RESEARCH ARTICLE



The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor

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Abstract

Context Landscape structure can affect seed dispersal, but the spatial scale at which such effect is maximized (scale of effect, SoE) is unknown.

Objectives We assessed patterns and predictors of SoE on the seed rain in two Mexican regions: the relatively well-preserved Lacandona rainforest, and the more deforested Los Tuxtlas rainforest. We hypothesized that source limitation at Los Tuxtlas makes seed dispersal more reliant on landscape patterns measured across larger spatial scales,

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especially when considering connectedness-related landscape metrics and dispersal-dependent responses. *Methods* We recorded the abundance and diversity of tree seeds in 20 forest sites per region, separately assessing local (dropping from neighboring trees) and dispersed (immigrant) seeds. We measured forest cover, fragmentation, and matrix openness in 11 concentric landscapes surrounding each site and tested for differences in SoE among regions, landscape metrics, response variables, and seed origins.

Results Contrary to expectations, SoE did not differ between regions and seed origins. Yet, as expected, forest cover tended to have larger SoE than matrix openness, with fragmentation showing intermediate values. Response variables also followed the predicted SoE pattern (abundance < diversity < species richness).

Conclusions Forest cover has larger SoE than matrix openness, possibly because forest cover is related to large-scale processes (e.g. long-distance dispersal) and matrix openness may drive small-scale processes (e.g. edge effects). Species richness may have larger SoE because of its dependence on long-distance dispersal. Therefore, to accurately assess the effect of landscape structure on seed dispersal, the optimal scale of analysis depends on predictor and response variables.

Keywords Landscape size · Multiscale analysis · Regional effect · Scale of effect · Seed dispersal · Source limitation

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Introduction

Deforestation, forest fragmentation, and creation of forest edges shape biodiversity patterns worldwide (Fahrig 2013, 2017; Pfeifer et al. 2017). Land use change modifies landscape structure, including the types and amounts of different land covers (landscape composition), and the spatial physiognomy of such land covers (landscape configuration). Yet, the effects of these two components of landscape structure on ecological patterns and processes remain poorly understood, especially because such effects depend on the spatial scale at which landscape variables are measured (Smith et al. 2011; Jackson and Fahrig 2015; Suárez-Castro et al. 2018). Therefore, landscape effects need to be assessed across several spatial scales to identify the one relevant to a given ecological pattern or process ("scale of effect", SoE; sensu Jackson and Fahrig 2015). Identifying the patterns and predictors of SoE is highly valuable for understanding the way species and ecological processes respond to landscape changes, and thus improve conservation strategies (Jackson and Fahrig 2015; Miguet et al. 2016; Martin 2018). Unfortunately, most landscape studies quantify landscape variables at one single spatial scale, and when measured across different spatial scales (i.e. multiscale approach), landscape studies are usually conducted at suboptimal scales (i.e. larger or smaller than the spatial scale relevant for the response variable; Jackson and Fahrig 2015). Furthermore, the available studies on SoE are focused on few taxa, and up-to now no study has assessed the scale of landscape effects on key ecological processes, such as seed dispersal (Miguet et al. 2016; Suárez-Castro et al. 2018).

The seed rain is essential for forest regeneration, and depends on seeds dropping from neighboring trees (local seeds, hereafter) and immigrant seeds dispersed by biotic and abiotic vectors (Martínez-Ramos and Soto-Castro 1993; Melo et al. 2010). These vectors, and thus the seed rain, can be affected by changes in landscape composition and configuration (Arroyo-Rodríguez et al. 2017a). Animal-dispersed seeds can be particularly vulnerable to landscape changes, especially to those changes that limit landscape connectedness (e.g. forest loss, inter-patch matrix openness; Ruffel et al. 2016; Boesing et al. 2018) and animal movements (Taylor et al. 1993). To our knowledge, however, there is only one study about the response of the seed rain to landscape structure (Jesus et al. 2012), but it measures landscape variables at one single spatial scale (800-m radius). This calls for cautious interpretations, as important response-landscape relationships may go undetected if assessed at incorrect scales (Jackson and Fahrig 2015; Martin 2018). Also, Jesus et al. (2012) do not differentiate between local and immigrant seeds, thus limiting our knowledge on seed dispersal patterns in human-modified landscapes (but see Melo et al. 2010).

In Mexico, contrasting land-use change patterns have resulted in regions with different spatial structure (Sánchez-Colón et al. 2009). For example, in the Los Tuxtlas rainforest (LTX), rapid deforestation since the early 1960's has resulted in the loss of about 70% of forest cover, and the remaining forest patches are embedded in a relatively homogeneous matrix dominated by cattle pastures (Guevara et al. 2004; Laborde 2004; Table 1; Supplementary material Fig. S1). Along with deforestation, this region has also suffered a defaunation process (sensu Dirzo and Miranda 1990), altering important animal-plant interactions, such as seed dispersal and seed predation (Dirzo and Miranda 1990; Mendoza and Dirzo 2007). In contrast, other Mexican regions, such as the Lacandona rainforest (LAC), have been deforested more recently (1980's onwards) so that defaunation there is incipient (Naranjo and Bodmer 2007; Garmendia et al. 2013). In Lacandona, $\sim 50\%$ of forest cover remains in different-sized forest patches surrounded by a heterogeneous matrix of agricultural lands, cattle pastures, and human settlements (Table 1; Fig. S1). As both regions share similar climate, fauna and flora, comparing the patterns and predictors of the SoE on the seed rain between these two regions can provide important clues on the role of landscape structure in shaping seed dispersal services in fragmented rainforests.

Here, we assessed the SoE of three landscape metrics of ecological significance (Table 2) on the abundance, species richness and diversity of tree seeds, separately assessing local seeds (dropping from neighboring trees) and wind- and animal-dispersed (immigrant) seeds. Landscape metrics were mostly independent between each other (Table S1), and included two metrics of landscape composition (i.e. forest cover and matrix openness) and one metric of landscape configuration (i.e. forest patch density). All landscape metrics were measured in 11 concentric 399–1784-m landscapes (buffers of radius)

Variable	Los Tuxtlas	Lacandona	Student t test
Location	18°36′N—94°6′W	16°7′N—90°53′W	
Altitude (m a.s.l.) ^a	0–1680	80–500	
Precipitation (mm/year)	3800	3000	
Matrix composition	Dominated by cattle pastures	Heterogeneous	
Land-use history (years)	60	35	
Percentage of forest cover ^b	14.9 ± 14.1	37.4 ± 16.8	t = 4.56, p < 0.0001
	(3.2–62.8)	(11.7-68.6)	
Percentage of open areas in the matrix ^b	87.7 ± 5.6	78.5 ± 16.7	t = -2.34, p = 0.03
	(77–98.7)	(18.7–97.3)	
Density of forest patches (n/ha) ^b	0.007 ± 0.004	0.022 ± 0.018	t = 3.61, p = 0.002
	(0.003–0.017)	(0.003–0.074)	

Table 1 General characteristics of the two studied regions from southeastern Mexico. The differences between regions in each landscape metric are also indicated

^aTo control the effect of altitude on the seed rain, all focal forest sites in both regions were located in lowland areas (< 600 m asl) ^bThese landscape metrics were measured in 1000-ha circular landscapes surrounding 40 focal patches (i.e. 20 landscapes per region). We indicate mean (\pm SD) values and range (in parenthesis) within each region

Landscape metrics	Metric description	Ecological interpretation	Refs ^a
Forest cover	Percentage of landscape area covered by old- growth forest cover	A proxy of landscape-scale habitat amount positively related to the availability of propagules and dispersal success (landscape connectivity)	1,2,3,4
Matrix openness	Percentage of matrix area covered by annual crops, human settlements, grasslands, roads, exposed soil, and water	Open-area matrices increase both negative edge effects (e.g. altered climatic conditions and increased mortality of adult trees) and seed dispersal limitation in the tropics	
Density of Number of forest patches divided by landscape forest area (n/ha) patches		A classical fragmentation metric, inversely related to mean patch size. Thus, for a given forest cover, fragmentation increases the edge-to-core ratio at the landscape scale, potentially increasing edge effects (i.e. small-scale process). Yet, as it is also positively related to landscape connectedness and to the number of (sub)populations (seed sources) in the landscape, it can also have stronger effects on seed dispersal over larger spatial scales	

Table 2 Definition and ecological justification of the landscape metrics measured in the present study

^aReferences: 1. Fahrig (2003); 2. Jesus et al. (2012); 3. Taylor et al. (1993); 4. Arroyo-Rodríguez et al. (2017a); 5. Pires et al. (2002); 6. Fahrig (2007); 7. Boesing et al. (2018); 8. Fahrig (2017)

surrounding each forest site, to test for differences in SoE among regions (i.e. LTX vs. LAC), landscape metrics, response variables, and seed origins.

Based on previous models (Arroyo-Rodríguez et al. 2017a), we hypothesized that the lack of adult trees in more deforested regions limits the availability of fruits and seeds (source limitation), potentially making the

seed rain more reliant on long-distance seed dispersal, and thus, on landscape patterns measured across larger spatial scales (Table 3). Thus, we predicted larger SoE in LTX than in LAC. Following a similar rationale, we hypothesized that landscape metrics driving dispersal success across larger spatial extents (i.e. long-distance seed dispersal) have larger SoE than metrics

Prediction^a LTX > LAC

FC > DF > MO

 ${}^{0}D > {}^{2}D > Ab$

AD > WD > LO

effect (SoE) on the seed rain in two tropical regions with different intensity of land-use change				
Predictor	Hypothesis			
Regional context	Source limitation in more disturbed regions makes the seed-dispersal process more reliant on landscape patterns measured across larger spatial scales			
Landscape	Landscape metrics more strongly related to long-distance seed dispersal (i.e. connectedness-			

metrics related to local seed dispersal (e.g. metrics related to edge effects)

scales than variables related to local drivers

 Table 3 Hypothesized effect of regional context, landscape metrics, response variables and seed origins on the scale of landscape effect (SoE) on the seed rain in two tropical regions with different intensity of land-use change

Landscape metrics: *FC* forest cover, *MO* matrix openness, *DF* density of forest patches. Response variables: *Ab* abundance of seeds, ${}^{0}D$ species richness, ${}^{2}D$ inverse Simpson concentration. Seed origins: *LO* local seeds (dropping from neighboring trees), *AD* animal-dispersed seeds, and *WD* wind-dispersed seeds

^aRegions: the relatively well-preserved Lacandona rainforest (LAC), and the more deforested Los Tuxtlas rainforest (LTX)

related landscape metrics) affect the seed rain over larger spatial extents than landscape

occurrence, species richness) are affected by landscape patterns measured across larger spatial

measured across smaller scales than dispersed (immigrant) seeds, especially when considering animal-dispersed seeds, which have longer dispersal distances than wind-dispersed species

Variables influenced by forces acting at larger spatial and temporal scales (e.g. species

Seeds dropping from neighboring trees (local seeds) are affected by landscape variables

associated with local seed dispersal. Long-distance dispersal largely depends on landscape connectedness (Nathan et al. 2008), which typically increases with increasing forest cover (Fahrig 2003, 2013; Table 2). Local seed dispersal is expected to be more strongly influenced by matrix openness, especially in the tropics, where open-area matrices (e.g. cattle pastures, annual crops) usually promote negative edge effects (Tuff et al. 2016; Arroyo-Rodríguez et al. 2017b). For example, the mortality rate of adult trees can increase at forest edges, especially in those surrounded by open-area matrices (Laurance et al. 1998; Mesquita et al. 1999). Thus, matrix openness can drive local edge effects, determining the availability of trees and seeds in the local landscape. Forest edges can also act as a barrier to animal movements (Tuff et al. 2016; Boesing et al. 2018) potentially limiting the influence of long-distance dispersal on the seed rain (i.e. dispersal limitation). Thus, it is reasonable to expect that matrix openness have smaller SoE than forest cover (Table 3). Forest fragmentation (i.e. density of forest patches) may have intermediate values of SoE (Table 3), as it can be related to both edge effects (i.e. small-scale process) and long-distance seed dispersal (Table 2).

Regarding the effect of biological responses on SoE, theory proposes that variables influenced by forces acting at larger spatial and temporal scales (e.g. species colonization and extinction dynamics) should have larger SoE than responses shaped by local drivers (Martin 2018). Thus, we predicted that responses based on combined occurrence information (e.g. species richness) show larger SoE than multi-species responses based on combined abundance information (Miguet et al. 2016; Martin 2018). A similar rationale can be applied to the effect of seed origins on SoE, i.e. both wind- and animal-dispersed seeds are expected to have a larger SoE than local seeds (Jackson and Fahrig 2012; Miguet et al. 2016; Suárez-Castro et al. 2018). Also, as animal-dispersed seeds have longer dispersal distances than wind-dispersed species (Clark et al. 2005), we expect larger SoE for animal-dispersed seeds than for wind-dispersed seeds (Table 3).

Methods

Study regions

The two study regions have a humid and hot climate and the same vegetation type (tropical rainforest), but show contrasting land-use change patterns and history (Table 1). The Los Tuxtlas Biosphere Reserve (LTX, hereafter) is located in Veracruz State, southeastern Mexico (Fig. 1). Although LTX was decreed a Biosphere Reserve in 1998, it has been subjected to heavy deforestation since the 1960's, mainly for cattle pasture expansion. It still maintains in their lowlands a

metrics

Response variables

Seed origins



Fig. 1 Location of the study rainforest regions in southeastern Mexico: Los Tuxtlas (a) and Lacandona (b). Dark gray indicates forested areas, light gray non-forested areas, and white water. The circles represent the 20 landscapes (1000 ha; 1784 m

relatively large forest reserve—the "Los Tuxtlas Tropical Biological Station" (700 ha)—that is functionally connected with few large private forest patches (200–300 ha). Yet, most of the lowlands in the region are nowadays composed of a large number of very small (i.e. ca. 85% of forest patches are < 8 ha, and only 10 patches are > 1600 ha; Guevara et al. 2004; Arroyo-Rodríguez et al. 2008) and defaunated forest patches (Dirzo and Miranda 1990). Although accurate information on population abundances in the remaining forest patches is lacking, most large-sized mammals (e.g. *Panthera onca, Tapirus bairdii, Pecari tajacu*), primates (*Ateles geoffroyi*), and birds (e.g. *Ara macao, Crax rubra*) show depauperated populations or are regionally extinct, even within the reserve.



radius) selected in each region (40 in total). There is also a landscape sample (c) with the 11 buffers (50–1000 ha) where landscape metrics were measured

The Mexican portion of the Lacandona rainforest (LAC, hereafter) is located in southeastern Chiapas State (Table 1; Fig. 1). This important biodiversity hotspot is part of the Mesoamerican Biological Corridor (Mora 2008). Here, the Montes Azules Biosphere Reserve protects 330,000 ha of continuous old-growth forest, however, outside the reserve, in the Marqués de Comillas county, recent deforestation (since 1980's) has resulted in the loss of approximately 50% of forest cover (Carabias et al. 2015). Different-sized forest patches remain, including very large (> 1000 ha) forest patches that are embedded in a heterogeneous matrix composed of secondary forests, annual crops (e.g. maize, chili), tree plantations (e.g. oil palm, rubber), cattle pastures, and human settlements. Large mammals (Garmendia et al. 2013; Muench and Martínez-Ramos 2016) and birds (Carrara et al. 2015) are still present in LAC, even in very small forest patches, although some mammal populations are less abundant outside the reserve (Naranjo and Bodmer 2007).

Study sites

In each region, we selected 20 forest sites, 19 oldgrowth forest patches (3-90 ha) and a well-preserved forest site within their respective reserves, i.e. the Los Tuxtlas Biology Station in LTX, and the Montes Azules Biosphere Reserve in LAC (Fig. 1). We defined "old-growth forests" as those without distinguishable signals of disturbance, with a continuous canopy of up to 30-40 m tall and with some emergent trees reaching up to 45 m tall. All sites were separated from each other by at least 2 km, and covered a wide range of variation in all landscape variables (Table 1; Supplementary material Fig. S2). Considering landscape sizes of 1000 ha, percent forest cover and patch density were lower in LTX than in LAC region (Table 1). In contrast, percentage of open areas in the matrix was higher in LTX than in LAC (Table 1).

Seed rain survey

We placed nine seed traps (trap area = 0.5 m^2 , 1 mm nylon mesh) at the center of each site in a grid of 8×8 m, with a separation of 4 m between traps (total sampling effort = $20 \times 9 = 180$ traps per region). Distance between traps and the nearest forest edge averaged 138 ± 83.2 m (mean \pm SD) in LTX (range = 47-377 m) and $180.7 \pm 156 \text{ m}$ in LAC (range = 54-612 m). The traps were hanging at approximately 90 cm above the ground (Fig. S3) and the contents of the traps were recovered every 15 days during one year (February 2015-February 2016). The material collected in the traps was dried and all intact seeds \geq 3 mm in length were counted and identified to the lowest possible taxonomic level using field guides (Ibarra-Manríquez et al. 2015) and the opinion of specialists from the MEXU Herbarium (Universidad Nacional Autónoma de México, Mexico City), the XAL Herbarium (Instituto de Ecología, A.C., Xalapa), and the seed collection at Los Tuxtlas Biological Station (UNAM). We classified seeds as wind- or animal-dispersed based on their morphology and scientific literature (Ibarra-Manríquez and Oyama

1992; Ibarra-Manríquez et al. 2015). Barochorousdispersed species were taken as zoochorous, since our traps were hanging above ground and the only way in which this kind of seeds could arrive to the traps was through animal dispersal. Also, we identified and counted all trees with diameter at breast height (dbh) > 10 cm, in a 40 m × 40 m plot around the seed traps. Then, following previous studies (Martínez-Ramos and Soto-Castro 1993; Melo et al. 2010), we compared the composition of the seed rain with the composition of local tree assemblage covered in the plot to classify the seeds from each site as local (i.e. those of same species present in the local tree assemblage, and thus, probably dropping from neighboring trees) or immigrant (i.e. those belonging to species that were not present in the local tree assemblage, and that would have been actively dispersed from external seed sources). Plant names followed the Missouri Botanical Garden database available at http://www.tropicos.org.

Response variables

We estimated the abundance (i.e. number of seeds) of local, wind- and animal-dispersed seeds for each study site in each region. We combined the data (i.e. sum) of the nine seed traps from each site to avoid pseudoreplication problems. We then evaluated the sampling completeness within each site using the estimator of sample coverage proposed by Chao and Shen (2010). This estimator indicates the proportion of the total number of individuals in an assemblage that belongs to the species represented in the sample. Sample coverage (in percentage) was very high in all sites (mean \pm SD per site; LTX = 98 \pm 2%, LAC = $95 \pm 5\%$), thus suggesting that our sampling effort was adequate, and that our estimates of species diversity were not biased by differences in completeness among sites (Chao and Jost 2012). In particular, we measured species diversity with Hill numbers (Jost 2006) using the entropart package (Marcon and Hérault 2014) for R software 3.3.0 (R Development Core Team 2013). We considered Hill numbers of order 0 (${}^{0}D$, species richness) and 2 (${}^{2}D$, inverse Simpson index). ⁰D is not sensitive to species abundances, and thus it allocates a disproportionate weight to rare species (Jost 2006). In turn, ^{2}D favors dominant species, being interpreted as the number of 'very abundant' or 'dominant' species in the community (Jost 2006). The formulas for the Hill numbers are detailed elsewhere (Jost 2006).

Landscape metrics

With high resolution (2.5 m \times 2.5 m) satellite images SPOT 5 (2012 for LTX and 2013 for LAC), we classified the land-covers using Quantum GIS 2.4.0 (QGIS Development Team 2014) through hand mapping assessed by field surveys and image interpretation. We differentiated ten land cover types, including old-growth and secondary forests, cattle pastures, arboreal (e.g. rubber, oil palm, orange) and annual crops (e.g. maize, chilli, pumpkin, watermelon), urban areas, water, riparian forest, and mangrove (only in LTX) and bamboo forest (only in LAC) (Fig. S1). With the SDMTools package (R v. 3.3.0) and FRAGSTATS (v. 4.2), we estimated three metrics of landscape structure in 11 circular buffers (399, 564, 798, 978, 1128, 1262, 1382, 1493, 1596, 1693, and 1784 m radius; i.e. landscapes of 50-1000 ha) from the center of each site (i.e. the place where seed traps were located). This range of buffer sizes comprises the home ranges and dispersal distances of seed dispersers, including birds (Holbroock 2011) and primates (Chaves et al. 2011). The largest buffer was selected to minimize spatial overlap between landscapes, and hence, avoid dependence (i.e. pseudoreplication) problems in our analyses (Eigenbrod et al. 2011). We calculated two metrics of landscape composition (i.e. percentage of forest cover, and matrix openness), and one metric of landscape configuration (i.e. density of forest patches) that were mostly independent (Table 2; Table S1).

Statistical analyses

We calculated the Moran's I index with the *ape* package (Paradis et al. 2004) for R (v.3.3.0) to test for spatial independence of our samples. The few models (6 of 54, 11%) in which we found significant spatial autocorrelation, showed very small Moran's I values (< 0.11, in all cases; Table S2), thus suggesting that they can be related to spurious correlations (Fortin et al. 2002). We therefore considered all study sites as independent samples in the following analyses. To identify SoE in each region we followed the protocol proposed by Jackson and Fahrig (2015). In brief, we used generalized linear models to assess the effect of

each landscape metric on each response, separately assessing local, wind- and animal-dispersed seeds within each region (e.g. effect of forest cover on the abundance of local seeds in LAC). Count response variables (abundance and ⁰D) were assessed with Poisson distribution error, whilst the continuous variable (^{2}D) was tested by assuming a Gaussian distribution in the generalized linear models (Crawley 2007). We did this for each landscape size, and then calculated the percentage of explained deviance as a measure of goodness-of-fit of each model (pseudo- R^2 ; Crawley 2007). We plotted the value of pseudo- R^2 of each model at each scale (dependent variable) against landscape size (predictor) to identify the spatial scale (landscape size) that makes response-landscape relationships the strongest (i.e. SoE) (Jackson and Fahrig 2012; Miguet et al. 2016). In particular, we estimated 54 values of SoE (i.e. 2 regions \times 3 landscape predictors \times 3 response variables \times 3 origins), so we had 27 values per region, 18 values per landscape metric, 18 values per response variable, and 18 values per seed origin (Supplementary Figs. S4 and S5; Table S3). Then, to assess if SoE differed among regions, landscape metrics, response variables, and seed origins, we carried out a four-way ANOVA, after verifying that the residuals followed a normal distribution (Shapiro-Wilk test). In 25 cases, SoE was equal to the smallest or largest landscape size evaluated (Fig. S4 and S5), suggesting that SoE was outside the studied range of landscape sizes (Jackson and Fahrig 2015). Yet, given the purposes of our study (i.e. to compare SoE among regions, landscape metrics, response variables, and seed origins) this suggests that our assessment is conservative, as the actual SoE must be lower than the minimum SoE or higher than the maximum SoE observed in this study. Therefore, the differences in SoE may actually be higher than those observed in this study. Finally, it is important to note that the variation of landscape metrics differed between regions and among scales (Fig. S2). As such variation can have major impacts on landscape-scale inference (Eigenbrod et al. 2011), we calculated the number of cases in which SoE coincided with the scale at which landscape metrics showed the highest coefficient of variation. We found a very weak association between SoE and coefficient of variation, with only 18.5% (10 of 54 cases) of coincidence. This suggests that differences in variation of landscape metrics between regions and among scales have a

weak effect on our results, and that SoE has biological significance in most cases (i.e. it is not a statistical artifact).

Results

We collected a total of 67,321 tree seeds, 56,892 seeds from 108 species at LTX, and 10,429 seeds from 111 species at LAC (Table 4). Heliocarpus spp. (31.8% of seeds), Dendropanax arboreus (20.7%) and Robinsonella mirandae (15%) were the most abundant tree seeds in LTX. In turn, the species with the highest number of seeds in LAC were Terminalia amazonia (37.7%), Dendropanax arboreus (10.8%) and Trichospermum mexicanum (10.6%). Regarding seed origin, we recorded 43,710 local seeds (77%) and 13,182 dispersed seeds (23%) in LTX. From dispersed seeds, 91% were dispersed by wind and only 9% by animals. In LAC, we recorded 7399 local seeds (71%) and 3030 dispersed seeds (29%). Yet, in contrast to LTX, animal-dispersed seeds in LAC were more abundant (90% of seeds) than wind-dispersed seeds (10%). Additional differences in seed origins and response variables between regions are indicated in Table 4.

Scale of landscape effects on the seed rain

SoE was highly variable among regions, landscape metrics, response variables, and seed origins (Figs. S4 and S5; Table S3). Mean SoE did not differ between LTX and LAC (F = 0.17, p = 0.68; Fig. 2a). Yet, matrix openness (863 ± 116 m, mean ± SE) tended to have a smaller SoE than forest cover (1244 ± 142 m), with patch density showing

intermediate values $(1055 \pm 121 \text{ m})$ (F = 2.93, p = 0.06; Fig. 2b). Regarding the differences among response variables, seed abundance $(800 \pm 128 \text{ m})$ had significantly smaller SoE than species richness $(1302 \pm 121 \text{ m})$, with Simpson diversity (^{2}D) showing intermediate values $(1061 \pm 118 \text{ m})$ (F = 3.64, p = 0.03; Fig. 2c). Finally, local and dispersed seeds showed a similar SoE (F = 0.06, p = 0.95; Fig. 2d).

Discussion

This study assesses, for the first time, the patterns and potential drivers of the scale of effect (SoE) of landscape structure on the seed rain in two fragmented tropical regions with contrasting disturbance level: the Los Tuxtlas (LTX) and Lacandona (LAC) rainforests. Contrary to our expectations, SoE did not differ significantly between regions or among seed origins. However, as predicted, matrix openness tended to have smaller SoE than forest cover. SoE also differed among response variables following the predicted pattern (i.e. seed abundance < species diversity < species richness). As argued below, these findings suggest that to accurately assess the effect of landscape structure on seed dispersal, the optimal scale of analysis mainly depends on landscape predictors and response variables.

The fact that forest cover shows the largest SoE, followed by forest fragmentation and matrix openness is not surprising, as it supports our hypothesis (Table 3). In particular, forest cover is probably related to large-scale dispersal success, and thus, its influence on the seed rain is stronger when measured across larger spatial scales (Miguet et al. 2016). The fact that forest fragmentation (i.e. density of forest

Table 4 Abundance and species diversity (mean \pm SD) of local and dispersed tree seeds in two fragmented rainforests from southeastern Mexico: Los	Seed origin	Response variable	Los Tuxtlas	Lacandona
	Local seeds	Abundance	2186 ± 3103	370 ± 748
		Species richness (⁰ D)	11.4 ± 3.7	8.8 ± 3.7
		Simpson diversity (^{2}D)	2.5 ± 1.5	2.6 ± 1.3
Tuxtlas and Lacandona	Animal-dispersed seeds	Abundance	89 ± 73	137 ± 256
		Species richness (⁰ D)	11.2 ± 3.5	8 ± 3.8
		Simpson diversity (^{2}D)	3.5 ± 1.6	3.1 ± 1.9
	Wind-dispersed seeds	Abundance	570 ± 1910	15 ± 29
		Species richness (^{0}D)	2.7 ± 1.3	1.6 ± 1.1
		Simpson diversity (^{2}D)	1.5 ± 0.6	1.2 ± 0.8



patches) has intermediate values of SoE suggests that this metric is probably related to both dispersal success across relatively large spatial scales (i.e. long-distance dispersal), and to local processes, such as edge effects

◄ Fig. 2 The scale of landscape effect on the seed rain in two Mexican tropical regions, separately assessing for differences between regions (a), landscape metrics (b), response variables (c), and seed origin (d). In total, we estimated 54 values of scale of effect (i.e. 2 regions × 3 landscape predictors × 3 response variables × 3 origins): 27 values per region, 18 values per landscape metric, 18 values per response variable, and 18 values per seed origin. The boxplots indicate the median (thick lines), the first and third quartiles (boxes) and the range (whiskers). The plus symbol (+) indicates the mean. Dots are the data points

(Table 3). In contrast, the seed rain can be more strongly related to matrix openness measured across smaller scales because this metric may shape local seed dispersal through small-scale mechanisms. For example, animal movements can be limited with increasing open-area matrices (Ricketts 2001; Boesing et al. 2018), potentially decreasing the effect of longdistance dispersal on the seed rain (i.e. dispersal limitation). Also, the likelihood that the seed rain is supplemented with tree seeds dispersed from the matrix through landscape supplementation dynamics (sensu Dunning et al. 1992) also decreases with increasing open-area matrices in the local landscape (also see Ricketts 2001; Vandermeer and Carvajal 2001). Finally, matrix openness can also promote negative edge effects (e.g. increased mortality of oldgrowth trees at forest edges than interior; Laurance et al. 1998; Mesquita et al. 1999; Laurance et al. 2002), thus limiting the availability of trees (and seeds) within the forest. In summary, the seed rain seems to be influenced by both long-distance dispersal mainly driven by forest cover across larger spatial scales, and by local seed dispersal mainly driven by matrix openness across smaller scales.

Regarding the response variables, our findings are also consistent with our expectations. In particular, SoE increases in the order: seed abundance < species diversity < species richness. This pattern is in agreement with the suggestion by Miguet et al. (2016) that multi-species responses based on combined abundance information (i.e. seed abundance and species diversity) should have smaller SoE than responses based on combined occurrence information (i.e. species richness). This is because the occurrence of one or several species in a given site is expected to be influenced by forces acting at larger spatio-temporal scales (e.g. colonization and extinction events, longdistance seed dispersal), than species diversity and abundance, which are strongly associated with smallscale drivers, such as tree abundance in the near vicinity of the site (Miguet et al. 2016; Martin 2018). Therefore, care should be taken when assessing the impact of landscape structure on several response variables, as each response can have different SoE.

The lack of differences in SoE between regions can be related to the fact that factors generating differences in one direction may be counteracted by factors pushing differences in the opposite direction. For example, a higher deforestation degree in LTX may increase source limitation, potentially making the seed rain more reliant on landscape patterns measured across larger spatial scales (i.e. predicted difference in SoE: LTX > LAC). This is particularly plausible because seed dispersers in LTX may need to move more and across longer distances to acquire sufficient resources (Lehouck et al. 2009; Herrera and García 2010; Herrera et al. 2011), which can increase the influence of long-distance seed dispersal on the seed rain (Nathan et al. 2008). Nevertheless, only 9% of dispersed seeds in LTX were dispersed by animals, and we found almost six times more local seeds (i.e. dropping from neighboring trees) in LTX than in LAC. This suggests that dispersal limitation is higher in LTX, probably because of its higher degree of deforestation-a landscape attribute that can limit dispersal success in fragmented landscapes (Fahrig 2003, 2013; Jesus et al. 2012; Arroyo-Rodríguez et al. 2017a). Dispersal limitation can actually push the differences in SoE between regions in the opposite direction (i.e. predicted difference in SoE: LTX < LAC). Yet, it seems that dispersal limitation in LTX was not strong enough to decrease significantly SoE at the regional scale. We propose at least two potential reasons: (i) this region still maintain a certain degree of landscape connectivity (e.g. it preserves $\sim 30\%$ of its original forest cover, and mean inter-patch distance in the northern portion of the reserve is about 100 m; Laborde 2004; Arroyo-Rodríguez et al. 2008); and (ii) defaunation in this region has mainly impacted largesized forest-specialist birds and mammals (e.g. macaws, spider monkeys), but generalist frugivores (including birds, bats and howler monkeys) are still relatively abundant, and can actively disperse seeds across the landscape (Guevara and Laborde 1993; Galindo-González and Sosa 2003; Arroyo-Rodríguez et al. 2008). Additional studies including a greater number of regions are needed to accurately test the importance of all these factors in shaping the SoE at the regional scale.

Surprisingly, SoE does not differ among seed origins. We predicted that dispersed (i.e. immigrant) seeds should have larger SoE than local seeds because, by definition, the former group interacts with its environment across larger spatio-temporal scales than the latter. The lack of such differences may be associated with our methodological approach. In particular, we classified seeds as 'local' if they belonged to the tree species present in the local tree assemblage (see Methods). Although this procedure has been used in previous studies (e.g. Martínez-Ramos and Soto-Castro 1993; Melo et al. 2010), it can underestimate seed dispersal, as some of the seeds classified as 'local' could have actually been dispersed from external seed sources. Godoy and Jordano (2001) actually demonstrate that some of the seeds falling under a given tree can come from other parental trees, helping to explain the large variation in SoE recorded for local seeds. Therefore, additional studies using molecular techniques are needed to accurately identify parent-offspring relationships (e.g. Godoy and Jordano 2001; Arroyo-Rodríguez et al. 2017c), and thus, draw stronger conclusions about the SoE of local vs. dispersed seeds.

We can therefore conclude that forest cover is related to the seed rain, especially to seed species richness, when measured at larger spatial scales. This suggests that this landscape metric has a stronger influence on long-distance seed dispersal. The seed rain can also depends on matrix openness at smaller spatial scales, probably because this variable drives local seed dispersal through small-scale mechanisms (e.g. edge effects, dispersal limitation, landscape complementation dynamics). Therefore, to accurately assess the effect of landscape structure on seed dispersal, the optimal scale of analysis depends on the landscape predictors and response variables. However, additional studies including a greater number of regions, and molecular techniques to accurately classify local and dispersed seeds are needed to better understand the role of regional context and seed origins in shaping the scale of landscape effect.

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References

- Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J (2008) Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. Am J Primatol 70:69–77
- Arroyo-Rodríguez V, Águilar-Barajas E, González-Zamora A, Rocha-Ramírez V, González-Rodríguez A, Oyama K (2017a) Parent-parent and parent-offspring distances in *Spondias radlkoferi* seeds suggest long-distance pollen and seed dispersal: evidence from latrines of the spider monkey. J Trop Ecol 33:95–106
- Arroyo-Rodríguez V, Melo F, Martínez-Ramos M et al (2017b) Multiple successional pathways in human-modified tropical landscapes: New insights from forest succession, forest fragmentation and landscape ecology research. Biol Rev 92:326–340
- Arroyo-Rodríguez V, Saldaña-Vázquez RA, Fahrig L, Santos BA (2017c) Does forest fragmentation cause an increase in forest temperature? Ecol Res 32:81–88
- Boesing AL, Nichols E, Metzger JP (2018) Biodiversity extinction thresholds are modulated by matrix type. Ecography 41:1520–1533
- Carabias J, De la Maza J, Cadena R (2015) Conservación y desarrollo sustentable en la selva Lacandona: 25 años de actividades y experiencias. Natura y Ecosistemas Mexicanos A.C., Mexico City
- Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, Schondube JE, Freitas SM, Fahrig L (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126
- Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547
- Chao A, Shen TJ (2010) Program SPADE: species prediction and diversity estimation. Program and user's guide. CARE, Hsin-Chu

- Chaves OM, Stoner KE, Arroyo-Rodríguez V (2011) Seasonal differences in activity patterns of Geoffroyi's spider monkeys (*Ateles geoffroyi*) living in continuous and fragmented forests in southern Mexico. Int J Primatol 32:960–973
- Clark CJ, Poulsen JR, Bolker BM, Connor EF, Parker VT (2005) Comparative seed shadows of bird-, monkey-, and winddispersed trees. Ecology 86:2684–2694
- Crawley MJ (2007) Statistical modelling in the R book. John Wiley & Sons Ltd, Chichester, UK
- Dirzo R, Miranda A (1990) Contemporary neotropical defaunation and forest structure, function, and diversity—a sequel to John Terborgh. Conserv Biol 4:444–447
- Dunning J, Danielson B, Pulliam H (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175
- Eigenbrod F, Hecnar SJ, Fahrig L (2011) Sub-optimal study design has major impacts on landscape-scale inference. Biol Conserv 144:298–305
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515
- Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. Func Ecol 21:1003–1015
- Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40:1649–1663
- Fahrig L (2017) Ecological responses to habitat fragmentation per se. Annu Rev Ecol Evol Syst 48:1–23
- Fortin M-J, Dale MRT, ver Hoef J (2002) Spatial analysis in ecology. In: El-Shaarawi A, Piegorsch WW (eds) Encyclopedia of environmetrics. Wiley, Chichester, pp 2051–2058
- Galindo-González J, Sosa VJ (2003) Frugivourus bats in isolated trees and riparian vegetation associated with humanmade pasture in a fragmented tropical landscape. Southwest Nat 48:579–589
- Garmendia A, Arroyo-Rodríguez V, Estrada A, Naranjo EJ, Stoner KE (2013) Landscape and patch attributes impacting medium- and large-sized terrestrial mammals in a fragmented rain forest. J Trop Ecol 29:331–344
- Godoy JA, Jordano P (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Mol Ecol 10:2275–2283
- Guevara S, Laborde J (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107(108):319–338
- Guevara S, Laborde J, Sánchez-Rios G (2004) Los Tuxtlas. El Paisaje de la Sierra. Instituto de Ecología, A.C., Xalapa
- Herrera JM, García D (2010) Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. Conserv Biol 24:1089–1098
- Herrera JM, Morales JM, García D (2011) Differential effects of fruit availability and habitat cover for frugivore-mediated seed dispersal in a heterogeneous landscape. J Ecol 99:1100–1107
- Holbroock KM (2011) Home range and movement patterns of toucans: implications for seed dispersal. Biotropica 43:357–364
- Ibarra-Manríquez G, Oyama K (1992) Ecological correlates of reproductive traits of Mexican rain forest trees. Am J Bot 79:383–394

- Ibarra-Manríquez G, Martínez-Morales M, Cornejo-Tenorio G (2015) Frutos y semillas del bosque tropical perennifolio. Región de Los Tuxtlas, Veracruz. Comisión Nacional para el Uso y Conservación de la Biodiversidad, Mexico City
- Jackson HB, Fahrig L (2012) What size is a biologically relevant landscape? Landscape Ecol 27:929–941
- Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–63
- Jesus FM, Pivello VR, Meirelles AT, Franco GADC, Metzger JP (2012) The importance of landscape structure for seed dispersal in rain forest fragments. J Veg Sci 23:1126–1136
- Jost L (2006) Entropy and diversity. Oikos 113:363-375
- Laborde J (2004) La Reserva de la Biósfera. In: Guevara S, Laborde J, Sánchez G (eds) Los Tuxtlas. El Paisaje de la Sierra. Instituto de Ecología, A.C., Xalapa, pp 271–281
- Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG (1998) Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology 79:2032–2040
- Laurance WF, Lovejoy T, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22 year investigation. Conserv Biol 16:605–618
- Lehouck V, Spanhove T, Vangestel C, Cordeiro NJ, Lens L (2009) Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? Ecography 32:789–799
- Marcon E, Hérault B (2014) Entropart, an R package to partition diversity (http://cran.r-project.org/package=entropart)
- Martin AE (2018) The spatial scale of a species' response to the landscape context depends on which biological response you measure. Curr Landscape Ecol Rep 3:23–33
- Martínez-Ramos M, Soto-Castro A (1993) Seed rain and advanced regeneration in a tropical rain forest. Vegetatio 107(108):299–318
- Melo FPL, Martínez E, Benítez-Malvido J, Ceballos G (2010) Forest fragmentation reduces recruitment of large seeded tree species in a semi-deciduous tropical forest of southern Mexico. J Trop Ecol 26:35–43
- Mendoza E, Dirzo R (2007) Seed-size variation determines interspecific differential predation by mammals in a neotropical rain forest. Oikos 116:1841–1852
- Mesquita RCG, Delamônica P, Laurance WF (1999) Effect of surrounding vegetation on edge-related tree mortality in Amazonian forest fragments. Biol Conserv 91:129–134
- Miguet P, Jackson HB, Jackson ND, Martin AE, Fahrig L (2016) What determines the spatial extent of landscape effects on species? Landscape Ecol 31:1177–1194
- Mora F (2008) Caracterización de la cobertura forestal en el Corredor Biológico Mesoamericano-México: patrones espaciales en la pérdida y fragmentación de los bosques. In: Importancia del capital ecológico de la región del Corredor Biológico Mesoamericano-México: evaluación de la biodiversidad, ciclo hidrológico y dinámica de la cobertura forestal. Comisión Nacional para el Uso y Conservación de la Biodiversidad, Mexico City, pp 55–84.

- Muench C, Martínez-Ramos M (2016) Can community-protected areas conserve biodiversity in human-modified tropical landscapes? The case of terrestrial mammals in southern Mexico. Trop Conserv Sci 9:178–202
- Naranjo E, Bodmer R (2007) Source-sink systems and conservation of hunted ungulates in the Lacandon rainforest, Mexico. Biol Conserv 138:412–420
- Nathan R, Schurr FM, Spiegel O, Steinitz O, Trakhtenbrot A, Tsoar A (2008) Mechanisms of long-distance seed dispersal. Trends Ecol Evol 23:638–647
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290
- Pfeifer M, Lefebvre V, Peres CA et al (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187–191
- Pires AS, Lira PK, Fernandez FAS, Schittini GM, Oliveira LC (2002) Frequency of movements of small mammals among Atlantic Coastal forest fragments in Brazil. Biol Conserv 108:229–237
- QGIS Development Team (2014) QGIS geographic information system. Open Source Geospatial Foundation. http://qgis. osgeo.org/en/site/
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/
- Ricketts T (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99
- Ruffel J, Clout MN, Didham RK (2016) The matrix matters, but how should we manage it? Estimating the amount of highquality matrix required to maintain biodiversity in fragmented landscapes. Ecography 40:171–178
- Sánchez-Colón S, Flores Martínez A, Cruz-Leyva IA, Velázquez A (2009) Estado y transformación de los ecosistemas terrestres por causas humanas. In: Capital natural de México, vol. II: Estado de conservación y tendencias de cambio. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City, pp 75–129
- Smith AC, Fahrig L, Francis CM (2011) Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. Ecography 34:103–113
- Suárez-Castro AF, Simmonds JS, Mitchell MGE, Maron M, Rhodes JR (2018) The scale-dependent role of biological traits in landscape ecology: a review. Curr Landscape Ecol Rep 3:12–22
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–573
- Tuff KT, Tuff T, Davies KF (2016) A framework for integrating thermal biology into fragmentation research. Ecol Lett 19:361–374
- Vandermeer J, Carvajal R (2001) Metapopulation dynamics and the quality of the matrix. Am Nat 158:211–220

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