Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes

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ARTICLE INFO

ABSTRACT

Fragmentation and habitat loss contribute considerably to global declines of amphibians and reptiles. However, few studies focus on forest edges, created during the fragmentation process, as proximate drivers of the local demographic structure of populations. Here, we use abundance data of amphibians and reptiles to study their responses to forest edges in nine fragmented forested landscapes of the Neotropics. Species-specific abundance data were collected in plots established at varying distances from their respective nearest forest edge. We tested for edge effects on the abundance of species, and used curve clustering techniques to group species with similar edge responses, i.e. species with either increasing or decreasing abundance from the matrix towards the forest interior. We also grouped species that showed no change in abundance with respect to the nearest forest edge and those whose abundance response was unimodal, peaking in either forest habitat or the surrounding matrix habitat. We found that 96% of all amphibians and 90% of all reptiles showed an edge response, with the abundance of 74.5% of amphibians and 57.3% of reptiles decreasing with increasing proximity to forest edges. However, species-specific edge effects were not always consistent, with some species having opposite edge responses when measured in different landscapes. The depth of edge effects exhibited by forest species, i.e. species that increased in abundance in the forest interior, extended up to one kilometre away from forest edges. We show that the median edge effect on forest species extends to 250 m within the forest interior, indicating that tropical forest patches with a mean diameter < 500 m (minimum area ≈ 78 ha) are unsuitable for half of forest-dependent species considered in this study.

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1. Introduction

Forest fragmentation acts on top of forest loss, as continuous forest habitats are broken up into increasingly smaller forest patches that are becoming increasingly isolated from each other (Fahrig, 2003). Fragmentation ultimately results in edge-dominated forest fragments, thereby edges or boundary zones differ structurally and functionally from both the original forest and the surrounding non-forest matrix (Saunders et al., 1991; Murcia, 1995; Cadenasso et al., 1997; Harper et al., 2005). Boundary zones are characterised by abiotic gradients such as wind, temperature or radiation and water fluxes (Didham, 2010), which cause first-order biological changes including altered species composition, distribution and abundance (Holt and Keitt, 2005; Ewers and Didham, 2006a). These biotic effects result in second-order biological changes, such as changes in trophic interactions (Fagan et al., 1999; Holt and Keitt, 2005) and parasitism (Schlaepfer and Gavin, 2001). Both abiotic gradients and biotic changes are examples of ecological phenomena grouped together under the broad concept of "edge effects".

Edge effects can be quantified by their magnitude, i.e. the difference between the lowest and the highest value of a variable measured across a forest edge, and by their extent, i.e. the distance over which the change can be detected (Ewers and Didham, 2006b). Both measures may vary with the quality of the matrix and forest habitat, the latter depending for example on structure and age of the forest patch, shaping the spatially variable patch-matrix contrast (Laurance et al., 2011).

Species respond to the edge differently depending on life history traits, including those linked to habitat specialisation, body size and

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dispersal capacity (Saunders et al., 1991; Ewers and Didham, 2006a; Stork et al., 2009). Specialisation allows species to adapt to micro-environments as specialized species have a narrower niche breadth, but it can exacerbate the effect of habitat loss (Houlahan and Findlay, 2003; Williams et al., 2008). Indeed, it may render species more vulnerable to habitat changes because forest fragmentation can reduce the probability that the species and its niche are both maintained in the remaining forest fragments (Harris and Silva-Lopez, 1992; Henle et al., 2004). Larger-sized animals are reportedly been more sensitive to fragmentation (Crooks, 2002; Henle et al., 2004; Pineda and Halffter, 2004), although empirical studies report a range of responses (e.g. Suazo-Ortuno et al., 2008; Mendenhall et al., 2014). Dispersal capacity affects the species ability to travel through suboptimal habitats, less able to provide resources or protection from predators, e.g. low tree cover matrix habitat for forest species (McGarigal and Cushman, 2002).

Biodiversity responses to anthropogenic land use changes are often analysed as species extinctions following habitat loss (Wearn et al., 2012). However, such responses are only the last step of a decline in abundance. Abundance signals in response to land use change, and in particular fragmentation, can be detected earlier, prior to actual species loss, and can be used to identify vulnerable species that are at risk from local extinctions. This information can then be used to design and implement conservation and management actions aimed at reversing local abundance declines. However, modelling the response of abundance-based biodiversity indicators to local drivers (e.g. fragmentation) requires high quality input data (Bellard et al., 2012) and would benefit from a more mechanistic understanding of driver-response relationships at landscape scale.

The abundance and species diversity and richness of mammals and birds typically decrease with increasing fragmentation (Andren, 1994; Laurance et al., 2011), even if some species are disturbance-adapted and can be found in the matrix (e.g. Pardini, 2004). Amphibians and reptiles are considered key indicators of environmental changes (Schlaepfer and Gavin, 2001; Blaustein and Bancroft, 2007), with habitat loss and degradation known to contribute to their observed worldwide declines (Gibbons et al., 2000; Houlahan and Findlay, 2003; Stuart et al., 2004; Cushman, 2006). Yet, comparatively little is known about their responses to fragmentation, especially when edge effects are considered (McGarigal and Cushman, 2002; Gardner et al., 2007a; Carvajal-Cogollo and Urbina-Cardona, 2008, 2015; Suazo-Ortuno et al., 2008). Edges are typically characterised by more open canopies, leading to reduced moisture and increased maximum daily temperatures (Didham and Lawton, 1999; Hardwick et al., 2015). These altered microclimates are particularly likely to affect abundance and distribution of amphibians (Lehtinen et al., 2003), as they respire primary through their moist skin and may thus be more sensitive to desiccation in drier environments. Low dispersal ability of both amphibians (Gibbs, 1998; Demaynadier and Hunter, 1999; Cushman, 2006) and reptiles (Araújo and Pearson, 2005) is likely to further amplify such edge effects.

Lehtinen et al. (2003) used randomisation techniques on species presence-absence data across forest fragments in Madagascar to identify edge responses in amphibians and reptiles, showing that they can display edge and non-edge avoiding strategies. However, their approach could not account for spatial variation in abundance, which may be a more sensitive to fragmentation and hence a more reliable indicator of edge effects on herpetofauna. This is important, as species may show a gradient in their sensitivity to the edge effect, reflecting their varying ability to exploit unique combinations of ecological conditions (Schlaepfer and Gavin, 2001). For example, species declining in abundance from the forest interior to the forest edge may be mislabelled as non-sensitive to fragmentation based on their presence-absence pattern, even though their abundance suggests the likelihood of a local extinction with continuing fragmentation and loss of forest core habitat.

Here, we analyse the abundance responses of 43 amphibian and 61 reptile species to the nearest forest edge in fragmented, human-modified Neotropical landscapes like plantations, primary and secondary forests. We hypothesize that abundance of forest and non-forest species show consistent signals in response to the forest edge, indicating causal impacts of habitat fragmentation, and that we can exploit these signals to monitor the ecological integrity of forests in the landscape. We quantify how far edge effects extend to within forest and matrix habitat by computing the depth of edge influence; and we then use this depth of edge influence to test to what extend habitat suitability decreases for forest species due to fragmentation. Finally, we compare edge responses of species across multiple landscapes to investigate whether edge responses are species-specific or whether they vary among fragmented landscapes, which would indicate that landscape specific characteristics can modify the edge effect.

2. Material and methods

2.1. Species abundance

We extracted amphibian and reptile datasets obtained at 11 Neotropical landscapes from the BIOFRAG database (Pfeifer et al., 2014a) in February 2014, including data from both published and unpublished sources. We subsequently excluded two datasets from our analysis, one of which because of the small number of plots (N = 9) and another one because it was conducted in urban environment. The datasets contain the raw abundance data, i.e. the number of individuals of each species found in each given plot along survey seasons. One dataset solely focussed on measuring abundance of reptiles (Table 1). We concentrated on amphibians and reptiles identified at the level of species (85.7% of all observations, 249 species retained). We excluded rare species from our analyses, defined as species whose abundance did not exceed three individuals at any plot, as their abundance patterns could not be analysed statistically. Therefore, we retained a total of 104 species (43 amphibian and 61 reptile species) for all subsequent analyses (see Supplementary material 2).

2.2. Study landscapes

The retained datasets originate from sampling in nine fragmented forest landscapes from Central and South America, whose characteristics are summarized in Table 1. The datasets encompass a variety of matrix types, including pasture, secondary regrowth or plantations. The sampling effort varies across datasets, with the number of sampling plots ranging from 15 to >150, and the number of known species sampled in these plots from 3 to 40.

2.3. Delineating the forest edge

Location of the forest edge was estimated from high spatial resolution tree cover maps generated from Landsat data between 2000 and 2003 (Hansen et al., 2013; Fig. 1A). We classified the continuous tree cover values as "forest" and "non-forest" using a three-step procedure: (1) homogeneous zones (tree cover variation <5%) were delineated using morphological segmentation (marker controlled watershed algorithm, Meyer and Beucher, 1990; Fig. 1B), (2) maps were transformed so that pixels in each homogeneous zones were given the value of the average tree cover in the zone and (3) we computed the value of the tree cover threshold between "forest" and "non-forest" classes so that the intra-class variance of the darkest (high tree cover) and brightest (low tree cover) regions of the image was minimized (Otsu's threshold, Otsu, 1979; Fig. 1C). Tree cover values above threshold were classified as "forest" and tree cover values below threshold as "non-forest". The delineation steps prior to thresholding ensure that neighbouring pixels of similar tree cover (differing by <5%) are classified within the same category. Therefore, the location of the forest edge, i.e. the interface between "forest" and "non-forest" zones, always corresponds to an edge in the landscape.