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Evaluation of multi-causal dynamics of variability composition of patch edges in temperate forest

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ABSTRACT

In this study, we examine the effect of 13 microenvironmental variables, 3 landscape variables and 8 anthropogenic pressure variables on species richness, abundance and diversity in the distribution of plant communities and the pattern of species diversity using multivariate statistics. Results of TWINSPAN classification have identified three compositional types of edge. DCA clearly distinguished these groups by the first two DCA axes. Both classification and ordination resulted in a clear demonstration of the vegetation pattern in the study area. The results obtained from the SEM showed that microenvironmental variations (canopy openness, litter layer) determine, to a large extent, the species composition of edges, and that landscape properties are correlated with these environmental variations, but anthropogenic pressures had no significant effect on them. This final model can be used as a tool for the application of management and conservation strategies in fragmented forests, as it contributes to identify the direct and indirect effects with the largest impacts on floristic variation.

1. Introduction

Fragmentation is a landscape-scale phenomenon defined as a change in the configuration, continuity and size of the habitat (Fischer and Lindemayer, 2007; Mitchell et al., 2014). One process emerging from forest fragmentation is the creation of edge or transition areas at the boundary of adjacent habitats (forest patches and the surrounding matrix), which modify environmental conditions inside the patch perimeter (Matlack, 1993). This process is known as edge effect (Fahrig, 2003; Harper et al., 2005; Tabarelli et al., 1999; Zheng and Chen, 2000) and directly affects biodiversity by modifying species richness and abundance patterns, causing changes in ecosystem composition, structure and processes (productivity, decomposition, and ecological interactions) (Ewers et al., 2007; Fahrig, 2003; Harper et al., 2005).

The literature on landscape ecology documents the relationship between ecological parameters in patches (e.g., species richness and composition) and ecological factors, such as microhabitat heterogeneity which, in turn, is modified by anthropogenic disturbances at the landscape level and spatial characteristics of patches (López-Barrera et al., 2007; Saunders et al., 1991; Stenhouse, 2004). The latter factors can be grouped into three distinct classes: (a) microenvironmental variation, including microclimate (Harper et al., 2005), soil and topography (Ewers et al., 2007); (b) anthropogenic pressure, including vegetation structure in the adjacent matrix (Grau, 2004; Ries et al., 2004), age of edge habitats (Cadenasso et al., 2003), and fire and disturbance regime (Cochrane and Laurance, 2002; Gascon et al., 2000); and (c) landscape characteristics such as patch size (Ewers et al., 2007), shape and connectivity (Lafortezza et al., 2010). The understanding of interactions between these factors has been limited, because the more spatial and temporal variables and their effects on species are considered, the more complex and dynamic the issue becomes, leading to multiple interpretations of the changes in edge composition (Ewers et al., 2007; Fletcher, 2005; Matlack, 1993; Saunders et al., 1991). Identifying the multi-causal dynamics responsible for the changes in edges composition at various spatial scales and the response of individual species to them is particularly important to extrapolate or predict edge effects in different patches and landscapes (Laurance, 2000). Such information provides the grounds for determining whether multiple edge effects should be incorporated into a predictive model to assist in the development of management and conservation strategies, particularly in

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rapidly changing landscapes (Laurance, 2000).

In forests fragmented by human activities, patches are usually surrounded by a low-biomass, homogenous and structurally simple matrix of grasslands, croplands or secondary vegetation. Such differences in structural complexity and biomass result in microclimate differences (Murcia, 1995). The edge zone typically has a higher light incidence, widely fluctuating daily temperatures, presence of wind, greater soil erosion, low humidity and high soil compaction. Such sites are usually favorable for the establishment of fast-growing, stress-tolerant species (Collinge, 1996; Grez and Bustamante, 1995). The environment under the forest canopy in core forest sites, by contrast, is cooler, more humid and more homogeneous. The microclimate differences between core and edge zones usually result in edge-interior gradients in temperature and humidity. Air temperature and humidity, vapor pressure deficit (VPD), soil moisture and light intensity usually vary between the edge and interior zones. In those cases, the differences disappear over the first 50 m inside the patch (Murcia, 1995). Responding to such a microclimate conditions at edge, some forest plant species show lower densities or are completely absent near the edge, whereas others either occur at higher densities or remain unchanged (Spies, 1998). On the other hand, the species that depend on the inner habitat may become excluded from the core of small patches due to the incidence of edge-related physical effects.

Examining fragmentation from the perspective of the landscape configuration, patch size will determine the total number of species that the site can accommodate, with larger patches offering more space, resources and environmental heterogeneity (soil, relief and microclimate) need to support and maintain more species versus smaller patches (Collinge, 1996; Pincheira-Ulbrich et al., 2009). Patch shape may also affect the intensity of edge effects; for example, the edge effects may be weaker in regular patches while the inner habitat of irregular shape patches is more strongly affected by matrix conditions. Landscape connectivity also plays an important role in offsetting the negative effects of fragmentation (Collinge, 1996; Grez and Bustamante, 1995; Mitchell et al.,2014). Patch isolation will influence negatively the total number of species and ecological functions the patch can sustain. Smaller populations in isolated patches have lower reproduction rates by hindering pair formation and endogamy (Collinge, 1996; Grez and Bustamante, 1995). Thus, the edge effect may be more pronounced as patches become more connected due to the arrival of immigrants who colonize inner zones of connected patches.

The consequences of the edge effect also depend on the surrounding matrix. Matrix conditions can permeate easily across small patches due to lack inner habitat, leading to stressful conditions for local species and fostering competition for limiting resources. In larger patches this effect can dissipate across the patch area and may not reach the inner habitat (Collinge, 1996). Highly anthropized environments such as crop fields, pasturelands and urban areas are highly disturbed sites showing soil erosion and compaction, conditions unsuitable for the establishment of native tree species. Such stressful conditions often facilitate the entrance of invasive species or weeds that proliferate in disturbed environments and, in the absence of competitors, are able to reproduce and disperse successfully (Castro-Díez et al., 2004; Collinge, 1996; Hoffmeister et al., 2005).

Altogether, these factors define the resulting edges ability to buffer the extreme microenvironmental fluctuations occurring in the surrounding matrix, its resilience following a disturbance (Asbjornsen et al., 2004), and its ability to foster or restrain ecological succession (Harper et al., 2005; Williams-Linera, 1990; Williams-Linera et al., 2002). Despite the importance of these factors for understanding floristic variability in edge environments, few studies addressing their combined effects are available (Cadenasso et al., 2003; Ferro and Morrone, 2014), since traditional approaches have focused on analyzing individual factors separately (Zheng and Chen, 2000). The complexity of analyzing this floristic variability (stemming from the multi-scale nature of the causal factors) have led to the use of multivariate methods to estimate the magnitude of the effect of causal factors on the formation of different compositional types of edge and their relationship with the differential response of vegetation in edge habitats (Podani, 2000).

One of such multivariate statistical methods is structural equation modeling (SEM), which has been widely used in ecology to evaluate the strength of causal relationships between multiple variables (Fan et al., 2016). For example, Gazol et al. (2012) used these models to understand how plant species richness is directly or indirectly related to landscape conditions and local environmental factors. Santibáñez-Andrade et al. (2015) built a SEM to include landscape indicators into a Pressure-State-Response model in temperate forests.

If we consider that microenvironmental variation, anthropogenic pressures and landscape characteristics lead to floristic variations at the patch edges (Romero-Torres and Ramírez, 2011; Varela et al., 2002), then the use of multi-causal statistical designs is necessary to answer the following questions: (a) do species respond differently (as evidenced by composition changes) to edges in different patches surrounded by a homogeneous matrix?; (b) what are the microenvironmental, anthropogenic or landscape-scale factors that determine the composition of edge communities in patches? and (c) how do these causal factors that operate at different scales relate to each other?

To address these questions, we conducted a study in a peri-urban forest in Mexico City. Previous studies on temperate forests in this zone have not evaluated the direct effects of environmental changes on the distribution of plant species. In this study, we examined the presence of different compositional types of edge – as identified from the vegetation composition and species associations – in a fragmented forest. Using multivariate classification and ordination methods, the existing floristic patterns in the edges of different temperate forest patches were identified and characterized. Finally, structural equation models were used to analyze direct and indirect effects of landscape properties, anthropogenic pressures and microenvironmental variations in the development of edges of distinct floristic composition.

We propose as hypothesis of this study: (a) that edge species will show differential responses (expressed as compositional changes) to the presence of different interior-edge environmental gradients, leading to the existence of different compositional types of edge; and (b) that factors operating at a larger scale – landscape properties and anthropogenic pressure , but specifically landscape configuration properties (size, shape or connectivity), could achieve significant effects on the species composition of edges; and (c) these larger scale factors indirectly affect those operating at a smaller scale – microenvironmental variation, which in turn directly affects the composition of edge vegetation.

2. Methods

2.1. Study area

We studied patches of pine-oak temperate forest located at the eastern slope of the Sierra de Monte Alto, center of Mexico (Fig. 1). The studied forest fragments occur between 2800 and 3100 m a.s.l., and its climate is temperate sub-humid with a summer rainy season, mean annual temperature between 10 and 16 °C and mean annual precipitation between 500 and 1500 mm (Rubio-Licona et al., 2011). The pine-oak forest forms dense communities where the genera *Pinus* and *Quercus* dominate over other tree species such as *Cupresuss, Salix, Alnus* and *Fraxinus*. The shrub layer is dense and rich in species, including genera such as *Baccharis, Eupatorium, Senecio, Gaultheria* and others.

We selected 29 forest fragments of anthropogenic origin and, homogeneous in terms of physiognomy, vegetation type and topography (Strayer et al., 2003). All of them face agricultural fields destined to the annual cultivation of corn, beans and vegetables, causing the maintenance of hard edges (high contrast between neighboring patches) (López-Barrera et al., 2007; Ries et al., 2004; Strayer et al.,