



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

C. Granados-Peláez<sup>a,\*</sup>, G. Santibáñez-Andrade<sup>b</sup>, F. Guerra-Martínez<sup>a</sup>, D. Serrano-Giné<sup>c</sup>,  
A. García-Romero<sup>a</sup>

<sup>a</sup> Department of Physical Geography, Institute of Geography, National Autonomous University of Mexico, 04510 Mexico City, Mexico

<sup>b</sup> National Center for Disciplinary Research in Conservation and Improvement of Forest Ecosystems of National Institute of Agricultural Forestry and Livestock Research, 04010 Mexico City, Mexico

<sup>c</sup> Department of Geography, Faculty of Tourism and Geography, Universitat Rovira I Virgili, Tarragona 43480, Spain



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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 (Laforteza 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

\* Corresponding author.

E-mail addresses: [cgrapel@ciencias.unam.mx](mailto:cgrapel@ciencias.unam.mx) (C. Granados-Peláez), [gabysant@ciencias.unam.mx](mailto:gabysant@ciencias.unam.mx) (G. Santibáñez-Andrade), [guerraf@comunidad.unam.mx](mailto:guerraf@comunidad.unam.mx) (F. Guerra-Martínez), [david.serrano@urv.cat](mailto:david.serrano@urv.cat) (D. Serrano-Giné), [agromero@igg.unam.mx](mailto:agromero@igg.unam.mx) (A. García-Romero).

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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 *Cupressus*, *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.,

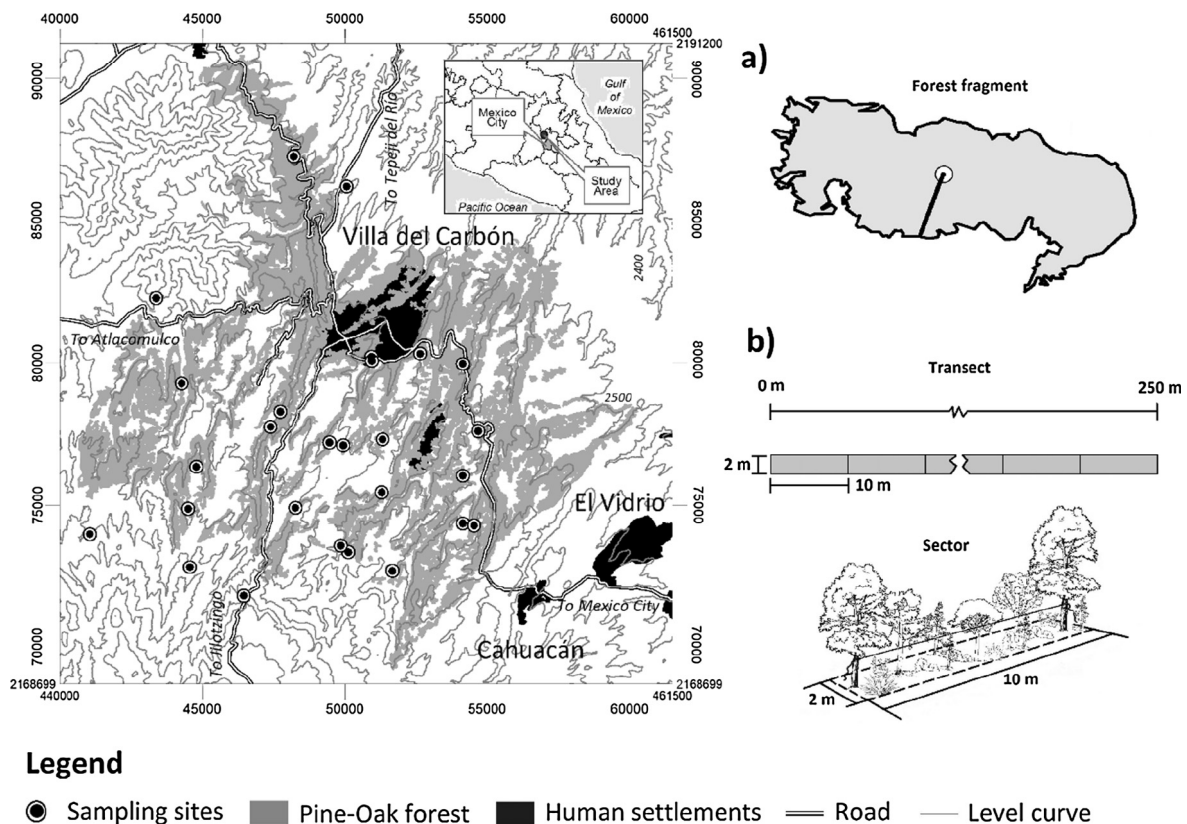


Fig. 1. Location of the study area at the eastern slope of the Sierra de Monte Alto, center of Mexico. Forest patches are shown in gray; dots represent sampling plots (5 × 50 m).

2003). Based on previously available information for the study area, we determined that the age of forest patches was  $40 \pm 5$  years since deforestation took place in the early 1970s caused by the expansion of the agricultural frontier (Fig. 1) (Granados et al., 2014). Because of their fragmented state and the variability of microenvironmental conditions, and the continued anthropogenic pressure from agriculture, patches of temperate forest in the study area were an appropriate site for studying changes in plant species composition due to edge effects in response to human intervention.

## 2.2. Variables

Edge-interior transects measuring 50 m long by 5 m wide were laid across 29 forest patches. Each transect was divided into  $10 \text{ m} \times 2 \text{ m}$  ( $20 \text{ m}^2$ ) contiguous sample plots (segments), the abundance and species identity of all tree individuals ( $> 5 \text{ cm dbh}$ ) and shrub species on each sample plot were recorded. Using a Geographic Information System and the software FRAGSTAT ver-4 (McGarigal et al., 2012), variables that describe the landscape properties of patches were evaluated, including patch size, patch shape and distance to the nearest larger patch (connectivity index).

Variables describing anthropogenic pressures were recorded along the edge-interior transect, in the center of each plot. To evaluate the impact of grazing, the number of browsed plants and the presence and width of cattle trails were recorded. To describe the impact related to the patch surroundings, the nature of the adjacent matrix (agriculture, pasture or planted forest) was recorded. To assess the impact of logging, the number of logged trees and stumps were recorded. Finally, to assess the impact of human activities, the number of trails, intensity of disturbance in relation to road width and type (paved/unpaved road) were also recorded.

In the center on each plot, the information on key microenvironmental variables including air temperature, soil temperature, relative

humidity, soil relative humidity, canopy openness, global site factor (GSF, estimated from hemispheric photographs using the software gap light analyzer), soil compaction (in  $\text{m}^2/\text{square inch}$ ), thickness of the litter layer, percentage of soil covered by litter, percent coverage of live vegetation, percentage of bare soil and the terrain slope (in degrees) were recorded. Temperature and relative humidity (RH) were logged using waterproof digital thermometers at 50 cm above soil level to the air and with 15 cm deep for soil. Canopy openness and GSF were estimated from hemispheric photographs using the software gap light analyzer. Thickness litter layer was measured employed soil compaction DICKEY-John<sup>®</sup>. Cover of litter, live vegetation and bare soil were calculated in relation on plot.

## 2.3. Determination of compositional types of edge

A primary matrix containing abundance data for each of the 39 species recorded at the edge of patches (first 50 m) was constructed (Laurance, 2000). To explore if different compositional types of edge could be recognized (Fletcher, 2005), patches were classified based on their species composition and abundance in response to similar/different environmental conditions, using a two-way indicator species analysis (TWINSPAN) (Hill, 1994). The results were summarized in a dendrogram showing clusters of patches representing different compositional types of edge, with the characteristic species in each group. Species richness, the Shannon-Wiener diversity index, the Simpson dominance index, and the equitability of each compositional type of edge were calculated using the software EstimateS ver-8 (Colwell, 2006).

An indirect ordination analysis was performed using a Detrended Correspondence Analysis (DCA) to determine whether the species composition of the edge types responds to the presence of environmental gradients and thus confirm that the clustering of patches is similar to the grouping obtained in TWINSPAN (McCune and Mefford,

2006).

#### 2.4. Evaluation of the independent effects of causal variables on compositional types of edge

To examine the effect of landscape properties, anthropogenic pressure and microenvironmental variables on the compositional types of edge identified, a direct ordination analysis was carried out using the Canonical Correspondence Analysis (CCA) (Jongman et al., 1995; ter Braak, 1987). CCA is a direct gradient analysis technique that seeks for relationships between the floristic variation (in terms of species composition and abundance data) in the communities analyzed and the variables leading to such variation (Vogiatzakis et al., 2003). Subsequently, a Monte Carlo permutation test was carried out to explore the statistical significance of the results ( $P < 0.05$ ).

To avoid multi-collinearity effects (Jongman et al., 1995; ter Braak, 1987), the variables used were first subjected to a correlation analysis using Pearson's correlation coefficient. Only one variable from each pair of highly correlated ( $r > 0.7$ ;  $P < 0.01$ ) variables was used for the analysis. Thus, the secondary matrix included six microclimatic variables, five anthropogenic variables and two variables describing the spatial configuration. A Monte Carlo test was used to explore the significance of the correlation between matrices. All the statistical tests were performed with the software SPSS version 2015. Classification and ordination analyses were performed in PC-ORD ver-5.10 (McCune and Mefford, 2006). With these results, potential interrelations (correlations between explanatory variables) were identified and used as *a-priori* information to support the structural model and explore the multi-causal dynamics.

Additionally, to review the absence of spatial autocorrelation of data, the statistical test of the Moran's I was applied using the residuals of the CCA models, through the *vegan* package in the R software ver-3.3.3. To identify the amount of the variance explained by each group of explanatory variables, as well as their combined effects, a variance partition was performed (Borcard et al., 1992) using adjusted  $R^2$  in redundancy analysis ordination (RDA) in the *vegan* package of the R software ver-3.3.3.

#### 2.5. Evaluation of the multicausal dynamics of edge effects

Finally, to assess the multi-causal dynamics and the intensity of the relationships between variables on the compositional types of edge identified, an *a-priori* model of hypothetical relationships was built using a structural equation model (SEM). Structural equation modeling is a method to evaluate complex hypotheses involving multiple causal pathways between variables (Curran, 2003; Kline, 2015; Mehta and Neale, 2005). The proposed relationship between latent and observed variables used in this analysis based on previous theoretical knowledge is shown in Fig. 2. It assumes that factors operating at a larger scale (landscape properties and anthropogenic pressure) indirectly affect those operating at smaller scales (microenvironmental variation), which in turn directly affect the composition of edge types.

From this general model and using the CCA results, we select those variables that would explain the variation in the floristic composition. Only six relationships were tested using a structural equation model (SEM). The method eliminated those relationships that were considered not significant based on their critical ratios (CR), and added those relationships that would improve the model's fit (Byrne, 2013) based on the modification index (MI). The goodness of fit of the resulting model was evaluated with the following indices: Chi-square ( $\chi^2$ ) and its associated probability level; the root mean square error of approximation (RMSEA) and the comparative fit index (CFI). RMSEA values below 0.06 and CFI values above 0.90 are indicative of a good-fitting model (Byrne, 2013). This analysis was performed using the software AMOS ver-4.0, within the SPSS statistical package (Arbuckle, 2007).

### 3. Results

#### 3.1. Determination of compositional types of edge

TWINSPAN identified three different clusters of patches based on species composition and abundance (Fig. 3). Eleven of the 39 species were identified as weeds, and some of them were characteristic of compositional types of edge (Table 1).

Species richness showed little variations between the three compositional types of edge; type 2 had the greatest species richness and type 3 the lowest. Note that species richness of type 1 was very similar to that of type 2 even though type 1 was only represented by four patches. However, those four patches were the largest in the sample examined, and this might be the reason why they had a species richness comparable to that found in the eleven and fourteen patches included in the other groups. Species diversity (Shannon-Wiener's and Simpson's indices) was also very similar across the three compositional types of edge. The physiognomic characteristics and species composition of the edge types (clusters) identified by TWINSPAN are described below.

Compositional type of edge 1. A low-contrast edge type with a dense understory (Fig. 4a). Characterized by a shrub understory composed of *Gaultheria acuminata*, *Baccharis heterophylla* and *Senecio salignus*; the species that are unique to this group are *Cestrum nitidum*, *Gaultheria acuminata*, *Monnina ciliolata* and *Senecio sinuatus*. Weed species found in edge type 1 include *Agave salmiana* (2 individuals), *Baccharis conferta* (1), *Buddleia cordata* (20), *Pinus patula* (2), *Prunus serotina* (5) and *Senecio salignus* (30) (Fig. 5). Weeds accounted for 14.53% of the total abundance of all species.

Compositional type of edge 2. A high-contrast edge type with madrone and oak trees, with no understory (Fig. 4b). Characterized by a strong association between *Arbutus xalapensis* and *Quercus crassipes*, with no understory. *Crataegus mexicana* is a species unique to this group. Edge type 2 includes the largest number of weed species: *Agave salmiana* (1 individual), *Baccharis conferta* (29), *Bouvardia termifolia* (1), *Buddleia cordata* (10), *Buddleia parviflora* (1), *Crataegus mexicana* (4), *Pinus montezumae* (19), *Pinus patula* (24), *Prunus serotina* (10), and *Solanum cervantesii* (3) (Fig. 5). Weeds accounted for 19.81% of the total abundance of all species.

Compositional type of edge 3. A low-contrast edge type with an incipient understory (Fig. 4c). Defined by a shrub understory composed of *Eupatorium glabratum* and saplings of *Prunus serotina* and *Quercus rugosa*. The species unique to this group are *Cestrum thyrsoides*, *Fuchsia thymifolia* and *Pinus pseudostrubus*. Seven weed species occur in edge type 3: *Baccharis conferta* (32 individuals), *Buddleia cordata* (10), *Buddleia parviflora* (6), *Pinus patula* (4), *Prunus serotina* (49), *Senecio salignus* (4) and *Solanum cervantesii* (2) (Fig. 5). Weeds accounted for 22.60% of the total abundance of all species.

#### 3.2. Evaluation of the independent effects of causal variables on compositional types of edge

DCA identified environmental gradients correlated with the spatial configuration of the species along the ordination axes, grouping them into three clusters of species corresponding to the three compositional types of edge.

Fig. 6a, shows the DCA ordination diagram of patches and species; for easier reference, the clusters identified in TWINSPAN are superimposed on this diagram. The eigenvalues corresponding to the first two ordination axes were 0.45 and 0.24. The spatial arrangement of the patches shows a clustering according to their species composition, which also match with the clusters obtained in TWINSPAN. On the other hand, this analysis shows that the different compositional types of edge identified are related to the presence of environmental gradients.

The results of CCA of landscape properties (Fig. 6b) were not statistically significant (axis 1 eigenvalue = 0.4, axis 2 = 0.3; variance accounted for = 28.5%, species-environment Pearson's

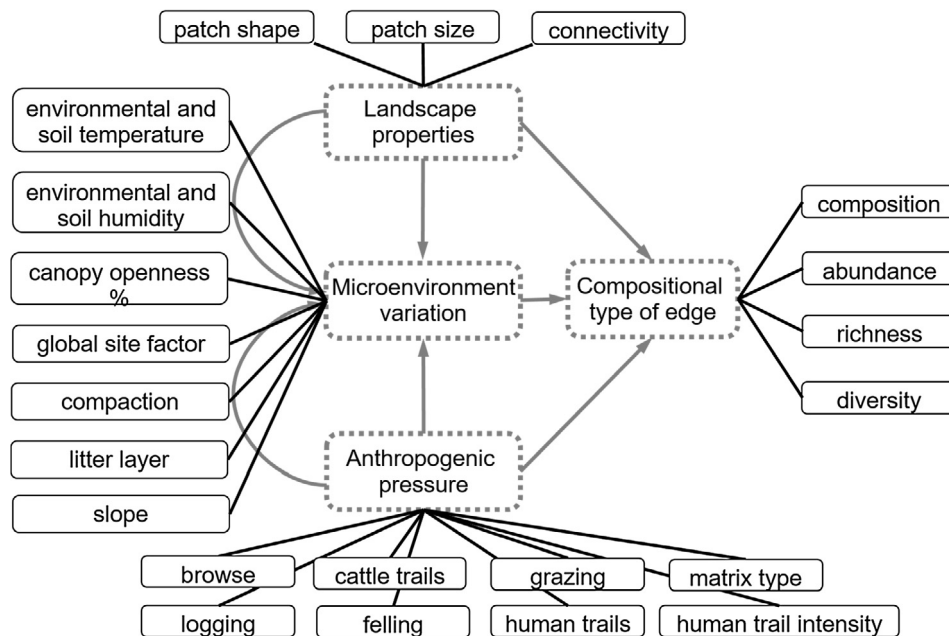


Fig. 2. Hypothetical relationships between latent and observed variables used in the structural equations model. Boxes with broken lines = latent variables; boxes with solid lines = observed variables.

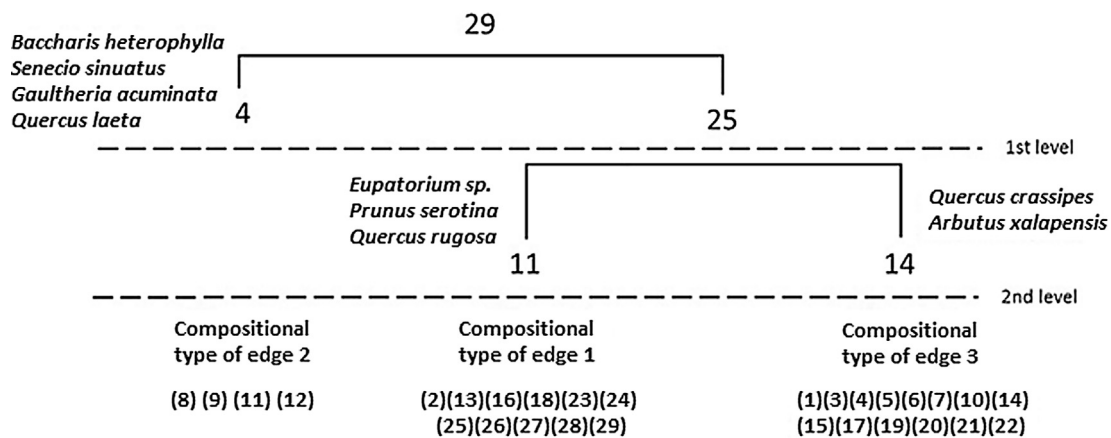


Fig. 3. Results of the two-way indicator species (TWINSpan) analysis for 29 forest patches. Numbers in parentheses represent individual patches; the species characteristic of each cluster are listed.

Table 1

Characteristics of the species composition of the edge types identified in 29 forest patches in the San Jeronimo river watershed, Mexico.

Edge type	Number of patches	Abundance	Richness	Shannon-Wiener	Simpson	Equitability	Weeds richness	Weeds Abundance
1	4	413	28	1.18	0.9	0.81	6	60
2	14	515	30	1.07	0.85	0.72	10	102
3	11	469	23	1.12	0.88	0.82	7	106

correlation = 0.87; Monte Carlo test: P = 0.33). However, the three variables examined, i.e. patch shape, patch size and connectivity, were determinant of compositional types of edge: patch shape and size were correlated with the presence of type 1, while connectivity was related to the presence of types 2 and 3.

The results of CCA of anthropogenic variables (Fig. 6c) were not statistically significant (axis 1 eigenvalue = 0.4, axis 2 = 0.3; variance accounted for = 30.8%; species-environment Pearson's correlation = 0.89; Monte Carlo test: P = 0.25). Only two variables were correlated with the presence of compositional types of edge: logging was related to type 1; browsing – an indicator of grazing – was correlated with the presence of type 2.

By contrast, the results of CCA of microenvironmental variables (Fig. 6d) were statistically significant (axis 1 eigenvalue = 0.5, axis 2 = 0.3; variance accounted for = 60.7%; species-environment Pearson's correlation = 0.98; Monte Carlo test: P = 0.01). Light and temperature were the variables most closely correlated with the arrangement of patches in the ordination. Canopy openness was correlated with the presence of compositional type of edge 1, whereas air and soil temperature were correlated with types 2 and 3 to a lesser degree.

The residuals of the CCA models analyzed by the Moran's I showed that the samples are spatially dispersed. Although some samples are apparently grouped, the statistical test indicates that the main floristic groups of the area are spatially dispersed. The results of the Moran's I

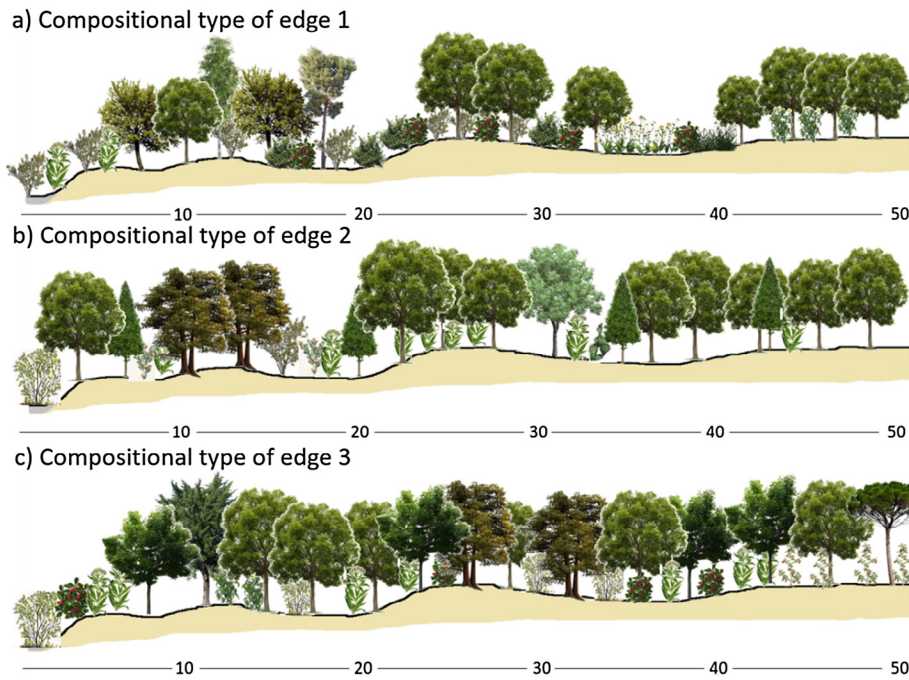


Fig. 4. Vegetation profile of the compositional types of edge identified by a TWINSpan of 29 patches along a 50 m edge-interior transect.

applied to the residuals of the CCA models of the landscape properties (observed = -0.0079, expected = -0.0018, sd = 0.0007, P = 0.000), the CCA of the anthropogenic variables (observed = -0.0084, expected = -0.0018, sd = 0.0007, P = 0.000) and the CCA of the microenvironmental variables (observed = -0.0106, expected = -0.0018, sd = 0.0007, P = 0.000). Observed values close to 0 and the statistically significant P value indicate that the sampling

points are more spatially dispersed than would be expected if the underlying spatial processes were random.

The variance partitioning test shows that microenvironmental variables explain 20% of the variance, landscape variables explain 18%, meanwhile, the combined effect of the three groups explain 13% of the variance. Finally, the anthropogenic variables only explain 1% of the variance.

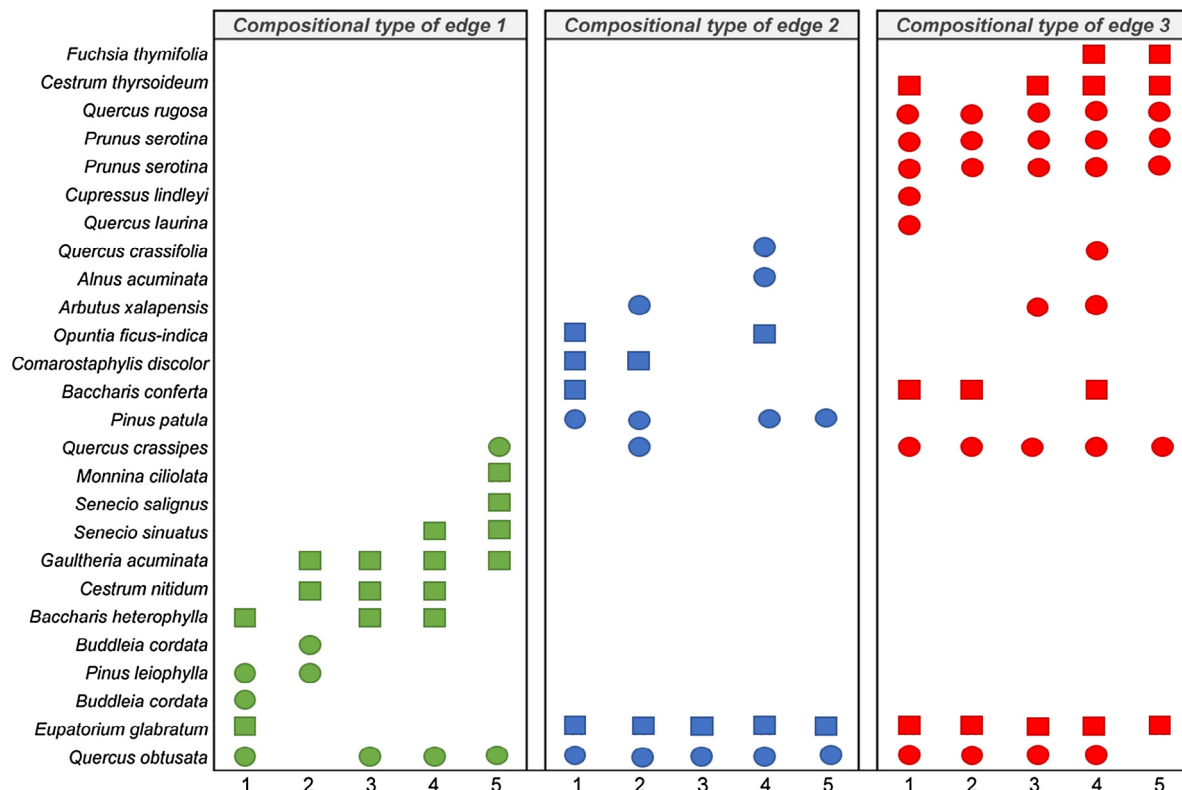
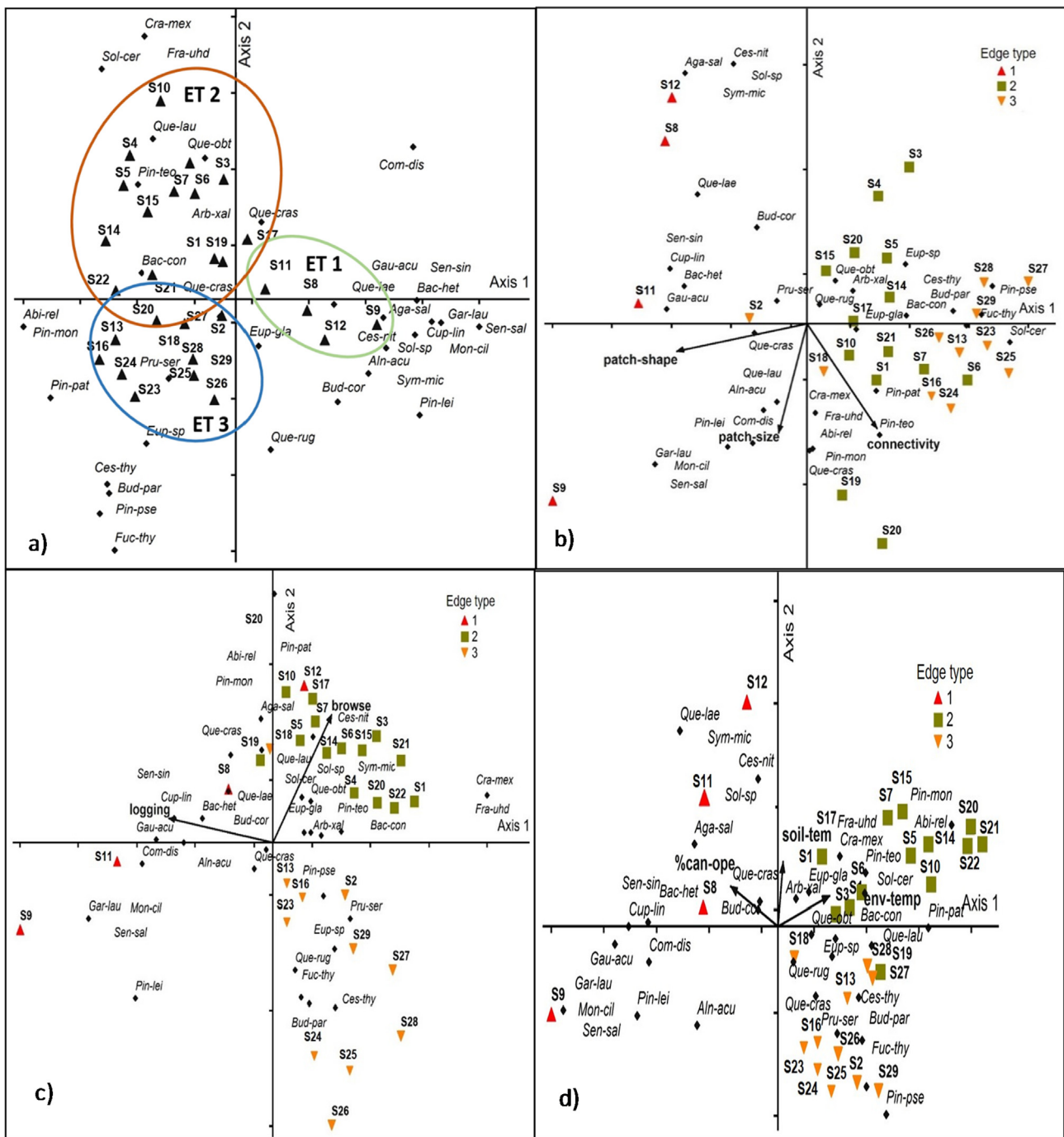


Fig. 5. Species-presence and differences in the compositional types of edge identified by a TWINSpan of 29 forest patches in the San Jeronimo river watershed, Mexico. Tree (circle) and shrub (square). Axis x show sections from 10 m along a 50 m edge-interior transect.



**Fig. 6.** Results of the correspondence analysis of species and compositional types of edge in 29 forest patches in the San Jeronimo river watershed, Mexico. (a) Detrended correspondence analysis (DCA), (b) canonical correspondence analysis (CCA) of landscape variables, (c) CCA of anthropogenic pressure variables, and (d) CCA of environmental variables.

### 3.3. Evaluation of the multi-causal dynamics of edge effects

The best fit model ordered cause and effect as shown in Fig. 7. The goodness of fit of the final model was acceptable, according to the three indices used (AIC = 10.17, RMSEA = 0.053, GFCI = 0.995;  $\chi^2 = 12.179$ ,  $df = 11$ ,  $P = 0.350$ ). The relationships between the latent variables outlined in the initial hypothesis did not hold, as landscape properties were the only variables that had a significant effect (path coefficient  $r = 0.6$ ) on the microenvironmental variations in edge types (Fig. 7). In turn, microenvironmental variation was the latent variable with the greatest effect on the species composition of edges. Regarding the independent effects of variables on compositional types of edge, out

of the several landscape properties tested, only patch shape and size showed a statistically significant effect on types 2 and 3; with the effect of patch size being greater on edge type 3 ( $r = 0.6$ ). As for the micro-environmental variables tested, only canopy openness and the amount of leaf litter had significant effects on the compositional types of edge. Canopy openness had the largest effect on types 1 and 3 ( $r = 0.5$  and  $r = 0.6$  respectively); the amount of leaf litter influenced type 2 ( $r = 0.5$ ).

### 4. Discussion

The analyses of the edge vegetation of forest patches in central

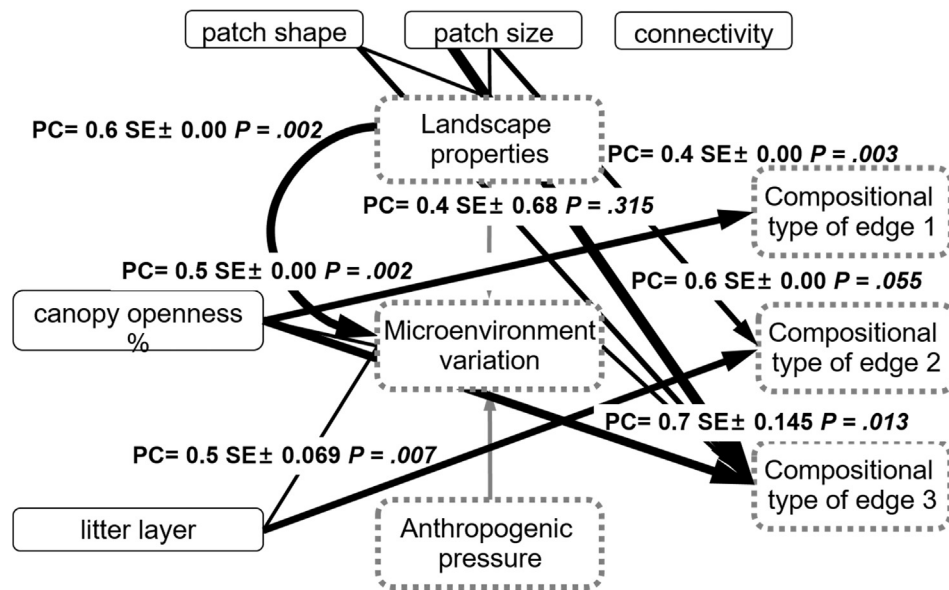


Fig. 7. Final best-fit model describing the relationships of landscape, anthropogenic pressure and microenvironmental variables with compositional types of edge. Arrow thickness denotes the magnitude of the PC = path coefficients ( $r$ ) and SE = standard error between variables.

Mexico led to the identification and characterization of three distinct compositional types of edge. Floristic differences between the edge communities due to their different environmental conditions were also correlated with differences in species composition and abundance. Such contrasts in species composition and abundance also suggest differences in the dynamics of communities or patches that result from differences in the prevailing environmental or spatial conditions in different compositional types of edge (Asbjornsen et al., 2004, Harper et al., 2005), for example, the presence of weed species in the different compositional types of edge might also denote the level of forest degradation (Hansen and Cleverger, 2005). Weeds were most abundant in compositional type of edge 2, followed by types 3 and 1.

According to Granados et al. (2014), the temperate forests of the northern slope of the Sierra de Monte Alto have core areas that extend more than 50 m from the edge of the fragments. In that transition the values of composition (diversity, wealth and abundance) decrease, as well as, the abundance of hardwood species in relation to the conifers. Although the present study does not include data for the interior of the fragments, it is notable that the tree species found in our compositional types of edge, coincide with hardwood species that show preference for edge environments (*Arbutus xalapensis*, *Crategus mexicana*, *Quercus crassipes*, *Q. rugosa* and *Prunus serotina*), and with widely distributed cultivated pines (*Pinus patula*) (Granados et al., 2014). For the above, the compositional type of edge 2 (a high-contrast edge type with madrone and oak trees, with no understory) would correspond to a lower ecological quality, since it includes the largest number of species considered as indicators of environmental edge, in addition to including the largest number of weed species, which accounted for 19.81% of the total abundance of all species.

To explore whether these vegetation patterns are due to variations in environmental factors, a DCA was conducted. This analysis effectively identified environmental gradients correlated with the three compositional types of edge. The identification of the variables that most contribute to explain the data variation required the assessment of their independent effects through a canonical correspondence analysis, as well as an integrated analysis of their effects by means of a structural equations model including all the variables recorded.

Although the results of the CCA of landscape properties were not statistically significant, the three variables used were correlated with the presence of the different compositional types of edge. Connectivity was an important factor for edge types 2 and 3, as patches included in

them were smaller than those included in edge type 1. Connectivity helps prevent soil erosion, besides favoring a constant flow of organic matter associated with areas with dense layers of plant material that increase humidity in the inner habitat. Compositional types of edge 2 and 3 were, in fact, those where the highest amount of litter was recorded (Grez and Bustamante, 1995; Mitchell et al., 2014).

On the other hand, patch shape and size were the variables most closely correlated with the species composition and abundance of patches included in edge type 1. These patches were the largest, in agreement with literature reports pointing out that a large patch will have a greater capacity to support and maintain more species than a small one (Collinge, 1996; Pincheira-Ulbrich et al., 2009). Regarding the CCA of anthropogenic pressure variables, it should be noted that such variables did not produce the expected effect, perhaps due to the strong pressures that the system withstands throughout the study area. Only logging caused some effect on edge type 1, and the presence of livestock (as indicated by browsing) had some effect on edge type 2. None of the variables considered had a statistically significant effect on the composition of edge type 3. The relationships identified through the canonical analysis of anthropogenic pressure variables would have been more informative had the objective of the analysis been to examine the disturbance level at each edge type and relate it to the presence of weeds (as disturbance indicators). However, the effect of these variables was weak, which restrained the identification of these effects (Saunders et al., 1991; Cadenasso and Pickett, 2000; Pauchard and Alaback, 2006; Saunders et al., 1991).

In the CCA of microenvironmental variables, only three of the seven variables considered showed a statistically significant effect on the composition of the edge types. In general, insolation (as measured by canopy openness) was strongly related to edge type 1 due to the physiognomy of this group of patches, in which the understory predominates over the tree layer. Therefore, plants in these patches are subject to higher temperature coupled with lower humidity and soil moisture (Oosterhoorn and Kapelle, 2000). On the other hand, soil and air temperature are a determining factor for species in edge type 2; this agrees with the physiognomy of this group, where the tree layer predominates over the understory, fostering cooler conditions. Similarly, in this analysis no factor had a statistically significant effect on the composition of edge type 3. It is worth mentioning that other studies have shown that most microclimatic variables included in this analysis do have significant effects on vegetation cover. However, such variables



may not have the same effect on the composition variables of the different compositional types of edge (Matlack, 1993).

The use of structural equation models was key for identifying direct and indirect effects of causal factors of edge effect at different scales. The comprehensive model of multi-causal dynamics built in this study led to results that confirmed those obtained by the analysis of the independent effects of variables on the species composition of edge types. For example, the results of the CCA of anthropogenic pressure variables were only marginally significant, while the effects of these variables were null in the SEM. These results are contrary to other studies suggesting that the type of surrounding matrix (agriculture, pastureland or forest plantation) determines to a great extent the edge type (Fahrig, 2003; Pauchard and Alaback, 2006; Ries et al., 2004; Williams-Linera et al., 2002), while confirming the results reported by Santibáñez-Andrade et al. (2015), who found that anthropogenic pressures had only a weak effect on the ecosystem composition, structure and function for forests in southern Mexico City.

However, some microenvironmental variables were strongly correlated with the composition of compositional types of edge, particularly canopy openness and the presence of leaf litter. This agrees with the results obtained by Matlack (1993) and Marchand and Houle (2006). As these edges are wider and more recently exposed, it has been shown that the increase in solar radiation governs microclimate in several forest ecosystems; besides, several studies have demonstrated that physical gradients depend on light availability. In relation to the CCA results, it is worth stressing that temperature was not a determining factor; on the contrary, the amount of litter – which was not considered initially – was one of the explanatory variables included in the final SEM.

Finally, the hypothesis proposed about the relationship between the ecological conditions of patches (biological composition) and small-scale ecological factors (such as habitat heterogeneity)—which, in turn, were affected by factors acting at a larger scale such as the spatial attributes of landscape and anthropogenic disturbances—was only partially accepted (Saunders et al., 1991).

Because of this, one of the expected results of the multivariate and SEM analyses was that factors acting at a broad scale (i.e. indirect factors) would have some effect on factors acting at a smaller scale (i.e. direct factors). In other words, we expected that the spatial attributes of patches and anthropogenic pressure factors would affect the environmental characteristics and, consequently, the floristic composition of edges (Fischer and Lindemayer, 2007). However, this relationship was not clearly observed in our model.

The microenvironmental variables (mainly canopy openness and leaf litter) are the most direct drivers of vegetation composition. The spatial attributes of the fragments (size and shape of the fragments), which have been of higher hierarchy (Collinge, 1996; Pincheira-Ulbrich et al., 2009), should be understood as significant indirect factors of the edge dynamics, by exercising control over micro environmental variables. However, the expected control by the anthropogenic variables was not clear, probably because, although the various human activities are highly impacting on the ecosystem, they do not occur through an interior-border gradient.

Finally, understanding the effects of habitat fragmentation requires comprehending the edge effects to account for regional variations in the sensitivity of species to fragmentation, where the relative importance of the factors analyzed is likely to vary depending on the study scale (Fletcher, 2005; Laurance, 2000).

## 5. Conclusions

The use of multivariate statistical methods allowed us to gain a deeper understanding of the multi-causal dynamics of edge effects in temperate forest patches in the periphery of Mexico City. The statistic TWINSpan results showed that, the species composition of edge environments makes it possible to differentiate three distinct

compositional types of edge. One of the advantages of using edge responses and evaluating the impacts of habitat change is that these can finetune the design of conservation strategies and the planning of ecological corridors (Sisk et al., 2002). Microenvironmental factors such as canopy openness and leaf litter percentage did have a significant causal effect on the compositional types of edge; among landscape properties, patch size and shape also had a statistically significant effect. However, none of the anthropogenic pressure factors recorded showed any significant effect on the species composition of edges. The hypothesis proposed, namely that factors operating at a larger scale—landscape properties and anthropogenic pressure—indirectly affect those operating at a smaller scale—microenvironmental variation, which in turn directly affects the composition of edge vegetation—was partially correct. However, only landscape properties had an indirect effect on microenvironmental variation.

To note, few studies have addressed the overall effect of all these factors on edge environments, as traditional approaches have focused on analyzing each individual factor separately. The complexity of the analysis of this floristic variability (derived from the multi-scale nature of the factors involved) leads to the use of multivariate models to evaluate more precisely the effect of causal factors on the formation of different edge types and their relationship to the differential response of vegetation (Podani, 2000). The final model obtained here can be used as a tool for the implementation of management and conservation strategies in fragmented forests, identifying the direct and indirect causes that exert the greatest impact on floristic variation.

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