010, 1st level beta diversity was generally higher in unlogged control sites, regardless of the relative weight given to abundant species (UF profiles Fig. 2A.b–d). Only at order $q = 0$ did both UF and LF reach identical levels in 2011 (Fig. 2A.a). UF exhibited the greatest inter-year dynamics for all orders of q (compare UF, LF, and PLF variation over time, Fig. 2A.a–d).

Dissimilarity between newly logged and unlogged sites (2nd level beta diversity) in 2011 only increases (heterogenization) when weight is given to abundant species (PLF/UF profile at q = 2, Fig. 2B.c). This trend is canceled out when superabundant species are emphasized (PLF/UF profile at q = 3, Fig. 2B.d). While the dissimilarity between logged and pre-/post-logged forests is generally lower than between either of these sites and unlogged forests, regardless of the order of q (compare LF/PLF profile with UF profiles, Fig. 2B.a–d), the two logged sites exhibited an additional decrease in beta diversity at orders q = 1 and 2 in 2011 (after logging in PLF, Fig. 2B.b–c). Combinations including UF again showed higher inter-year dynamics (Fig. 2B). Landscape level beta diversity (3rd level beta diversity) remained constant from 2010 to 2011 and generally increased with increasing q (calibration curve “Combined,” Fig. 2B.a–d).

ENVIRONMENTAL DETERMINANTS OF COMPOSITIONAL SHIFTS.

The ordination of transects in species space and subsequent SIMPROF validation yielded significant results in only two cases (2010 & 2011). Patterns retrieved for 2009 were not distinguishable from random patterns (NMDS stress > 0.2, no significant cluster distinction in SIMPROF). For 2010, NMDS produced two clearly separated groups (VG1–VG2, P = 0.001) that mainly separated unlogged forest transects (UF) from logged (LF) and pre-/post-logging (PLF) transects prior to logging in PLF, indicating a higher concordance between LF and PLF (compare VG1 vs. VG2, Fig. 3A). UF exhibited a distinct yet not unique species assemblage, with three LF transects falling in the same group (VG2, Fig. 3A). In 2011, community structure shifted significantly, resulting in the formation of six clearly separated groups (VG1–VG6, P = 0.001, Fig. 3B). The unlogged forest site (UF) currently exhibits a distinct within-site differentiation, with two groups markedly separated from LF and PLF in species space (VG 1 & VG 3, Fig. 3B). Transects in LF and PLF (after logging) fell into four clearly separated groups (VG2 & VG4– VG6, P = 0.001, Fig. 3B), representing composites of both LF and PLF (VG 2 & VG 4) and unique site-specific groupings (VG6: LF, VG5: PLF).

Compositional shifts in assemblages were partly explained by environmental determinants. The PERMANOVA results show that environmental variables explained 49% of the variation in species composition in 2009 (only four contributing variables) even though NMDS did not produce significant non-random patterns, 63 percent in 2010 (five contributing variables), and 70 percent in 2011 (six contributing variables and one interaction term), respectively. In all cases, logging-related variables (Artificial lentic water bodies: ART, Canopy Openness: Copen, Skid roads: Skid) contributed to the variation, with more than half of the total variance explained; ART was the most important of these factors (Table 1).

EFFECTS OF CLIMATIC EXTREMES.

Effects of two different extreme climatic events (severe drought in 2009 and severe flooding in 2010) were detected, with varying consequences to 1st level beta diversity in different sites (LF & PLF vs. UF). In the case of LF (logged forest) and PLF (pre-/post-logged forest), this also depended on the order of q (weight given to abundant species). General patterns remained congruent across all orders of q in UF and across $q > 0$ in LF & PLF.

Although the drought of 2009 resulted in initially low 1st level beta diversity, with subsequent increases after the exceptionally wet year of 2010 in both LF and PLF (heterogenization, with $q > 0$, Fig. 2A.b–c), the opposite was true for unlogged forests (profiles of UF at all orders of q, Fig. 2A.a–d). The most severe effects of the climatic anomalies on diversity pattern shifts were observed in UF (compare UF between years, Fig. 2A).

Pairwise dissimilarity for 2nd level beta diversity reflected these patterns (Fig. 2B). While the 3rd level beta diversity remained constant in 2010 and 2011, it was slightly higher for $q \leq 1$ in 2009 (calibration curve “Combined” Fig. 2B.a–d).

DISCUSSION

Our analysis of beta diversity patterns and subsequent mechanistic explanatory approaches proved to be sensitive for detecting both single and multi-driver impacts and their potential interactions. Three important patterns emerge: (1) to detect homogenization or heterogenization processes following disturbance events, it is crucial to differentiate between different beta diversity components (weighting rare vs. abundant species). For the presence/absence-based dissimilarity measures, there is a tendency to detect homogenization at local scales (1st level beta diversity) and to a lesser extent at regional scales (2nd level beta diversity), while abundance-based measures tend to detect heterogenization processes. (2) Focusing on large-scale dynamics ignores important local-scale dynamics that are more informative in terms of evaluating disturbance impacts. In our study, dramatic 1st and 2nd level beta diversity pattern changes were not detectable at the landscape level, that is, 3rd level beta diversity remained basically unchanged throughout the study period, regardless of the weight given to rare versus abundant species. (3) Addressing interactions between different drivers of beta diversity change is crucial, but the results can be counterintuitive. Two seemingly synergistic drivers, each previously reported to have negative impacts on biodiversity, may turn out to generate potentially mitigating rather than enhancing effects when interacting under specific circumstances. Moreover, our analyses clearly showed that logging disturbance is a multifaceted driver composed of factors that contribute to biodiversity pattern changes in different ways.

EFFECTS OF LOGGING: HOMOGENIZATION VERSUS HETEROGENIZATION.

Studies addressing beta diversity shifts, that is, homogenization and heterogenization, in human-modified tropical landscapes suggest that these processes are largely scale dependent (Keil et al. 2012, Arroyo-Rodrıguez et al. 2013). Our results support this notion, as patterns observed at local scales did not reflect patterns observed at higher scales (incongruence between 1st, 2nd, and 3rd level beta diversity). However, our results are even more alarming from a management perspective because they highlight the fact that scale dependency is not the only decisive factor: patterns observed when stressing species presence/absence components of beta diversity differed from those observed when abundances are given increasing weight (incongruence between orders of q in multipleassemblage dissimilarity profiles). While a role has been acknowledged for local-scale processes in setting upper limits of species accumulation and thus for determining beta diversity in disturbed landscapes (Flohre et al. 2011), the importance of different beta diversity components in detecting such disturbance-induced processes had not been tested systematically. Our results demonstrate these dependencies clearly.

Shifts in the abundance of a species usually occur faster than extinctions that may come after (extinction debt sensu Tilman et al. 1994). Detecting these early shifts can therefore be crucial when the aims are (1) to implement immediate post-impact measures designed to maintain or restore the ecosystem, its biodiversity, resources, and landscapes (compare FSC Principle 6 & 7, FSC 2012) and (2) to guarantee post-impact monitoring assessments that demonstrate progress toward the original management objectives, with the ultimate goal of maintaining high conservation value forests (compare FSC Principle 8 & 9, FSC 2012).

Processes that shift abundance are crucial to understanding actual impacts in our study system. Observed heterogenizations are mainly due to abundance shialthgoufts in two leptodactylid species, Leptodactylus petersii and Physalaemus ephippifer, whose abundance increased in sample units containing newly created artificial breeding sites (water-filled skid roads) used as alternative reproductive habitats. The creation of novel aquatic habitats has previously been shown to affect population sizes in neotropical hylid frogs (Tocher et al. 2001). However, our results clearly show that these artificial habitats can alter the organization of entire communities and therefore, beta diversity patterns. Changes in the dominance of particular species also directly affect important biotic interactions, such as competition and trophic interactions (Tylianakis et al. 2008). Even short-term changes can therefore influence important ecosystem processes in the long run.

Although shifts in the abundance of particular species and dispersal of resident species across the disturbed matrix are detectable shortly after logging, colonization processes can only be observed over longer time spans. When looking at longer term impacts (2–4 yr after logging), we found beta diversity to be generally higher than in recently logged sites. In the wet year of 2010, beta diversity in older recovery stages was higher than in unlogged forest, resulting from selective invasion processes of (1) species recruited from regional forest species pools and (2) additional invasions by non-forest species, along with (3) long-term abundance increases of resident species. Divergent patterns between the different disturbance stages are therefore a result of individually varying species' responses and different time spans since logging. Eventually, extinction-replacement processes resulting from the colonization and invasion of pre-adapted species become operable. These species may subsequently increase in both frequency and abundance. While accounting for taxonomic changes is important, it neglects more subtle yet potentially important patterns at the community functional level. The winners and losers of these replacement processes are usually not randomly distributed (Ernst et al. 2006). Instead, invasion success and vulnerability are defined by the interaction between intrinsic species traits and extrinsic environmental characteristics (Olden et al. 2004). Environmental filtering processes contribute to these dynamics (compare Ernst et al. 2012) and may be an important element in biotic homogenization (Karp et al. 2012). This pattern deserves more attention and needs to be addressed using a refined approach aimed at correlating heterogenization and homogenization processes at the taxonomic level with those at the functional and phylogenetic level.

CLIMATIC EXTREMES AND LOGGING – INDEPENDENT EFFECTS AND INTERACTIONS.

Habitat modification and climate change have both opposing and synergistic effects on the temporal and spatial frequency and occurrence of organisms, with both drivers acting independently as well as in combination (Fox et al. 2014). This can also be said for the major factors (logging and climatic extreme) driving biodiversity patterns in our study system, with the caveat that the response variable of interest was beta diversity.

The independent effect of the observed climatic anomalies was most prominently demonstrated by the unexpected response of our unlogged riparian forest (UF) assemblages. Here, beta diversity was highest during the extreme drought phase, while it decreased tremendously during the extreme flooding phase. Beta diversity in logging control sites (LF), on the other hand, remained stable across the study period, indicating no independent effect of the climatic extremes. At the same time, this value increased in pre-/post-logging forest (PLF) prior to logging but shortly after the drought phase. The key to explaining these seemingly contradicting patterns is the differences in water availability between sites. While UF represents a dynamic riparian forest in which water availability is influenced by regular flooding events and aquatic habitats are normally not limited, our PLF site is located in mixed forest not directly influenced by the dynamics of larger lotic systems. Here, aquatic habitats are naturally rather limited. Under natural conditions (i.e., without disturbance), the two forests therefore represent opposing ends of a continuous gradient of water availability. The importance of forest type in determining alpha diversity patterns in selectively logged forests was demonstrated in African leaf litter anurans (Ofori-Boateng et al. 2013), but this cannot fully explain the beta diversity patterns observed in our study system. During extended dry periods, the availability of aquatic habitats is much more limited in unlogged versus logged forest sites. In the latter, artificial water bodies act as surrogates for dried out natural aquatic sites. These artificially created habitats also tend to be larger and more permanent, even under severe water stress. In unlogged forest, a reduced subset of species tends to aggregate at the few remaining reproductive sites during drier periods. These sites are not homogenously distributed across the forest matrix. As a result, beta diversity increases (heterogenization). In wetter years, the availability of aquatic sites is not limited. An extended set of species disperses more or less freely across the matrix, causing a significant decrease in beta diversity (homogenization).

While fluctuations are more extreme in pristine riparian forest assemblages, they do show high resilience. However, prolonged extreme conditions that persist over several population cycles may put the viability of entire populations at serious risk and pave the way for a tipping point (Lenton 2011), beyond which a return to initial conditions becomes impossible. The occurrence of extreme anomalies will likely increase and become more intense in the future (Cox et al. 2008, Gloor et al. 2013). This could have lasting negative effects on amphibian populations in the primary lowland rainforests of the Guiana Shield and elsewhere, ultimately affecting entire communities and ecosystems.

While it was suspected that severe drought conditions would enhance the negative effects of logging on anuran diversity, the unique combination of a severe drought and the presence of novel breeding habitats resulted in a somewhat paradoxical situation. Amphibian communities in previously disturbed areas are in fact buffered against further decay in diversity from extreme climatic events, which presents an unexpected managementconservation conflict. An integral part of the codes of practice for sustainable timber harvesting is the renaturation of impacted habitats (compare GFC 2002). This includes the removal of ruts on any kind of logging road once operations have ceased. However, under the outlined conditions, these artificially created habitats may increase resilience of the system and therefore aid post-logging recovery of amphibian assemblages. This novel situation needs to be taken into account when designing post-logging management strategies.

Both opposing and synergistic effects of two interacting drivers have previously been reported, but the synergistic effects have usually been found to be enhancing (Laurance & Useche 2009, Schweiger et al. 2010, Fox et al. 2014) rather than mitigating. However, logging and drought can be regarded as an additive filter, “selecting” only for species that have pre-adaptations that allow them to cope well with these novel environments while filtering out others that decline or even go extinct. In the long run, this may result in the loss of functional diversity (compare Ernst et al. 2006).

CONCLUSIONS

As pristine forest biomes are continuously being disturbed (Asner et al. 2009), the importance of modified or secondary habitats for retaining and preserving biodiversity increases (Edwards et al. 2014). It therefore becomes ever more important to apply scientifically sound and sensitive methods and techniques to a) assess the impacts of these activities on forest biodiversity and b) meet the international strategic biodiversity targets laid out in the various action plans issued by the CBD and its signatory states. The “multiple drivers/multiple diversity components approach” proposed here could be a vital step for conservation biologists and practitioners. This approach is sensitive for detecting impacts at different scales, and it has the power to reveal potential management conflicts. Our approach can thus help shape, remodel, and improve strategies currently implemented in various selective logging and certification schemes (e.g., FSC Principles, FSC 2012). Moreover, the conceptual framework can easily be adapted to take into account other important diversity elements pertaining to possible ecosystem functions and services (compare Ernst et al. 2012, Bassler et al. 2014). Facing this complexity and disentangling the interplay of different drivers that ultimately affect biodiversity across both intact and modified landscapes over longer time periods in threatened habitats represents a major frontier in applied ecology and conservation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Locality map showing study region and site location.

FIGURE S2–S4. Exact locality maps of study site showing transect location.

FIGURE S5. Precipitation diagram for study site and detailed information about weather phenomena in 2009 and 2010.

TABLE S1. List of environmental variables.

TABLE S2. Full species list.

TABLE S3. List of observed species richness per site and year.

TABLE S4. Bootstrapped CqN – measures for 1st, 2nd, and 3rd level beta diversity.

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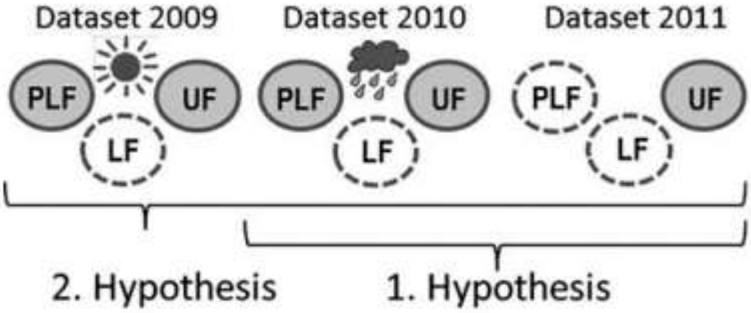
Figures

Figure 1: (A) Datasets and how they were used to test the overarching hypotheses. Sun represents the severe drought year, cloud the year with exceptional rainfall, dashed lines indicate logged sites, continuous lines unlogged sites. LF, logged forest; PLF, pre-/post-logged forest; UF, unlogged forest. (B) transects per site and respective data allocation to beta diversity analyses at different levels.

(a)



(b)

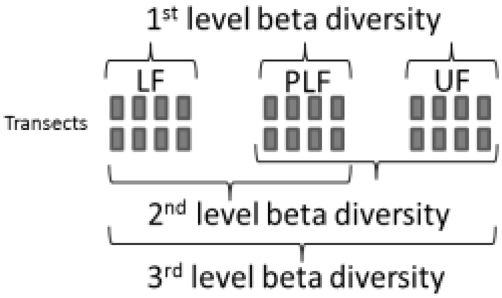
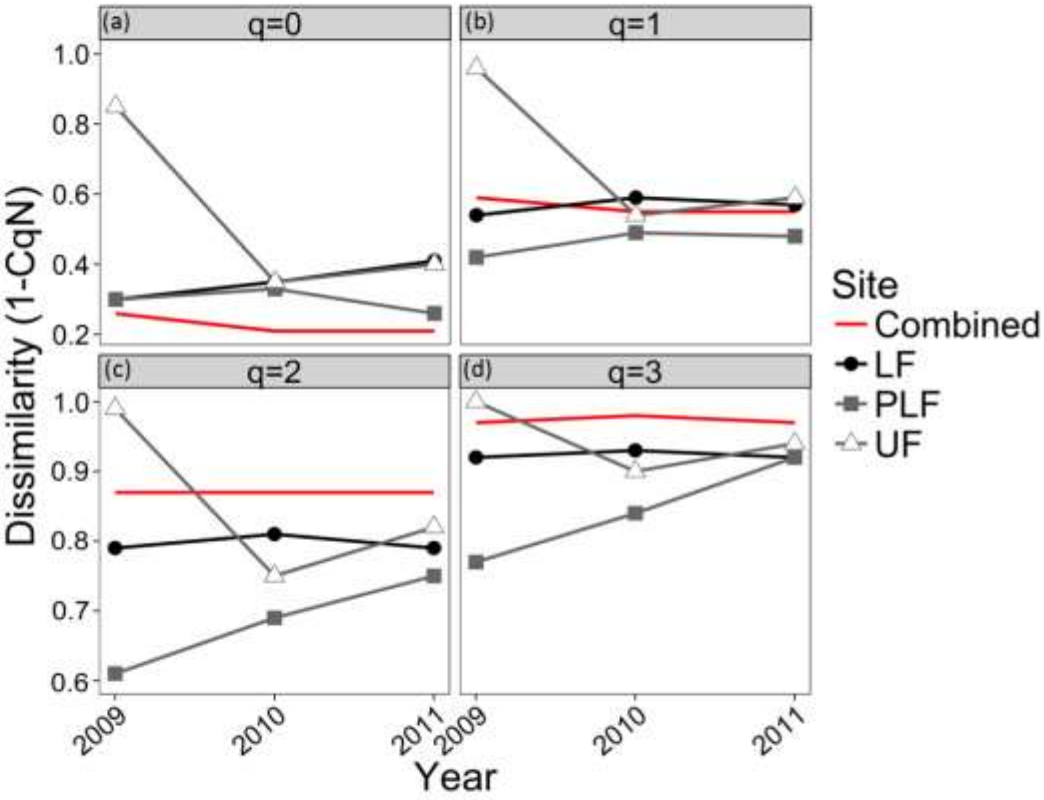


Figure 2: (A) 1st level beta diversity (1-CqN) calculated between transects within sites. (B) 2nd level beta diversity (1-CqN) for pairwise comparisons between sites across years, both calculated with different relative weights given to rare versus abundant species, where increasing q = increasing weight assigned to abundant species. Red line represents 3rd level beta diversity, given as the overall spatial calibration curve (total variability per year). Changes in trends were validated using bootstrapping routines (10,000 replications). To improve readability, standard errors are not shown (see Table S4)



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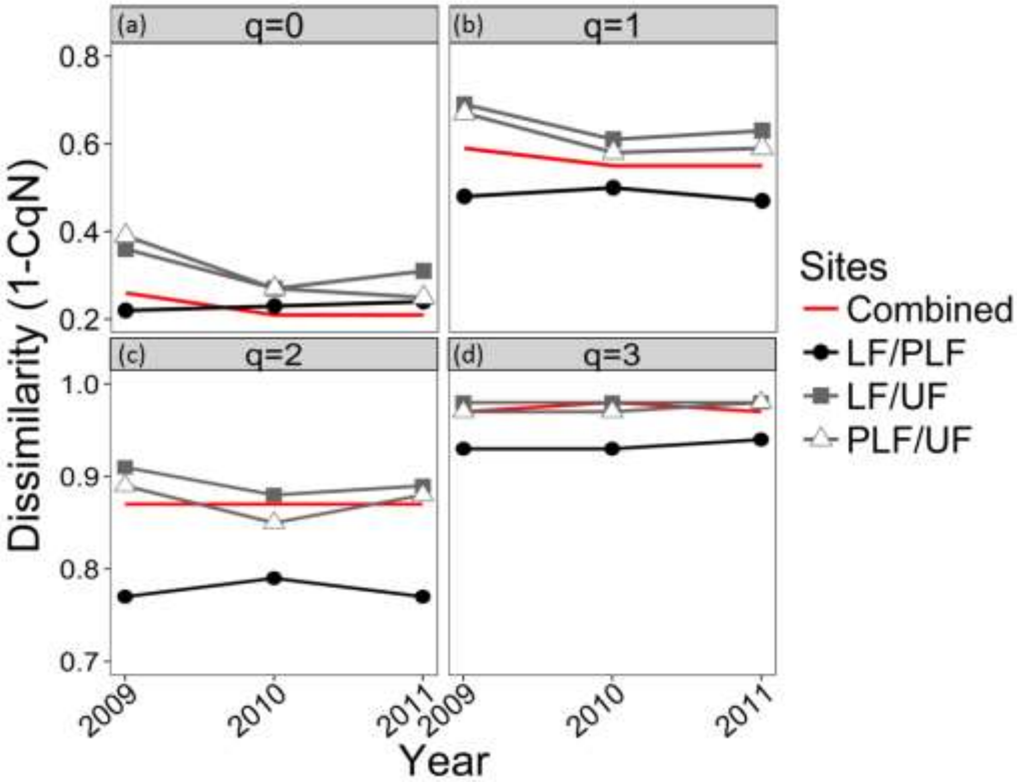

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Figure 3: Non-metric multidimensional scaling (NMDS) based on the Horn index, depicting compositional differences between transects. (A) 2010 dataset. (B) 2011 dataset. 2009 not shown (low stress value). Only two dimensions are given to facilitate interpretation. Significant SIMPROF validated groups (P = 0.001) are represented by different colors. Different symbols represent different study sites. VG, validated group; I-II, transects that do not significantly cluster in any group; LF, logged forest; PLF, pre-/post-logged forest; UF, unlogged forest.

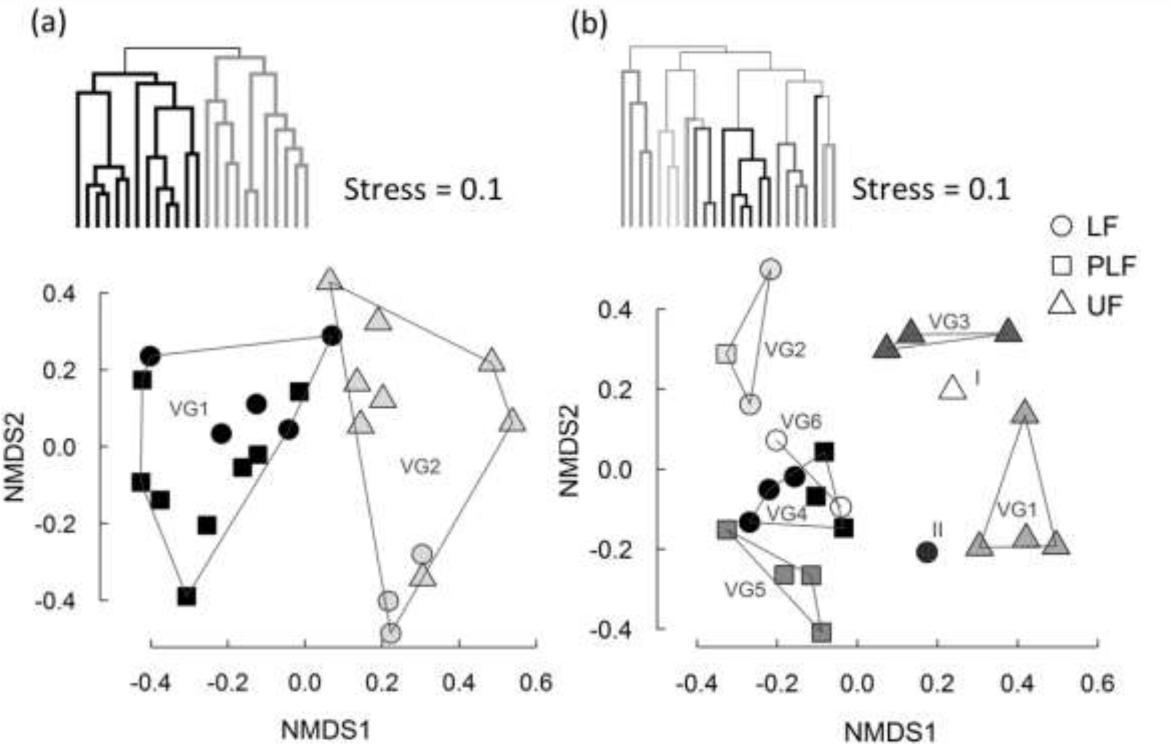

Figure legends

Fig. 1. (A) Datasets and how they were used to test the overarching hypotheses. Sun represents the severe drought year, cloud the year with exceptional rainfall, dashed lines indicate logged sites, continuous lines unlogged sites. LF, logged forest; PLF, pre-/post-logged forest; UF, unlogged forest. (B) transects per site and respective data allocation to beta diversity analyses at different levels

Fig. 2. . (A) 1st level beta diversity (1-CqN) calculated between transects within sites. (B) 2nd level beta diversity (1-CqN) for pairwise comparisons between sites across years, both calculated with different relative weights given to rare versus abundant species, where increasing q = increasing weight assigned to abundant species. Red line represents 3rd level beta diversity, given as the overall spatial calibration curve (total variability per year). Changes in trends were validated using bootstrapping

routines (10,000 replications). To improve readability, standard errors are not shown (see Table S4).

Fig. 3. Non-metric multidimensional scaling (NMDS) based on the Horn index, depicting compositional differences between transects. (A) 2010 dataset. (B) 2011 dataset. 2009 not shown (low stress value). Only two dimensions are given to facilitate interpretation. Significant SIMPROF validated groups (P = 0.001) are represented by different colors. Different symbols represent different study sites. VG, validated group; I-II, transects that do not significantly cluster in any group; LF, logged forest; PLF, pre-/post-logged forest; UF, unlogged forest. **Fig. 4.** Non-metric multidimensional scaling (NMDS) based on Horn index, depicting compositional differences between sample units. (a) 2010 data set (b) 2011 data set. 2009 not shown (n.s. extremely low stress value). Only two dimensions are given to facilitate interpretation. Significant SIMPROF validated groups (*P* = 0.001) are represented by different colours. Different symbols represent different study sites. VG = validated group, I-II = transects that do not significantly cluster in any group, LF = logged forest, PLF = pre-/post logged forest, UF = unlogged forest.

Tables

Table 1 Results of Per(mutational) MANOVA showing contribution of environmental variables to variability in amphibian assemblage composition

Variable	df	Sums Sqs	*F*-Model	R^2	P-value[a]
2009					
NAT [b]	1	1.576	6.914	0.221	0.0001**
FType[c]	1	0.793	3.478	0.111	0.002*
ART[d]	1	0.582	2.554	0.082	0.006*
Copen[e]	1	0.569	2.495	0.080	0.001*
Residuals	11	2.507		0.352	
Total	20	7.120		1.000	
2010					
FType	1	1.743	10.321	0.208	0.0001 **
ART	1	1.336	7.913	0.159	0.0001 **
NAT	1	0.889	5.263	0.106	0.0001 **
Copen	1	0.678	4.017	0.081	0.0004 **
LOT[f]	1	0.390	2.312	0.068	0.0224 *
Residuals	15	2.533		0.302	
Total	23	8.387		1.000	
2011					
FType	1	1.924	12.520	0.228	0.0001 **
NAT	1	1.269	8.261	0.151	0.0001 **
ART	1	0.797	5.185	0.095	0.0001 **
Skid[g]	1	0.603	3.927	0.072	0.001*
LOT	1	0.444	2.890	0.053	0.005*
Copen	1	0.396	2.575	0.047	0.009*
ART x Skid	1	0.377	2.452	0.045	0.018*
Residuals	11	1.909		0.227	
Total	23	8.428		1.000	

[a] Only significant results shown at *$P < 0.05$ and **$P < 0.001$.

[b] Natural lentic water bodies.

[c] Forest type.

[d] Artificial lentic water bodies.

[e] Canopy openness.

[f] Lotic water bodies.

[g] Skid roads.