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Research Article

Association between small rodents and forest patch and landscape structure in the fragmented Lacandona rainforest, Mexico

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Abstract

Identifying the main factors that shape biological communities in human-modified tropical landscapes has key ecological and conservation implications. In these emerging landscapes, the maintenance of biodiversity may depend on both forest patch and landscape attributes, but this topic has been poorly investigated. Here we assessed the landscape (forest cover, degree of fragmentation, and matrix composition) and patch metrics (tree basal area, patch size, and isolation) that best predicted the abundance and diversity of small terrestrial rodents in the Lacandona rainforest, Mexico. In 2011 and 2012, we sampled rodent communities in 12 sites (9 patches and 3 areas within a continuous forest). We assessed the landscape characteristics within a 100-ha buffer from the center of each site. In total, we captured 78 individuals in 2011 and 82 individuals in 2012 from four species: Desmarest's Spiny Pocket Mouse (*Heteromys desmarestianus*), Rice Rat (*Oryzomys* sp.), Mexican Deermouse (*Peromyscus mexicanus*), and Toltec Cotton Rat (*Sigmodon toltecus*). Only the abundance of rodents was strongly associated with forest patch and landscape attributes, but the best predictors differed between years. The degree of fragmentation, matrix composition, and patch isolation showed the lowest impact on rodents, probably because the region is dominated by a highly heterogeneous anthropogenic matrix. Community composition was weakly related to patch and landscape attributes in both years. Overall, our findings suggest that almost a half-century of land use in the region has not led to significant changes at the community level, but additional long-term studies including arboreal species are needed before a strong conclusion can be drawn.

Keywords: Fragmentation *per se* · *Heteromys desmarestianus* · Hyperdinamism · Long-term studies · *Sigmodon toltecus*

Resumen

Identificar los factores principales que moldean las comunidades biológicas en paisajes tropicales fragmentados tiene implicaciones ecológicas y de conservación muy importantes. En estos paisajes antropogénicos, el mantenimiento de la biodiversidad puede depender de atributos espaciales del fragmento y del paisaje, sin embargo, este tema ha sido pobremente investigado. En este trabajo evaluamos las métricas del paisaje (cobertura forestal, grado de fragmentación y composición de la matriz) y del fragmento (área basal de árboles y tamaño y aislamiento del fragmento) que predicen de mejor manera la diversidad y abundancia de roedores terrestres pequeños en la selva Lacandona, México. En 2011 y 2012 muestreamos las comunidades de ratones en 12 sitios (9 fragmentos y 3 sitios dentro del bosque continuo). Evaluamos las características del paisaje dentro de un buffer de 100-ha a partir del centro de cada sitio. En promedio, capturamos 80 individuos de cuatro especies cada año: la rata espinosa (*Heteromys desmarestianus*), la rata arrocera (*Oryzomys* sp.), el ratón mexicano (*Peromyscus mexicanus*) y la rata algodonera (*Sigmodon toltecus*). Solamente la abundancia de roedores estuvo fuertemente asociada a los atributos del fragmento y del paisaje, pero los mejores predictores difirieron entre años. El grado de fragmentación, la composición de la matriz y el aislamiento del fragmento mostraron el menor impacto sobre los roedores, debido probablemente a que la región se encuentra dominada por una matriz altamente heterogénea. La composición de la comunidad estuvo débilmente asociada a las métricas espaciales. En conjunto, nuestros hallazgos sugieren que casi medio siglo de cambio de uso de suelo en la región no ha resultado en cambios significativos a nivel de comunidad, sin embargo, es necesario realizar estudios a largo plazo que incluyan a las especies arborícolas antes de generar conclusiones definitivas.

Palabras clave: Fragmentación per se · Heteromys desmarestianus · Hiperdinamismo · Estudios a largo plazo · Sigmodon toltecus

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Introduction

With the expansion of croplands, pastures, plantations, and urban areas in tropical forests, increasing proportions of continuous forests have been transformed into fragmented landscapes [1]. These landscapes differ in structure, that is, in composition (land cover types) and configuration (the spatial arrangement or physiognomy of each land cover [2]). The remaining forest patches can also differ in size, shape, isolation, and resource availability [3]. Because each of these patch and landscape structural modifications can shape biological communities in human-modified landscapes [4-6], assessing the response of biodiversity to both forest patch and landscape attributes is needed to improve management and conservation plans [7-9].

Important discussions in fragmentation studies have been poorly tested in tropical forests [6, 10]. For example, because fragmentation *per se* (the breaking apart of forest while controlling for forest loss; *sensu* Fahrig [11]) results in smaller forest patches and more forest edge, to which tropical species usually respond negatively [12], it has been proposed that, unlike temperate forests, tropical forest fragmentation *per se* (fragmentation, hereafter) could be substantially more important than forest loss in determining patterns of species diversity [11, 13-14]. It has also been proposed that the response of biodiversity to landscape changes depends on the composition of the surrounding matrix, and that matrix quality can actually drive the maintenance of species in fragmented tropical landscapes [15-19]. Finally, because individuals in forest patches also face significant reductions in food availability, animal populations and communities may be more affected by local changes in food availability than by landscape characteristics, particularly forest-dwelling species with small home range sizes and low vagility (e.g., terrestrial mammals [20-21], primates [22]).

Small rodents are involved in key ecological processes for forest regeneration, such as seed dispersal and seed predation [23-25]. At the same time, these mammals are the primary prey for many birds, mammals, and reptiles. Thus, assessing the impact of forest patch and landscape attributes on small rodents has key ecological and conservation implications. Unfortunately, this topic has been poorly investigated in tropical forests, as most studies have been performed at the patch scale [e.g., 26-31] or in island ecosystems [32-33]. This implies that landscape-scale inferences are not possible [11], and that comparisons with countryside ecosystems are very difficult because the matrix is functionally different from island ecosystems [19, 34]. Furthermore, variations in biological attributes among species, such as body size, longevity, fecundity, and arboreality [35-36], as well as differences in the remaining forest cover in the landscape [10, 37-38], cause great variability in the response of species to human-imposed disturbances

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among different regions [17, 38-40]. Further studies are therefore required to determine the main drivers of rodent diversity in human-modified tropical landscapes.

Here we adopted a multi-scale approach to assess the landscape (forest cover, degree of fragmentation, and matrix composition) and patch metrics (tree basal area, patch size and isolation) that best predicted differences in the abundance and taxonomic diversity of small terrestrial rodents in a biodiversity hotspot – the Lacandona rainforest, Mexico. This rainforest is one of the biologically richest Mexican ecosystems, with 25% of Mexican terrestrial mammal species [41]. The region has suffered severe land-use changes during recent decades, but only one study in the region has evaluated the response of small mammals to these changes [26]. Medellin & Equihua [26] show that the number of rodent species is similar in abandoned crop plots and mature forests. However, there is no information on the impact that forest patch and landscape characteristics may have on the abundance and diversity of rodent communities within old-growth forest patches.

Because the region still maintains its original fauna, including a large number of predator species [14, 41], we first expected that, in general, the abundance of rodents would be low, as predators prevent the increase of rodent abundance within ecosystems [42], and evidence indicates that the density of rodents is lower in sites occupied by predators than in sites where predators have disappeared [43]. Nevertheless, because in this region the number of mammal species (including several predators of rodents) is positively related to patch size [14], and because the abundance and species richness of small mammals can increase in smaller forest patches [31], we predicted that the abundance and diversity of rodents would be negatively related to forest patch size and to the amount of forest cover in the landscape [but see 28]. Regarding fragmentation, positive, negative and neutral effects have been reported for several taxa, including mammals [11, 13], but according to Malcolm [31], the high productivity associated with forest edges may favor small rodents by increasing resource availability. Thus, because forest fragmentation increases forest edges [11], we would expect a positive effect of fragmentation on the abundance and diversity of rodents. In contrast to forest edges, cattle pastures are expected to contain fewer resources and refuges for forest-dwelling mammals, and we therefore predicted that the abundance and diversity of rodents will decline in patches surrounded by a matrix dominated by cattle pastures [17, 30, 44]. Finally, because almost all rodent species in the Lacandona rainforest are granivores [41], and tree basal area in tropical forests is an accurate estimator of fruit availability [45], local tree basal area will be positively associated with the abundance and diversity of rodents. In fact, tree basal area has been shown to be a good predictor of mammal species richness [21] and primates' distribution [46] in neighboring Mexican forests.

Methods

Study area

The Mexican portion of the Lacandona rainforest is located in southeastern Chiapas State. It is delimited to the south and east by the Guatemalan border and to the north and west by the Chiapas highlands (16º05'58'' N, 90º52'36'' W; 80-500 m a.s.l.; Fig. 1). This region represents the largest tropical rainforest remnant in Mexico and is considered a biodiversity hotspot [47]. Unfortunately, this rainforest has been extensively deforested during the last 40 years, particularly in the Marqués de Comillas region (MCR). The area was originally covered by over 1.4 million ha of rainforest, but deforestation has eliminated 60% of the original forest cover [48-49], with an annual deforestation rate of 2.1% between 1990 and 2010 [50].

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The remaining old-growth forest patches are nowadays surrounded by a matrix of cattle pastures, agricultural lands (oil palm, rubber, corn, rice, beans, lemon), secondary forests, and human settlements. The climate is hot and humid. Average monthly temperature ranges from 24 °C to 26 °C, and annual precipitation averages 2,500 to 3,500 mm, with the greatest rainfall concentration between June and November. In this forest, fruits and seeds are available the whole year around, but there are three distinguishable annual peaks in fruit production: the first in January, the second during the dry season (March and April) and the third during the rainy season (September-October) [51].

Study sites

This study is part of a larger project in which we are evaluating the relative impact of forest patch and landscape metrics on different taxa [14, 22]. The fieldwork was conducted in MABR, comprising 331,200 ha of old-growth forest, and in MCR, comprising 203,999 ha of forest patches and human-modified lands (Fig. 1). The two areas are separated by the Lacantun River (ca. 150 m wide). We selected three reference sites within MABR, separated > 4 km from each other and at least 1 km from the border of the Lacantun river to avoid edge effects. In MCR we selected nine forest patches ranging from 3 to 92 ha (Fig. 1; Appendix 1).

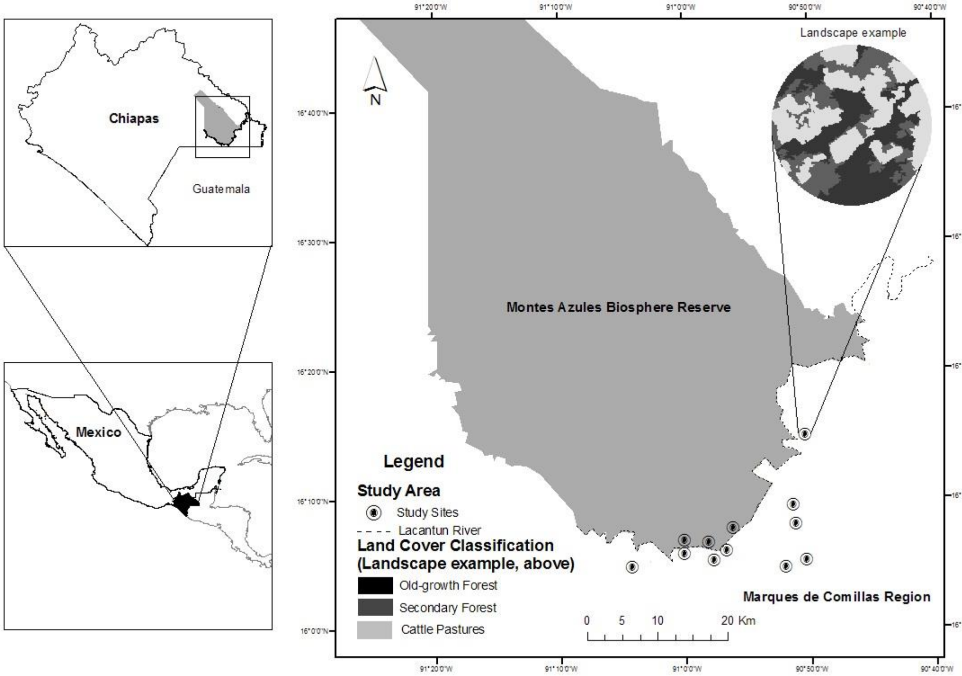

Fig. 1. Location of the study sites in the Lacandona rainforest, Mexico. We show the location of the nine fragmented landscapes in the Marqués de Comillas region and the three reference areas in the Montes Azules Biosphere Reserve. We described the landscape spatial pattern of all sites considering a buffer (i.e., concentric circle) of 100 ha (see an example in the upper right side). The figure was modified from Garmendia *et al*. [14].

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Rodent surveys

Small rodents were sampled within each site during two field sessions, from April to August in 2011 and 2012, encompassing parts of the dry and rainy seasons of both years. We placed 120 Sherman traps in each site for 8 consecutive nights (960 trap-nights per site and year, totaling 23,040 trap-nights). Sites were sampled following a randomly selected order to avoid bias related to differences in tree phenology and resource availability among sites. Sherman traps were placed in a grid of 90 x 110 m, with a distance between traps of 10 m. The grid was located in the center of each forest patch (avoiding tree-fall gaps) to control for edge effects [12]. Within reference sites, the grid was located in the center of a circular area (i.e., landscape) of 100 ha. Traps were baited with a mixture of oats, sunflower seeds, and vanilla. Animals were marked with gentian violet to identify recaptures. This non-invasive short-term marking technique allows the identification of marked individuals for several months, and has no adverse physiological effects on mammals [52]. Because traps were placed on the ground, all captured arboreal species were excluded from further analyses: i.e., Big-Eared Climbing Rat (*Ototylomys phyllotis*), Peters's Climbing Rat (*Tylomys nudicaudus*), and Mexican Mouse Opossum (*Marmosa mexicana*). Because all these arboreal species showed very low abundances, the inclusion of these species in the analyses would increase the probability of finding spurious associations. Finally, *Oryzomys* (=*Handleyomys*) species were treated at the genus level because of inconsistencies in their taxonomy in the region and the non-invasive nature of this study.

Spatial metrics

Following Fahrig [53], we used a sample site-landscape approach. We characterized the spatial composition and configuration of the landscape surrounding each sampling site within a 100-ha buffer from the center of each site, using recent SPOT 5 satellite images (March 2011) and the GRASS GIS program. We selected this buffer size because it is large enough to include the home range of several populations of small rodents, which usually have small home ranges (< 0.4 ha [54]). In particular, we used a supervised classification with SPRING GIS [55] considering six land cover types: old-growth forests, secondary forests, tree crops (i.e., palm and rubber plantations), shrub crops (i.e., corn and bean plantations), cattle pastures, and human settlements. The overall classification accuracy was 77% (see Garmendia *et al*. [14]).

Within each 100-ha landscape we estimated the percentage of remaining forest cover, the degree of fragmentation, and matrix composition. We also estimated the density of forest/non-forest edges (expressed as meters per hectare) in the landscape, but as described below it was excluded from the analyses to avoid multicollinearity problems. The degree of fragmentation was evaluated as the ‘effective number of forest patches’:

$$EN = \frac{A_{forest}^2}{\sum_{i=1}^{n} A_i^2}$$

where A_{forest} is the area covered by forest in the landscape and A_i is the area of forest patch *i* (J. A. G. Jaeger and L. Fahrig, unpubl. data). This novel metric is independent of total forest cover in the landscape, and it is therefore a measure of fragmentation *per se* (*sensu* Fahrig [11]). Regarding the matrix composition, we estimated the percentage of the matrix covered by cattle pastures, as this land cover type dominates many human-modified tropical landscapes [1]. Also, it represents the highest contrast with the original vegetation and is expected to provide very few food resources, cover, or opportunities to disperse among

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forest patches [5]; it can thus show a negative impact on small mammals [30]. At the forest patch scale, we estimated the size and isolation of each patch. The isolation was measured as the mean inter-patch isolation distance (i.e., mean Euclidean nearest-neighbor distance of the focal patch to all patches within the 100-ha landscape). Furthermore, we quantified tree basal area within each site by summing the basal area of all trees with a diameter at breast height (dbh) ≥ 2.5 cm within five circles of 8-m radius each: one circle located in each trap's grid corner, and another one in the center of the grid.

Structure of rodent communities

We first evaluated the sampling completeness within each site using the estimator of sample coverage proposed by Chao & Shen [56]:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right]$$

where f_1 and f_2 are the number of singletons (species with one individual) and doubletons (species with two individuals) in the sample, respectively, and n is the number of individuals. The sample coverage varied notably among sites because of large variations in the number of singletons and doubletons. Sample coverage averaged (± SD) 88.8 ± 16.9% per site in 2011, and 88.8 ± 12.4% in 2012 (Appendix 2).

Species richness is not sensitive to species abundances and so gives a disproportionate weight to rare species [57]. It is thus strongly dependent on variations in sample coverage; i.e., in the number of rare species [58]. Therefore, to avoid biases related to variations in the number of rare species among sites and years, we also considered two diversity metrics that are less sensitive to variations in rare species and sample coverage: the exponential of Shannon's entropy (${}^1D$), and the inverse Simpson concentration (${}^2D$). These three metrics (species richness or ${}^0D$, ${}^1D$, and ${}^2D$) are considered true diversities (*sensu* [57]) because they obey the replication principle, which is required in biodiversity assessments as it conserves uniqueness of each species that compose an assemblage [59], being thus increasingly recommended in diversity evaluations [57-60]. The formulas are detailed elsewhere [e.g., 57, 60]. ${}^1D$ weights each species according to its abundance in the community, and can be therefore interpreted as the number of 'common' species in the community [60]. ${}^2D$ favors abundant species, and can be interpreted as the number of 'dominant' species in the community [57, 60].

Data analyses

To include reference sites in the regression models that are described below, we considered them as having 100 ha, zero isolation, zero edge density, 100% forest cover, *EN* = 1, and zero percentage of cattle pastures in the matrix. To avoid collinearity between the predictor variables and multivariate models, we first checked the relationships between all the predictor variables with Pearson correlations and each predictor´s variance inflation factor (VIF) [61]. VIFs were calculated for each predictor as the inverse of the coefficient of non-determination [$1/(1-R^2)$] for a regression of that predictor on all others. A VIF > 4 indicates "possible" collinearity, and VIF > 10 indicates "severe" collinearity [61]. Only edge density was strongly correlated to the percentage of the matrix covered by cattle pastures ($r = 0.91$, $P < 0.05$, VIF = 5.8), and hence, it was eliminated from the analyses. Due to our small sample size (12 sites) we could not test the impact of patch and landscape metrics simultaneously, so we performed two independent analyses, one to evaluate the association with patch metrics, and another with landscape metrics.

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To identify the landscape and patch attributes with stronger influence on the response variables described above, we used multiple regression analyses with generalized linear models (GLM). Using a multi-model inference approach [62], we identified the subset of models with stronger levels of empirical support. To this end, we considered two approaches. First, we considered the subsets of models with a difference in AICc values (ΔAICc) between the best model (i.e., with the lowest AICc value) and model *i* lower than 2 (i.e., ΔAICc < 2). This set of models can be considered the most plausible [62]. We used Akaike weights (w_i) to rank the importance of variables and produce model-averaged parameter estimates [62]. The relative importance of each predictor was evaluated with the sum of Akaike weights (Σw_i) of each candidate model in which each predictor appeared. In fact, Σw_i represents the probability that a given predictor appears in the best approximating model [62]. We also considered the set of models for which Σw_i was 0.95: we sequentially summed w_i of ranked models until the total was $\geq$ 0.95 [63]. This represents a set of models for which we have 95% confidence that the set contains the best approximating model to the true model [62-63]. Model-averaged parameter estimates and their unconditional variances were calculated from the 95% confidence set of models to assess the association between each predictor and each response variable [62]. As suggested for count response variables, GLMs for species richness (^0D) and total abundance were constructed using a Poisson error and a log-link function. Because overdispersion is common in GLMs with Poisson errors [64], we corrected overdispersion by using QAICc values instead of AICc in such models [65]. GLMs for ^1D and ^2D were tested using a Gaussian error structure, after testing that they showed a Gaussian distribution (Shapiro-Wilk test). We built models using the package *glmulti* for R (version R 2.15.3), which facilitate multimodel inference based on every possible first-order combination of predictor variables [65]. Because poor predictors are not expected to have w_i close to zero [63], we estimated the goodness-of-fit of the models by estimating the percentage of deviance explained by the complete (full) model compared with the null model (i.e., the model that includes only the intercept [64]).

To identify the landscape and patch attributes with stronger influences on the abundance of each species we used Canonical Correspondence Analysis (CCA) using the *vegan* package [66] for R (version R 2.15.3). This is a simple method for arranging species along environmental variables, and is very useful for detecting species–environment relationships. In fact, it is commonly used in ecological studies because it seems to be immune to most of the problems of other ordination techniques, such as Correspondence Analysis and Detrended Correspondence Analysis [67]. We used four CCAs: one for each year (2011 and 2012) and spatial scale (landscape and patch scales).

Results

Overview

We recorded 78 individuals in 2011 and 82 individuals in 2012 from a total of four terrestrial rodent species: Desmarest's Spiny Pocket Mouse (*Heteromys desmarestianus*), Rice Rat (*Oryzomys* sp.), Mexican Deermouse (*Peromyscus mexicanus*), and Toltec Cotton Rat (*Sigmodon toltecus*) (Appendix 2). The species with a higher number of individuals in each year were *H. desmarestianus* (41% and 30.5% of individuals sampled in 2011 and 2012, respectively) and *Oryzomys* = *Handleyomys* sp. (14.1% and 40.2%), followed by *S. toltecus* (23.1% and 17.1%) and *P. mexicanus* (21.8% and 12.2%). Three species were recorded within both continuous and fragmented forests, but *S. toltecus* (= *hispidus*) was only recorded in forest patches.

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Patch and landscape metrics associated with rodent communities

The metrics that best predicted the abundance of rodents differed between years. In 2011, the abundance of rodents was mainly (and positively) related to patch size ($\Sigma w_i = 0.82$; Fig. 2A; Appendix 3), whereas in 2012 it was principally associated (negatively) with tree basal area ($\Sigma w_i = 0.82$; Fig. 2B; Appendix 3). At the landscape scale, the number of individuals in 2011 increased principally in landscapes with higher forest cover ($\Sigma w_i = 0.94$; Fig. 2C; Appendix 3), whereas in 2012 the abundance of individuals was weakly related to differences in landscape structure (with only 12% of explained deviance by the complete model; Fig. 2D Appendix 3).

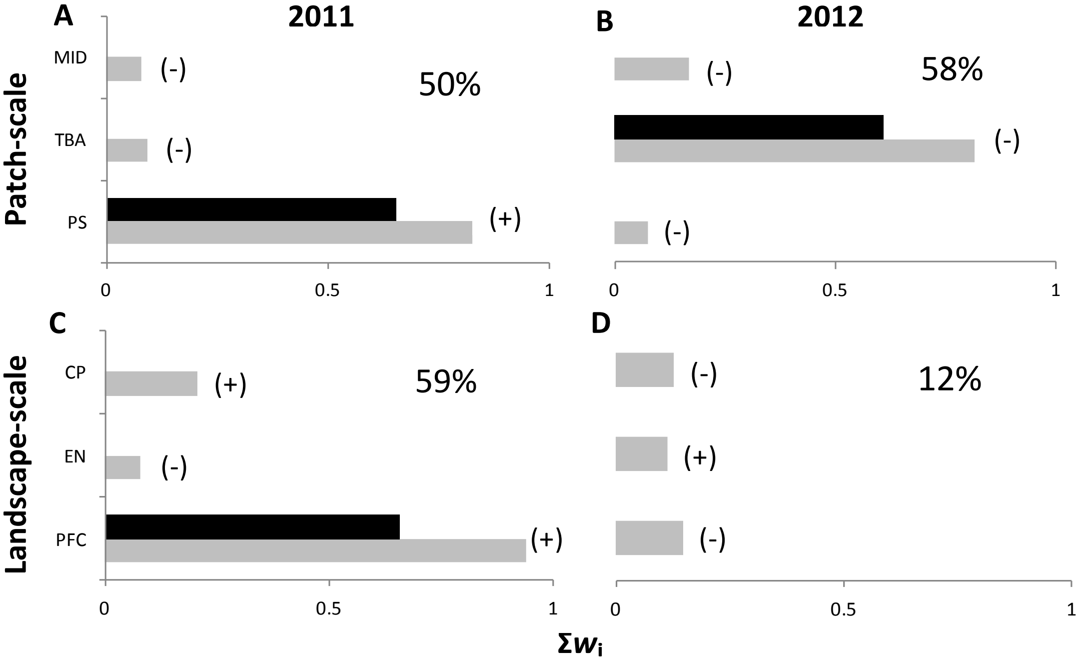

Fig. 2. Patch and landscape predictors included in the ΔAICc < 2 set of models (black bars) and 95% set of models (gray bars) for the abundance of small rodents in 2011 (A, C) and 2012 (B, D) in the Lacandona rainforest, Mexico. The importance of each predictor is showed by the sum of Akaike weights of all the models for which such variable was included. We show the sign of model-averaged parameters in each case (+/-) to indicate the direction of predictor effects on each response variable (see details in Appendix 3). We also indicate the percentage of explained deviance by each complete model. Predictors: PS = patch size; TBA = tree basal area; MID = mean inter-patch isolation distance; PFC = percentage of forest cover; EN = effective number of patches (fragmentation *per se*); CP = percentage of the matrix covered by cattle pastures.

As in the case of rodent abundance, the metrics that best predicted the diversity (${}^0D$, ${}^1D$, and ${}^2D$) of rodent communities also differed between years, but in this case the relationships were much weaker, with most models explaining less than 30% of deviance (Fig. 3). Species richness (${}^0D$) was associated with patch metrics only in 2012 (36% of explained deviance) and was negatively related to tree basal area ($\Sigma w_i = 0.29$; Fig. 3B; Appendix 3). The associations found for the number of common species (${}^1D$; Figs. 3E-H) were very

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similar to those found for the number of dominant species (^2D; Figs. 3I-L). In particular, both ^1D and ^2D were mainly related to patch metrics in 2012 (Figs. 3F and 3J), with the number of species decreasing with mean isolation distance. Yet ^1D (Fig. 3G) and ^2D (Fig. 3K) were weakly related to landscape metrics in both years, with ≤ 6% of explained deviance.

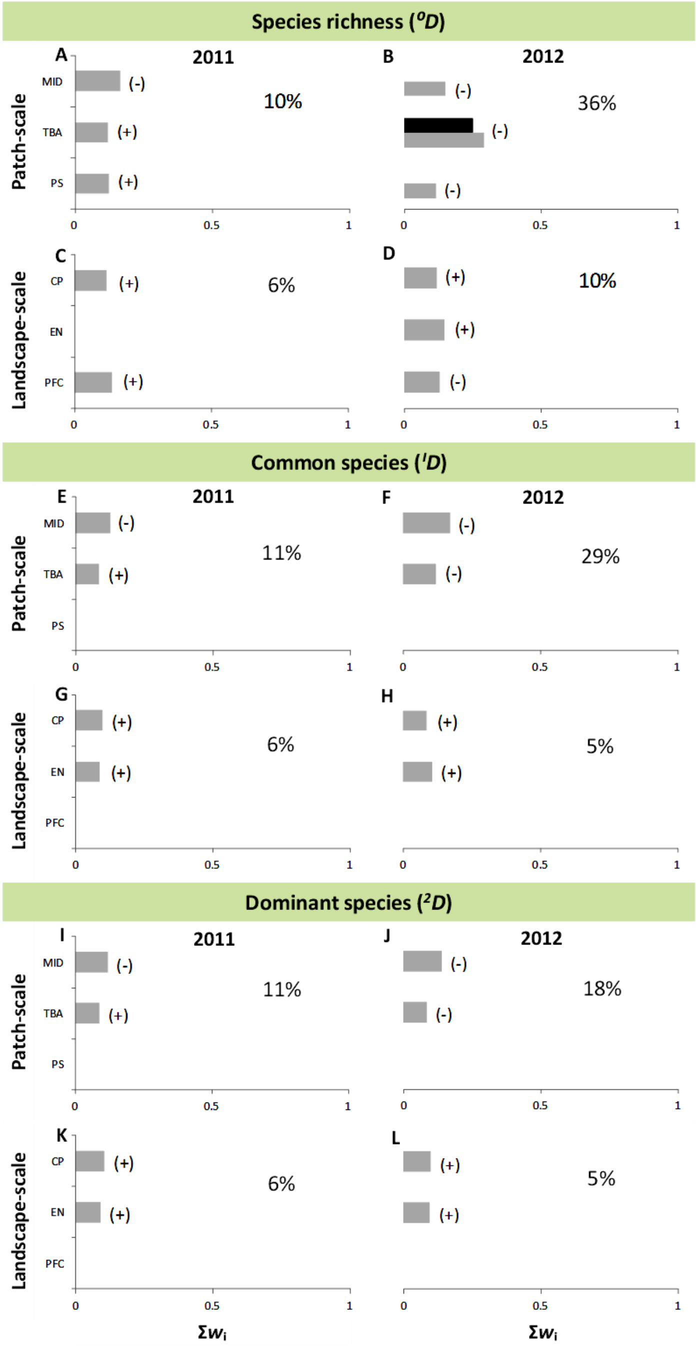

Fig. 3. Patch and landscape predictors included in the ΔAICc < 2 set of models (black bars) and 95% set of models (gray bars) for the diversity of rodent species (i.e., ^0D = species richness; ^1D = exponential of Shannon's entropy index; ^2D = inverse Simpson concentration) in 2011 and 2012 in the Lacandona rainforest, Mexico. The importance of each predictor is showed by the sum of Akaike weights of all the models for which such variable was included. We show the sign of model-averaged parameters in each case (+/-) to indicate the direction of predictor effects on the response variable (Appendix 3). We also indicate the percentage of explained deviance by each complete model. Predictors: PS = patch size; TBA = tree basal area; MID = mean inter-patch isolation distance; PFC = percentage of forest cover; EN = effective number of patches (fragmentation *per se*); CP = percentage of the matrix covered by cattle pastures.

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Patch and landscape metrics associated with species composition

The first two eigenvalues of CCAs at the patch and landscape scales in 2011 explained 26.5% and 43.0% of the variation in rodent composition, respectively (Fig. 4A and 4C), whereas in 2012, they explained 34.0% and 39.7% of the variation (Fig. 4B and 4D). This indicates that community composition was weakly related to patch and landscape attributes in both years. However, some tendencies can be highlighted. First, in 2012 the abundance of *H. desmarestianus* tended to be positively associated with tree basal area and patch size, whereas *S. toltecus* was negatively associated with tree basal area (Fig. 4B). At the landscape scale, in 2011 and 2012 the abundance of *H. desmarestianus* tended to be positively related to forest cover, whereas the abundance of *S. toltecus* increased in landscapes with higher percentages of cattle pastures (Fig. 4C and 4D).

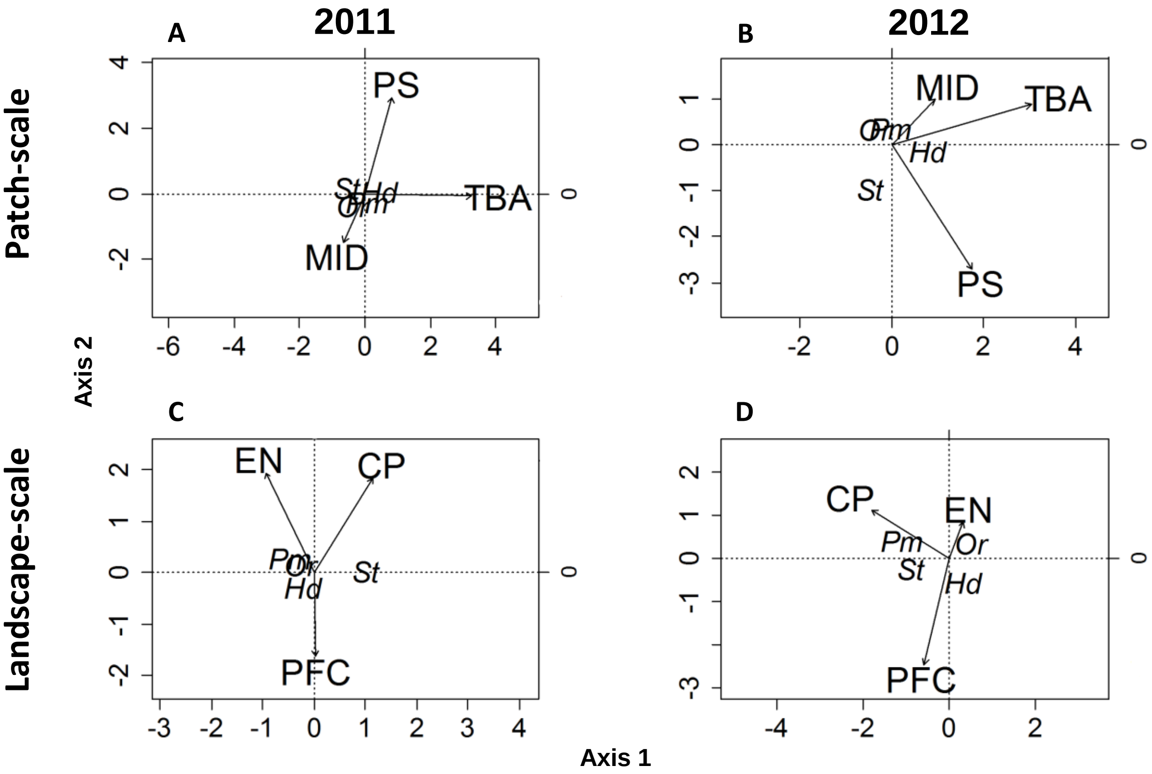

Fig. 4. CCA ordination diagrams displaying the rodent species recorded in the Lacandona rainforest, Mexico and its relationship with different spatial metrics (arrows) estimated at the patch (A, B) and landscape (C, D) scales in 2011 (A, C) and 2012 (B, D). Each arrow points in the direction of maximum change of that spatial metric across the diagram, and its length is proportionate to the rate of change in this direction. Spatial metrics: PS = patch size; MID = mean inter-patch isolation distance; TBA = tree basal area; EN = effective number of patches (fragmentation *per se*); CP = percentage of the matrix covered by cattle pastures; PFC = percentage of forest cover. Rodent species: Hd = *Heteromys desmarestianus*; Pm = *Peromyscus mexicanus*; Or = *Oryzomys* = *Handleyomys* sp.; St = *Sigmodon toltecus*.

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Discussion

This paper shows that, as expected, the abundance of rodents was very low in all sites, probably because the region has not experienced a significant defaunation process [14, 41], and hence, predators are preventing the increase of rodent abundances [42-43]. Yet the abundance of rodents was strongly associated with forest patch and landscape attributes, with most models explaining ≥50% of total deviance. In contrast, rodent diversity was weakly related to habitat spatial patterns. This would be related to the low number of species sampled. Further studies including arboreal species are needed to have a larger sample size, and our results should therefore be considered preliminary. Despite this limitation, however, some findings deserve special attention.

First of all, it was particularly interesting that the metrics that best predicted the abundance of rodents differed between years. For example, in 2011 the abundance of rodents was principally and positively related to patch size and landscape forest cover, whereas in 2012 it increased mainly in patches with lower tree basal area. This can be associated with the large variations in the abundance of rodents between years [68]. Because of their relatively small body sizes, small home range sizes, short generation times, and high reproduction rates, population sizes of small rodents are expected to be particularly variable among years in both continuous and fragmented forests [17, 68]. For example, *Oryzomys* sp. was rare in 2011, with 14% of individuals sampled, but in 2012, this species accounted for 40% of all individuals sampled. This species is known to have highly variable yearly population sizes [69], probably because of inter-year differences in food availability and disturbance regimes [70-71]. The variations in environmental stochasticity can also increase population and community dynamics, particularly in fragmented landscapes [72].

Second, contrary to the effect of patch size and landscape forest cover on the abundance of individuals, which was positive or negative depending on the year, tree basal area was negatively related to the abundance of rodents in both years (Appendix 3), and was actually the best predictor of species richness in 2012, with a negative effect. Although we predicted a positive association between tree basal area and the abundance and diversity of rodents, these negative associations can be explained by the absence of *Sigmodon toltecus* in continuous forests, and the higher abundance of *S. toltecus* and *Oryzomys* sp. in forest patches, in which we found the lowest values of tree basal area. *Sigmodon toltecus* and *Oryzomys* sp. are known to be common in perturbed areas [26, 73]. Both species have a generalist diet, which includes different plant items, not only seeds and fruits, allowing them to inhabit sites with low fruit availability. Therefore, in agreement with the 'intermediate disturbance hypothesis' [74], our results suggest that in the Lacandona rainforest, which has suffered a moderate land-use change, the abundance and diversity of rodents can be maximized in the fragmented portion of the region, in which we recorded both specialist and generalist rodent species. This is consistent with Malcolm [31], who found that the abundance and species richness of small mammals are higher in forest patches than in the continuous forest. The absence of predators in smaller patches [14] can also help to maintain higher abundances of these small mammals within the patches [see 42-43].

Finally, contrary to our prediction and with some empirical evidences [17, 44], forest fragmentation and the percentage of the matrix dominated by cattle pastures were not related to rodent communities. This can be explained by the fact that the matrix in the region is highly heterogeneous, potentially increasing the availability of food resources and refuges for rodents (see the 'landscape-moderated insurance

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hypothesis' [6]). In fact, as demonstrated for other forest-dwelling animals such as primates [75-76] and birds [77-78], small rodents can supplement their food intake by using resources from the surrounding matrix, including vegetation corridors, secondary vegetation, and even agricultural fields [26, 30-31], a process named 'landscape supplementation' (sensu Dunning *et al*. [2]). Medellin & Equihua [26] actually demonstrate that all rodent species in the region can be present in small abandoned crop plots, indicating that forest-dwelling rodents are able to cross and use these areas. Therefore, the very high heterogeneity of the matrix can help mitigate the potential negative effects of forest fragmentation and cattle pastures on small rodents in the region.

Implications for conservation

Although further study is needed before a strong conclusion can be drawn, our findings suggest that land-use changes in the Lacandona region have not resulted in significant alterations of rodent communities. This may be because deforestation in the region is a relatively recent event (< 40 years ago) and the region still maintains a relatively high amount of forest cover (ca. 40%) and a very heterogeneous matrix. Under this landscape scenario, the 'fragmentation threshold hypothesis' proposes slight (if any) responses of biodiversity to habitat spatial changes [38], as landscape connectivity is expected to be very high, allowing for greater ecological resilience [10, 38]. Thus, in agreement with other studies of plants [37; 79], birds [80], mammals [14, 22], and amphibians and reptiles [81], our findings indicate that in this region both small and large forest patches can be highly valuable for the conservation of rodent assemblages. Unfortunately, the future conservation of small rodents in the area is uncertain given the very high current rates of deforestation in the Marqués de Comillas region [51]. Thus, further long-term studies in the region will be required to monitor populations.

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Appendix 1. Patch and landscape (100-ha buffers) spatial attributes assessed in nine forest patches (P) within the Marqués de Comillas region, and three sites of continuous forest (CF) within the Montes Azules Biosphere Reserve, Lacandona rainforest, southeastern Mexico

	Patch metrics[a]			Landscape metrics[b]			
Site	PS	TBA	MID	PFC	EN	CP	ED
CF1	100	5.8	0	100	1	0	0
CF2	100	2.0	0	100	1	0	0
CF3	100	3.3	0	100	1	0	0
P1	2.8	1.8	355	3.1	1.2	16.2	14
P2	20.3	2.5	1,678	26.5	1.7	43.0	93
P3	20. 6	2.7	335	24.1	1.3	38.1	57
P4	22.4	2.5	982	41.1	2.4	75.6	95
P5	33.2	2.4	44	36.6	1.2	45.6	69
P6	33.4	2.3	251	37.8	1.3	82.6	102
P7	37.8	3.1	176	37.9	1.0	70.0	63
P8	65.5	3.4	608	65.8	1.0	61.7	92
P9	91.9	1.7	157	91.9	1.0	54.3	46

[a] PS = patch size (ha); TBA = tree basal area (m^2); MID = mean inter-patch isolation distance (m).
[b] PFC = percentage of forest cover (%); EN = effective number of patches (i.e., fragmentation *per se*); CP = percentage of cattle pastures in the matrix; ED = edge density (expressed as meters per hectare).

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Appendix 2. Abundance (Ab) and species richness (S) of small rodents captured in 2011 and 2012 in nine forest patches (P) and three areas of continuous forest (CF) in the Lacandona rainforest, Chiapas, Mexico. The number of singletons (f_1) and doubletons (f_2) are shown, as well as the sampling coverage ($\hat{C}$ = percentage of species recorded).

Site	2011					2012				
	Ab	S	f_1	f_2	$\hat{C}$ (%)	Ab	S	f_1	f_2	$\hat{C}$ (%)
CF1	4	2	1	0	75	7	3	2	0	71
CF2	10	3	1	0	90	4	2	1	0	75
CF3	18	3	0	1	100	7	2	0	0	–
P1	2	2	2	0	0	15	3	2	0	87
P2	0	0	0	0	–	3	1	0	0	–
P3	4	3	2	1	63	8	2	0	0	–
P4	5	3	0	1	100	7	3	1	1	89
P5	0	0	0	0	–	5	2	0	1	100
P6	10	3	1	2	93	12	4	2	0	83
P7	2	2	2	0	0	2	1	0	1	100
P8	9	2	0	0	–	3	1	0	0	–
P9	14	2	0	0	–	9	2	1	0	89

(–) With the formula proposed by Chao and Shen [56] it is not possible to estimate the sampling coverage in these sites.

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Appenidx 3. Results of information-theoretic based model selection and multimodel inference for assessing the impact of patch and landscape variables on rodent communities within the Lacandona rainforest, Mexico. We detail final model-averaged parameter estimates (β) and the unconditional variance for all model predictors.*

Scale/ Metrics[a]	Abundance				^0D				^1D				^2D			
	2011		2012		2011		2012		2011		2012		2011		2012	
	β	UV	β	UV	β	UV	β	UV	β	UV	β	UV	β	UV	β	UV
Patch[a]																
PS	0.016*	0.000	0.000	0.000	0.000	0.000	-0.001*	0.000	0.000	0.000	0.000	0.000	0.002*	0.000	0.000	0.000
TBA	-0.017*	0.008	-0.552*	0.105	0.025	0.025	-0.123*	0.079	0.019	0.038	-0.081	0.090	0.018	0.034	-0.013	0.013
MID	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Landscape[b]																
PFC	0.021*	0.000	-0.001*	0.000	0.001*	0.000	-0.001*	0.000	0.000	0.000	0.003*	0.000	0.000	0.000	0.000	0.000
EN	-0.011	0.029	0.002	0.013	0.015	0.043	0.052	0.055	0.030	0.081	0.062	0.121	0.032	0.076	0.023	0.029
CP	0.003*	0.000	-0.001*	0.000	0.000	0.000	0.000	0.000	0.001*	0.000	0.000	0.000	0.001*	0.000	0.000	0.000

*With asterisks we indicate the parameter estimates that are more accurate, as they were higher than the unconditional variance [62]

[a] Patch scale: PS = patch size (ha), TBA = tree basal area (m^2), MID = mean inter-patch isolation distance (m); Landscape scale: PFC = percentage of forest cover (%), EN = effective number of patches (i.e., fragmentation *per se*), CP = percentage of cattle pastures in the matrix

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