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Conservation value of tropical secondary forest: A herpetofaunal perspective

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ABSTRACT

In some areas of the tropics forests are recovering on abandoned cattle pastures. These secondary forests may be important habitats for conserving biodiversity, but we know little about their species composition over the long term. We studied herpetofaunal community changes in a 40 years chronosequence of forest succession on abandoned pastures in Puerto Rico. Twelve submontane sites (100–250 masl) represented four forest recovery stages: pasture, young (1–5 years after abandonment), intermediate (10–20 years), and advanced (40 years). Among these stages we analyzed the relationship of forest structure, microclimate, and herpetofaunal community structure. During succession total forest height increased, new strata of vegetation appeared in the understory, and the forest gained heterogeneity and complexity. Microclimate changed with changes in the physiognomy and structure of the vegetation. Microclimatic shifts were more dramatic in forest <20 years since abandonment. During 1 year we observed 7991 individuals of thirteen reptilian species (60% of observations) and six anuran species. Herpetofaunal richness was similar among stages, but the total abundance increased through succession. Relative abundance of anurans and reptiles was similar between stages, but species dominance changed with succession. Forest >20 years old resembles mature forest in some structural characteristics important to herpetofauna and can provide habitat for forest herpetofauna in disturbed areas.

1. Introduction

Humans have destroyed large areas of tropical forest around the world. Between 8 and 12 million square kilometers (35–50%) of the original closed canopy tropical forests have been removed (Wright and Muller-Landau, 2006). The most frequent proximate cause of tropical deforestation is the expansion of crop and pasture land. In Latin America, forest conversion to pasture for cattle has been greatest during the last 40 years (Geist and Lambin, 2001); however, a large area of that cleared land is regrowing with secondary forest (Wright, 2005). Under this deforestation/regrowth pattern, old growth tropical forests are likely to continue disappearing rapidly and to be replaced by secondary and logged forests (Chazdon, 2003; Perz and Skole, 2003; FAO, 2005; Wright, 2005). Although protecting remaining forest areas is a high priority, managing the forest regrowth on abandoned lands is also important, and this requires knowledge of forest regeneration after human disturbance (Brown and Lugo, 1994).

However, we know little about long-term patterns of tropical forest regrowth, because most regrowth studies have focused on early stages (Saldarriaga et al., 1988; Grau et al., 1997; Aide et al., 2000). Studies of succesional changes in animal communities during plant succession are relatively new and mainly focused on invertebrates (Barberena-Arias and Aide, 2003; Sánchez De-León et al., 2003) and endothermic vertebrates (Blake and Loiselle, 2001; William et al., 2002).

Puerto Rico offers an opportunity to study long-term forest regrowth and associated faunal changes using chronosequences of forest plots of different ages (Saldarriaga et al., 1988; Davis et al., 2003). In contrast to other tropical locations where there are only young forest patches (<30 years), Puerto Rico has secondary forests more than 60 years old (Aide et al., 1996, 2000). As in other Caribbean islands, in Puerto Rico large animals such as those found in mainland ecosystems are absent, and anoles and anurans constitute a substantial portion of the total animal biomass (Reagan, 1996; Stewart and Woolbright, 1996). Their abundance, widespread ecological distribution, and functional role as higher order consumers make them important components of animal communities throughout the Caribbean (Reagan, 1996). Currently, anurans are the most threatened (Stuart et al., 2004; IUCN, 2006) and least studied groups of terrestrial vertebrates in the world (Urbina-Cardona, 2008) and are a high priority for research.

Understanding the patterns of animal community structure during forest succession could be a useful tool for determining the value of secondary forest for conserving biodiversity. We

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studied changes in the herpetofaunal community in relation to changes in microclimate and forest structure on a 40 years successional chronosequence, to determine if secondary forest is an important habitat for conserving herpetofauna. We expected to observe changes in the herpetofaunal community in response to changes in habitat structure and microclimate during succession. Increasing heterogeneity and complexity of habitats with forest regrowth should produce diverse microhabitats for herpetofauna, suggesting the conservation value of secondary forests for these groups.

2. Methods

2.1. Study area

We located our study area in the Municipality of Luquillo in northeastern Puerto Rico (18°15′N, 65°45′W, USGS), between 100 and 250 m above mean sea level. The area is classified as subtropical moist forest (Ewel and Whitmore, 1973), with a wetter period between May and November, with ca. 400 mm monthly precipitation, and a drier period from January to April, with 200–250 mm monthly precipitation (García-Martinó et al., 1996). Mean monthly air temperatures range between 21 °C and 24 °C. In the last 70 years agriculture in this area has declined, while forest area has increased, including a mix of forests of different ages (Thomlinson et al., 1996). Forest fragments (<1 ha) ranging from <10 to >100 years in age predominate in the study area landscape, which mirrors an islandwide pattern (Lugo and Helmer, 2004).

2.2. Study sites

We selected twelve sites to represent pasture (grassland with a few cattle) and three ages of forest succession since pasture abandonment: young forest (1–5 years), intermediate forest (10–20 years), and advanced forest (40 years). We included the first 40 years of recovery because studies in Puerto Rico have shown that after 30–40 years, most measures of forest structure on abandoned pastures are similar to those in mature forest (Aide et al., 2000; Pascarella et al., 2000; Marcano-Vega et al., 2002). Pasture and each forest age were considered as successional stages, and were each represented in our study by three replicates. We used aerial photographs from 1951 to 2002 to select and date the abandonment of individual sites between 10 and 20 and 40 years ago. Site age was estimated by taking the mid-point between the last photograph that showed pasture and the first photograph that showed signs of abandonment (i.e., all grasses and herbs versus presence of shrubs or small trees). Age of the 40 years old forests was verified with landowners. Final selection of pastures and young forests was made by visiting the study sites. Only patches larger than two hectares were included, to minimize edge effects when plots where established. All sites were located in the buffer area of El Yunque National Forest.

2.3. Forest structure

To characterize forest structure and minimize edge effects (Didham and Lawton, 1999), we located one 20 × 50 m plot (1000 m^2 total) at the approximate center point of each site. In each plot we identified to species and measured the diameter of all trees ⩾10 cm dbh (diameter at 130 cm above ground). We also established an inner belt of 3 × 50 m inside each plot, in which all trees and stems of woody vegetation ⩾1 cm dbh where identified and measured for dbh. We compared species richness, dbh-class distribution (diameter classes 1.0–5.0, 5.1–10.0, >10 cm dbh), stem density, and basal area among stages using one-way ANOVA.

We estimated percent cover of shrub (woody plants <130 cm height, <1 cm dbh), fern, and herbaceous vegetation in ten 1.0 × 1.0 m subplots located each 5 m along the midline of the plot. Ground cover was estimated in the subplots as the percent of cover classes (bare soil, rock, litter, and herbs) relative to ground area. Comparisons of these variables among stages were made using a Multivariate Analysis Of Variance (MANOVA). We provided the Pillai trace statistic with its approximated F for the analysis. Although, Wilk's lambda is more commonly used, the Pillai trace may be more robust (Hammer et al., 2001). When MANOVA showed a significant overall difference between groups, the analyses proceed with pairwise comparisons through Hotelling's test.

We estimated canopy cover from ground level with a hand-held canopy densiometer in the 1.0 × 1.0 m subplots. To create a foliage height profile, at 25 points, one located each 2 m along the plot midline, we measured canopy height with a clinometer, and we recorded the presence or absence of live vegetation within height intervals (Fig. 1). We also recorded the presence of litter (dead vegetation) in the lower intervals. The percent of vegetation and litter cover for each height interval were calculated as the number of intercepts recorded for the height interval divided by the total number of points along the transect. Horizontal changes in vegetation were considered as a measure of heterogeneity, and vertical changes as complexity (Brokaw and Lent, 1999).

We used ordination analyses to describe the patterns in forest structure during succession. A principal components analysis (PCA) represented in axes the strongest covariation among all variables recorded for forest structure characterization. We used two axes and correlation coefficients to find the final configuration of the ordination (McCune and Grace, 2002).

2.4. Microclimate

We measured temperature and relative humidity at air and ground level for 1 year in the sites. We located two data loggers (HOBO) at the middle point of each vegetation plot, one at 10 cm (ground) and the other one at 2 m (air) above ground. We attached the data loggers to available woody plants. In the case of pastures where herb cover did not reach 2 m, we used shrubs or remnant trees in the plot to attach the instrument. Each data logger recorded hourly from December 2005 to November 2006. We considered four diurnal periods for analysis; early morning (1:00–5:59), morning (6:00–12:59), afternoon (13:00–18:59) and night (17:00–00:59). Yearly and daily variations were evaluated using Factorial ANOVA, while for sample periods we used one-way ANOVA.

With a principal components analysis (PCA) we related all microclimate measures to site distribution in ordination space. We constructed the PCA matrix using sites as rows (12), while the columns corresponded to the averages of daily variation (early morning, morning, afternoon, night) of relative humidity and temperature at air and ground level. We used two axes and correlation coefficients to find the final configuration of the ordination (McCune and Grace, 2002).

2.5. Herpetofaunal community structure

To describe herpetofaunal community structure we used Visual Encounter Surveys (Crump and Scott, 1994; Dood, 2010) by day and night at four different times during a year: November, March, June, and August. Eight continuous days of sampling constituted each sampling period, and each plot was visited on two different days during this period. The order of visits to sites was random to maximize the possibility of detecting species and recording variation. We located one 6 × 50 m herpetofaunal study plot (300 m^2 total) near the mid-point of the midline of