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Recovery of amphibian species richness and composition in a chronosequence of secondary forests, northeastern Costa Rica

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ABSTRACT

In some tropical regions, following the abandonment of agriculture and pastures, secondary forests can recover plant species richness and forest structure (e.g. canopy cover, biomass); however, the importance of these secondary forests for fauna is not clear. Secondary forests can benefit fauna by providing suitable habitats, connecting forests fragments, and increasing gene flow. Previous studies of forest regeneration have showed different levels of amphibian recovery. In Puerto Rico, 1–5 years old secondary forests achieved similar amphibian species richness and composition in comparison with old-growth forests, while in Brazil secondary forests from 14 to 19 years of recovery only recovered 60% of the species of old-growth forests. We evaluated amphibian recovery in secondary forests in northeastern Costa Rica, by assessing amphibian recovery in 12 secondary forests that vary in age of recovery and in three old-growth forests using visual and acoustic surveys. Our sites varied in terms of their landscape (e.g. amount of surrounding forest) and forest characteristics (e.g. forest age, aboveground biomass, basal area, number of tree species, number of stems, leaf-litter depth), but there was no relationship between these characteristics and amphibian species richness or species composition. We found that amphibians are recovering rapidly in secondary forests in Costa Rica, and even young forests (10–16 years) had similar species richness and composition in comparison with old-growth forests. These forests are providing suitable microhabitats conditions for amphibians. In addition, this study highlights the importance of landscape characteristics. The abundance of amphibian species sources (e.g. forest patches) and connections between forests appear to be helping the species colonize these sites. Worldwide, the area of secondary forests is increasing, and our results show that these habitats are suitable for a diversity of amphibian species, suggesting that these forests can help reduce amphibian population and species decline.

1. Introduction

Species richness and structure (e.g. canopy cover, biomass) of tropical forests can recover from different human activities such as deforestation, agriculture or pasture in 20–40 years (Aide et al., 2000; Janzen, 2002; Letcher and Chazdon, 2009). In some tropical regions the rates of deforestation are decreasing and the rates of reforestation are increasing (Aide and Grau, 2004; Rudel et al., 2005). For example, in Dominican Republic and Puerto Rico secondary forests have emerged from abandoned agriculture lands (Rivera et al., 2000; Grau et al., 2003, 2007; Lugo and Helmer, 2004). Secondary forests have also emerged from abandoned pastures for cattle in Puerto Rico, Dominican Republic and Costa Rica (Aide et al., 1996; Rivera et al., 2000; Janzen, 2002); and there are examples of forests recovery from forest plantations (Mayaux et al., 2005), and following slash and burn agriculture (Rudel et al., 2005) in other neotropical ecosystems. Most of this recovery has occurred due to changes in socioeconomic patterns that involve rural–urban migration, increasing industrialization, and modern agriculture practices (Aide and Grau, 2004; Wright and Muller-Landau, 2006). These secondary forests can be important reservoirs for mature forest plant species (Wright and Muller-Landau, 2006; Chazdon et al., 2009), although their value for fauna is still poorly understood (Dunn, 2004; Gardner et al., 2007).

Secondary forests can benefit fauna by providing suitable habitats (Faria et al., 2009), connecting forests fragments (Faria, 2006), and increasing gene flow (Pardini et al., 2005). For example, secondary forests from 25 to 30 years old have similar ant species composition in comparison with 60 years old secondary forests in Puerto Rico, because they provide similar microhabitats (Osorio-Pérez et al., 2007). Similarly, the diversity, abundance and trophic structure of amphibians and reptiles increased as forest complexity and

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microclimate diversity increased during secondary succession (Heinen, 1992; Williams et al., 2002; Gardner et al., 2007; Ríos-López and Aide, 2007; Ficetola et al., 2008; Herrera-Montes and Brokaw, 2010). Birds and mammals also increase in diversity and abundance as the habitat structure complexity increases during secondary succession (Johnston and Odum, 1956; Barlow et al., 2007; Jayat et al., 2008).

Furthermore, it has been shown that secondary forests can provide corridors between old-growth forests and plantations for bat populations in the Atlantic rainforest of Brazil (Faria, 2006); and small mammal total abundances and levels of gene flow are higher in forests connected by secondary forests than in isolated forests fragments (Pardini et al., 2005).

Because amphibians are sensitive to environmental changes (Collins and Storfer, 2003; Ríos-López and Aide, 2007; Blaustein and Bancroft, 2007), and are less mobile than other vertebrates (Sinsch, 1990; Semlitsch et al., 2009), it is important to understand how amphibian species richness and species composition vary in secondary forests. Since habitat degradation and habitat loss are major causes of the current amphibian decline (Blaustein, 1994; Collins and Storfer, 2003; Stuart et al., 2004; Todd et al., 2009), forest recovery can be especially important for tropical species. A restoration project in Puerto Rico showed that all the amphibian species from the surrounding forests had recolonized an abandoned pasture in only 3 years (Ríos-López and Aide, 2007). However, this site was less than 1 ha in area and was surrounded by older forests, which were sources for amphibian species. In another study of secondary forests in Puerto Rico, young (1–5 years), intermediate (10–20 years) and advanced secondary forests (>40 years) shared six species of amphibians (two exotic), but their abundances varied with forest age (Herrera-Montes and Brokaw, 2010). Although this study covered a greater number of sites (n = 12) and a larger region (24 km^2), most sites occurred within 0–100 m of an old-growth forest (i.e. sources of amphibians). These examples of rapid amphibian species recovery in Puerto Rico occurred in a region with low amphibian diversity and in a landscape that often included nearby sources of amphibians (i.e. patches of old-growth forest).

In contrast, in other tropical regions land use often occurs at a larger scale, and, thus the distance to sources of fauna can be much greater. For example, a study in Amazonia, Brazil, covered 15 sites across a larger region (3900 km^2) and the distance between the sites and old-growth forests varied between 650 and 2800 m (Gardner et al., 2007). In this study, secondary forests and plantations had lower species richness in comparison with high amphibian diversity old-growth forests. These secondary forests shared only 60% of the species observed in old-growth forests (Gardner et al., 2007). These findings suggest that the landscape characteristics and the spatial scale of analysis are important factors influencing amphibian species recovery in secondary forests.

In the present study, we evaluated amphibian species richness and composition recovery in tropical secondary forests of different age in northeastern Costa Rica. This region has a diverse amphibian community (Guyer and Donnelly, 2005), and the landscape is a mosaic of mature forests, secondary forests, agricultural and pastures (Sánchez-Azofeifa et al., 1999; Bell and Donnelly, 2006, Letcher and Chazdon, 2009). We assessed amphibian recovery in 12 secondary forests that vary in age of recovery and in three old-growth forests. We sampled amphibians' species richness and composition using visual and acoustic surveys. We hypothesized that (1) amphibian species richness will increase as forest age increases, and if amphibian species respond like they did in Puerto Rico, older secondary forests (30–40 years old) will have similar species richness in comparison with old-growth forests; and (2) amphibian species composition in older secondary forests will be more similar with old-growth forests than with younger forests, because specialist species will need microhabitats that will only be available in older secondary and old-growth forests. Because of the high amphibian diversity in this region, we do not expect species richness and composition to recover as fast as in the studies in Puerto Rico (Ríos-López and Aide, 2007; Herrera-Montes and Brokaw, 2010). But, we do expect amphibian recovery to be more rapid in our sites in comparison with the Brazil study (Gardner et al., 2007), because our sites are not as isolated from old-growth forests. The results from the present study provide valuable information on the suitability of secondary forests as habitat for amphibian species recovery; habitats that can potentially mitigate the negative effects of deforestation and habitat loss that are causing amphibian population and species decline.

2. Methods

2.1. Study sites and sampling design

The study was carried out in the northeastern region of Costa Rica (10°26′N, 86°59′W), Sarapiquí, Heredia. This region has been characterized by deforestation for agriculture, mainly banana plantations, and cattle for pastures since 40 years ago (Butterfield, 1994). By 1994, forest area was reduced to 34% (Sánchez-Azofeifa et al., 1999), and the major current land uses in this region are cattle pastures, banana and pineapple plantations (Butterfield, 1994; Sánchez-Azofeifa et al., 1999; Bell and Donnelly, 2006; Letcher and Chazdon, 2009). More recently, some of these agricultural areas have been abandoned, and have transformed into secondary forests (Chazdon et al., 2003).

We selected a series of secondary forests that are recovering following cattle pasture abandonment and that vary in age of recovery (Fig. 1, see Appendix A). Specifically, we selected three sites within each of five age classes: 10–16 years old, 17–23 years old, 24–28 years old, 36–48 years old, and old-growth forests as controls (see Appendix A). Seven of these 15 sites were located within La Selva Biological Station (LSBS). Two of these forests sites were adjacent to old-growth forests, but the other sites were located between 700 and 2500 m away from old-growth forest. Two of the old-growth forests sites were located in LSBS. None of the sites included rivers, creeks or ponds, because water sources could be a potential confounding factor (de Souza et al., 2008; Ficetola et al., 2008).

LSBS covers 1536 ha, and approximately 75% is forested. The majority of the forest is old-growth, with secondary forests in areas recovered from abandoned pastures and plantations (McDade and Hartshorn, 1994). LSBS receives approximately 4 m of precipitation per year, and it is included in the tropical wet forest Holdridge's life zone (McDade and Hartshorn, 1994). There are approximately 50 species of amphibians documented for LSBS, 46 of them are frogs (Guyer and Donnelly, 2005).

2.2. Visual survey

We established three transects (2 × 50 m) in each site to census amphibian species richness, composition and abundance during the day and night. We used the visual encounter survey (VES) (Crump and Scott, 1994), and each transect was censused by two people for 20 min. Transects were censused in 2010 during the dry season (February and March), transition period (April–May), and wet season (October and November). During each of the three sampling periods, each of the three transects per site were sample by two people for 20 min during the day and night. In total, we spent 12 person hours per site conducting visual censuses.

2.3. Acoustic survey

We used acoustic surveys to increase species detection, particularly of species that are difficult to observe (e.g. arboreal, cryptic).