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The value of forest fragments for maintaining amphibian diversity in Madagascar

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ABSTRACT

Forest fragmentation often causes biodiversity loss, but there is no consistent pattern on species' reactions. Considering the alarming rate of deforestation in the tropics, and the fact, that large areas of protected continuous forest are limited, it becomes increasingly important to determine the biodiversity value of fragmented forests. In order to investigate fragmentation effects on rainforest frogs in Madagascar and to assess the conservation value of these fragments, we analyzed amphibian diversity in a continuous rainforest and nearby forest fragments. We hypothesized that species richness is lower in fragments compared to continuous forest, and that fragmentation leads to altered assemblage composition. We found no fragmentation effects on species richness, demonstrating that fragments may maintain local species richness comparable to continuous forest. The presence of streams was the most important factor for high species richness, independent of fragmentation status. However, we detected fragmentation effects on species composition. As expected, several species were restricted to continuous forest, but many species occurred in both forest types, and some species were only found in fragments. Rainforest amphibians in our study area were less sensitive to fragmentation than expected. Adaptations to natural disturbances like cyclones could be one reason to explain this. However, as some species exclusively occurred in continuous forest and species composition differed between continuous forest and fragments, we conclude that fragments cannot substitute continuous forest blocs, but are generally important for maintaining amphibian diversity in Madagascar, especially if they comprise streams. Forest fragments should hence be included in conservation planning.

1. Introduction

Habitat loss and fragmentation are major threats to biodiversity (Dirzo and Raven, 2003). Forest fragmentation is a process resulting in the decrease of total habitat amount, an increasing number of smaller-sized and isolated habitat patches, and an increasing ratio of edge to interior habitat. Generally, forest fragments exhibit severe ecological changes including species extinctions and altered ecosystem functions (Laurance et al., 2011). However, reactions to anthropogenic habitat alterations and fragmentation can differ markedly between species, taxonomic groups and ecosystems (Fahrig, 2003; Gardner et al., 2009; Irwin et al., 2010; Laurance et al., 2011).

Deforestation in the tropics proceeds at an alarming rate (Hansen et al., 2013). Protected areas are limited in area and connectedness, and their current coverage fails to protect overall global biodiversity including numerous threatened species (Rodrigues et al., 2004). The forest cover outside protected areas has declined markedly in tropical forests since the 1980s (DeFries et al., 2005). Considering the ongoing agricultural expansion in the tropics (Laurance et al., 2014), it can be assumed that fragmented forest will become the dominant forest type in human altered tropical landscapes in the future. To be able to maintain overall tropical biodiversity in the long-term, it is hence essential to determine the biodiversity and conservation value of human-modified landscapes (Daily, 2001; Gardner et al., 2009; Irwin et al., 2010). So far, most attention has been drawn to secondary habitats. There is increasing evidence that secondary forests and fragments may have the potential to contribute to biodiversity conservation (Barlow et al., 2007; Gillespie et al., 2012; Mendenhall et al., 2014). However, there is still a considerable lack of knowledge concerning the degree to which tropical biodiversity can persist in human-modified landscapes (Gardner et al., 2009).

More than one third of extant amphibian species are currently considered threatened (Stuart et al., 2004). Various, often interacting factors have been identified as causes of this global amphibian crisis, habitat loss and alteration belonging to the most severe causes (Sodhi et al., 2008; Stuart et al., 2004). Accordingly, the majority of fragmentation

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studies addressing amphibians so far revealed negative effects on their diversity (e.g., Bell and Donnelly, 2006; Cabrera-Guzmán and Reynoso, 2012; Vallan, 2000). However, increased amphibian diversity in forest fragments has also been observed (Tocher et al., 1997).

Madagascar is one of the world's biodiversity hotspots with an outstanding degree of endemism (Myers et al., 2000). Amphibian species richness, including many so far undescribed candidate species, is expected to comprise up to 465 native and endemic species (Vieites et al., 2009). Madagascar's rich and unique ecosystems are threatened by high rates of deforestation and the remaining forest cover is highly fragmented (Green and Sussman, 1990; Harper et al., 2007). A recent review of species' responses to anthropogenic disturbances in Madagascar revealed that overall very little is known and responses differ even within lower taxonomic levels and between ecoregions (Irwin et al., 2010).

Our study aims to contribute to a better understanding of the response of highly diverse tropical amphibian assemblages to habitat fragmentation for the implementation of future conservation strategies with special emphasis on the conservation value of forest fragments. We examined patterns of amphibian diversity in a continuous rainforest and nearby forest fragments to reveal fragmentation effects on rainforest frogs in Madagascar. A fragmented landscape where a relatively large continuous forest part that can act as control site is still present is an ideal model system to learn about the value of forest fragments as amphibian habitats. In particular, we compared species richness between forest fragments (<20 ha) and continuous forest (non-fragmented area of Ranomafana National Park, >40,000 ha), and evaluated patterns of assemblage composition in both forest types. We investigated stream and terrestrial habitats to equally account for stream depending species (either semiaquatic or stream breeding species) and for species that are completely independent from running waters. We hypothesized for both habitat types that 1) species richness is lower in forest fragments compared to continuous forest, and that 2) fragmentation leads to altered assemblage composition in forest fragments.

2. Material and methods

2.1. Study system

Field work was conducted in the Ranomafana National Park (RNP, 21°02′–21°24′S, 47°20′–47°35′E), East Madagascar, and in forest fragments located east of RNP (Fig. 1). RNP comprises 43,500 ha of continuous mid-altitude montane rainforest (500–1300 m a.s.l.) with an annual precipitation between 1700 and 4300 mm (Wright and Andriamihaja, 2003). It provides most of the remaining rainforest habitat in the Ranomafana region. The remaining forest fragments around RNP are embedded in a matrix of cultivated land (slash and burn agriculture; "tavy"), clear cut, and secondary bush and shrub vegetation. We chose nine different forest fragments that range in size between two and 16.5 ha (Fig. 1, Appendix A). Five forest fragments comprise streams, including one fragment with two streams. Aerial photographs from 1950 showed that all but two of the studied fragments were separated from continuous forest by that time already and interviews with local people revealed that all studied fragments were at least 50 years separated from RNP.

The Ranomafana region corresponds to one of the centers of amphibian diversity within Madagascar with almost 120 taxa known (Glaw and Vences, 2007; Vieites et al., 2009; own unpubl. data).

2.2. Sampling design

We determined species richness and composition on transects distributed along streams and in terrestrial forest parts inside RNP and forest fragments. We included stream and terrestrial habitats to equally account for stream depending species (either semiaquatic or stream breeding) and for species that reproduce independent from streams (i.e., phytotelmata, pond or terrestrial breeders). As not all studied fragments comprise streams, data from stream and terrestrial transects were analyzed separately. In the following, we refer to stream and terrestrial transects as habitat types, and continuous forest and forest fragments as forest types.

We established a total of 38 independent line transects (50×2 m; Marsh and Haywood, 2010): 22 transects were located inside RNP (control sites) and represented continuous forest (terrestrial: 11, streams: 11), and 16 transects were spread over nine different forest fragments (terrestrial: 10, streams: 6). Following the sampling scheme of terrestrial transects (searching a band of 2 m width), stream transects included one meter riparian vegetation on each stream bank in addition to the water body. Terrestrial transects were at least 50 m apart from the next stream. We kept a minimum distance of 200 m between transects of the same habitat type, and stream transects had no direct upstream connections. Transects were geographically spread over RNP as far as possible according to accessibility and logistic constraints to control for geographic distances between fragments and transects located within RNP. Transects inside forest fragments followed the topography of the respective fragment and were initially at least 50 m apart from the next forest edge, except two stream transects that were about 25 m from the next forest edge.

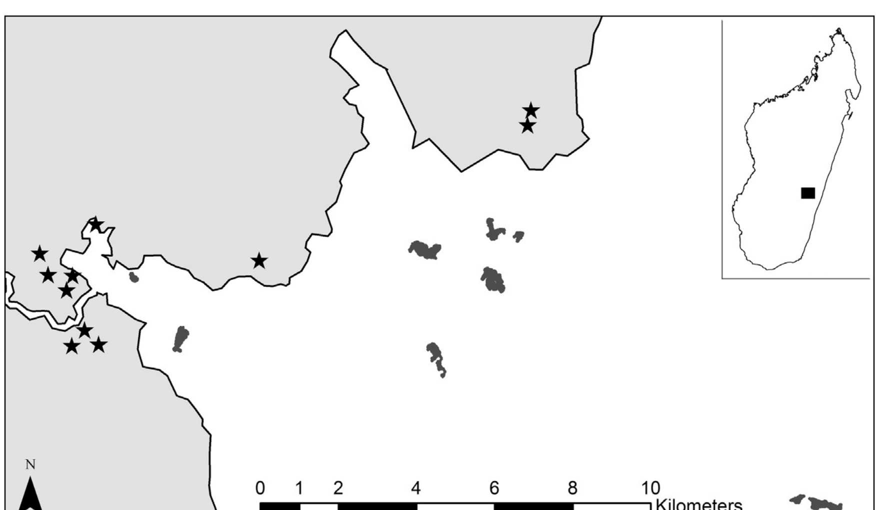

Fig. 1. Schematic view of the study area and its position on Madagascar (insert). Shown are study sites (black stars) inside Ranomafana National Park (gray area; black line: park border) and studied forest fragments (dark gray areas).