Biological Conservation 204 (2016) 417–425

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Importance of the matrix in determining small-mammal assemblages in an Amazonian forest-savanna mosaic

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ARTICLE INFO

Article history:
Received 4 June 2016
Received in revised form 4 October 2016
Accepted 24 October 2016
Available online 14 November 2016

Keywords:
Eastern Amazon
Connectivity
Patch size
Landscape ecology
Conservation

ABSTRACT

Patch-size and connectivity effects on organisms are usually strong, but may be positive or negative, depending on the landscape context. A binary habitat/non-habitat perspective that fails to consider matrix heterogeneity often explains these inconsistent results, as matrix influences patch quality and connectivity differently for different species. Here we tested the effects of patch size, connectivity and matrix type on non-volant small-mammal assemblages in an eastern-Brazilian Amazonian forest-savanna mosaic. We sampled 14 forest-patches and 2 continuous-forest plots, using 60 baited live traps and 8 pitfall traps (60 L) per plot in 3 field expeditions. We estimated connectivity using the Proximity Index and matrix type as the proportions of savanna or regrowth forest around patches. We used one-dimensional NMDS, ANCOVA and multiple regression to test the relationships among species composition, species traits and predictor variables. We captured 178 individuals of 16 small-mammal species and an NMDS ordination showed a pattern of assemblage change that was strongly related to matrix type. Connectivity and patch size had no statistically significant effect on assemblage composition. Species associated with patches in regrowth-forest matrix were mostly rodents, relatively large and mainly frugivorous, while species associated with savanna-matrix patches were smaller, mostly insectivorous, marsupials. This may be related to how matrix is used by small mammals and affects patch quality, rather than how it limits animal movements. Composition of small-mammal assemblages in patches depended on the type of surrounding matrix, so matrix heterogeneity enhances small-mammal assemblage diversity in this landscape and should be taken into consideration in regional conservation-unit management plans.

1. Introduction

Understanding landscape dynamics can lead to better comprehension of ecosystem functions and species persistence. Land use accentuates natural landscape dynamics, causing habitat alteration and fragmentation. Fragmentation, by reducing habitat patches and increasing patch isolation, affects species diversity and abundance. As predicted by the species–area relationship (Preston, 1962), patch size usually has strong effects on the number of species occupying a patch (Laurance et al., 2011). However, these effects are not always positive (Laurance et al., 2011; Fahrig, 2003), mostly because patches are commonly considered as closed communities and because the amount of habitat in the area surrounding the patch is frequently ignored (Fahrig, 2013). This can lead to results that are inconsistent among studies (Debinski and Holt, 2000; Fahrig, 2003).

Habitat isolation also has strong effects, usually showing negative relationships with the number and abundance of species (Debinski and Holt, 2000; Bailey et al., 2010), and causing changes in species composition (Pardini et al., 2005; Vieira et al., 2009). Isolation can be measured in terms of connectivity, though some connectivity measures are considered more realistic than others (Kindlmann and Burel, 2008; Rayfield et al., 2011; McGarigal, 2015). The use of less-appropriate connectivity measures, such as the nearest neighbor distance, can lead to misleading conclusions (Fahrig, 2013; Bender et al., 2003) and connectivity measures that consider the area of patches located in a buffer around the focal patch are generally more appropriate to indicate effective local connectivity (Bender et al., 2003).

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http://dx.doi.org/10.1016/j.biocon.2016.10.037
0006-3207/

The patch size-connectivity perspective is a result of the binary landscape concept of habitat and non-habitat, originated in island biogeography (MacArthur and Wilson, 1967) and metapopulation theories (Levins, 1969). This approach ignores the heterogeneity of the matrix (Ricketts, 2001; Prevedello and Vieira, 2010), which can lead to inconsistent results (Laurance, 2008). The matrix may influence patch quality and connectivity in many ways (Laurance et al., 2011). Matrix effects have received increasing attention and recent studies have shown that matrix type may have different effects on different species or taxa (Ricketts, 2001; Prevedello and Vieira, 2010; Watling et al., 2011). In the Prevedello and Vieira (2010) meta-analysis, 95% of studies showed effects of matrix type, but in 56% of those studies patch and isolation variables had greater effects than did the matrix. In the tropics, non-flying mammal-species richness and composition may be affected by matrix type (Daily et al., 2003), and matrix was important to predict species richness and persistence in Amazon forest patches (Gascon et al., 1999). Therefore, matrix effects are relevant, but may have varied intensities and their importance in relation to patch and isolation variables is still poorly understood.

The Amazon tropical forest remains one of the largest and least fragmented in the World, but it has already lost about 12% of its original extent and shall lose another 9 to 28% by 2050, especially in drier areas along its southern border (Soares-Filho et al., 2006). Threats to the Amazon are mainly from cattle and soy-bean culture, which frequently cause fragmentation of natural habitats, and highways pose a threat that usually accompanies agricultural activities (Soares-Filho et al., 2006). A large portion of the Brazilian state of Pará, situated in the eastern Amazon, is subject to impacts caused by the BR-163 Highway, which links the city of Cuiabá, in Mato Grosso state, to the township of Santarém in Pará (Fearnside, 2007). The area around Alter do Chão village, Santarém Municipality, is covered by a landscape containing forest patches surrounded by different matrix types, and was designated as an Environmental Protection Area (EPA). This landscape offers the opportunity to investigate how matrix and patch characteristics affect organisms, which could improve the efficiency of future management actions in the region.

Non-volant small mammals clearly respond to changes in the landscape caused by fragmentation and habitat loss (Gascon et al., 1999; Pardini et al., 2005; Umetsu and Pardini, 2007; Santos-Filho et al., 2012), so they are a suitable group to study these effects. Differences in small-mammal functional traits, such as diet, body size and locomotory habits, may facilitate species coexistence (Galetti et al., 2016), and some of these traits have been associated with landscape characteristics (Pardini, 2004; Holland and Bennett, 2009). They also play important ecological roles as primary and secondary consumers (Paglia et al., 2012), prey of many species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011), and seed predators and dispersers (Vieira and Izar, 1999; Pimentel and Tabarelli, 2004), and may be keystone species in some environments (Ernest and Brown, 2001).

Here, we test the effects of patch size, connectivity and matrix type on the structure of small-mammal assemblages of forest patches in the Alter do Chão landscape. Our objective was to determine which of these landscape variables is most related to small-mammal assemblage structure. We also tested if species functional traits were associated with the variables related to species composition. We measured assemblage structure through species composition, because species complementarity among sites is recommended for selecting sites for conservation (Margules and Pressey, 2000) and because recent studies have shown that species composition responds strong and clearly to environmental changes, much more so than the frequently-used measure of species richness (Su et al., 2004; Solar et al., 2016).

2. Material and methods

2.1. Study area

Alter do Chão is a village on the right bank of the Tapajós River, located in Santarém Municipality, Pará State, in eastern Brazilian Amazonia. The climate is humid tropical, with rainy season between December and June and dry season between July and November. Mean annual rainfall is 2192 mm, most rain falls between February and April (919 mm) and least between August and October (115 mm). Mean annual temperature is 27.5 °C and mean monthly temperature varies little throughout the year (INMET, 2009).

The village is surrounded by a mosaic composed mainly of forest patches immersed in an Amazonian-savanna matrix, the latter surrounded by continuous forest. All forests in the area are classified as semi-deciduous tropical (Cintra et al., 2013). The savanna is covered mostly by herbs and grasses with sparse trees, even though there is a gradient of tree cover (Magnusson et al., 2008). The forest has a relatively open understory and >50 tree families, but Myrtaceae, Flacourtiaceae and Leguminosae are the most common (W.E. Magnusson and I. Amaral, unpubl. data). The whole landscape was probably forested approximately 2000 years ago (Sanaiotti et al., 2002). There is no certainty about forest-patch origins, but the observations of Bates (1892) are the earliest record of forest patches in the region, so they are at least 150 years old, probably much older. The matrix transition to savanna may have been a consequence of the fires induced by paleoindian agriculture (Iriarte et al., 2012), as this region has been inhabited for millennia (Stenborg et al., 2012).

The savannas around Alter do Chão burn at intervals of 1–3 years, mainly due to human activities (Magnusson et al., 2010). However, there is an area of forest-transition vegetation, which is probably an old savanna that has not burnt entirely for at least the past 30 years (A.P. Lima, unpubl. data; W.E. Magnusson pers. obs.). Some savanna patches that existed in this area around 20 years ago have had their size reduced due to reduced burning (W.E. Magnusson pers. obs.). The matrix around the forest patches in that area is mainly regrowth forest with little or no grass cover. According to the Mausel et al. (1993) classification, this matrix is a forest in advanced secondary succession (>30 years) and the forest patches and continuous forest are mature forest. Regrowth forest is drier and shorter than mature forest (10–20 and 20–30 m high, respectively), with trees much thinner and in higher density (C. Borges-Matos, pers. obs.). We considered the regrowth-forest matrix a "natural" land-cover, since it is part of a local succession process of forest reestablishment. The savanna is a natural physiognomy; in Alter do Chão its origin and expansion may be related to ancient human activities, but not to modern changes in land-cover, such as clearing for plantations or pasture. Hence, we considered the savanna matrix a "semi-natural" land-cover.

2.2. Site samples

All plots were sampled for small mammals in May/June (wet season), August/September and October/November (dry season) of 2015. We sampled 16 plots located in 14 forest patches and in 2 continuous-forest sites (Fig. 1). Patches were chosen according to facility of access and to maintain little overlap among their buffers (see Section 2.4). The standard plot consisted of four parallel 250 m straight lines that summed a total length of 1 km, separated from each other by 50 m. Four plots had either 3 or 5 lines, due to local restrictions or because patches were small and too irregular in shape, but the total length of their lines was also 1 km, so the area sampled was equal for all plots.

The savanna matrix was not sampled because we were interested only in forest-dwelling small mammals, and all species previously registered for the plots (Souza, 2002; A.P. Lima, unpubl. data) are considered forest species (Rossi and Bianconi, 2011; Oliveira and Bonvicino, 2011). In addition, the savanna matrix has been surveyed intensively for small mammals during the past 29 years (Magnusson et al., 1995; Layme et al., 2004; Magnusson et al., 2010; W.E. Magnusson and A.P. Lima, unpubl. data) and the only species of small mammal regularly found was *Necromys lasiurus*, a species that has not been recorded in forest in the region. The only forest species captured during these decades of research were a few individuals of the genus *Proechimys* (species not