

Capítulo 7

Efectos sinérgicos de la fragmentación y la perturbación local en la diversidad de árboles de bosques tropicales montanos

Este capítulo reproduce el texto del siguiente manuscrito, a excepción de la sección de Métodos, que aparece resumida:

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Resumen

Establecimos la hipótesis de que la fragmentación forestal y la perturbación local actúan de manera sinérgica y modifican la diversidad del estrato arbóreo. Esto cuestiona el valor predictivo de los modelos basados en la teoría de biogeografía de islas.

En este estudio analizamos datos de diversidad de especies de árboles de 195 inventarios forestales repartidos en 16 fragmentos de bosque tropical montano en los Altos de Chiapas, México. Evaluamos los efectos de la fragmentación forestal y la perturbación local en el conjunto de especies de árboles, así como en especies pioneras y especies sucesionales tardías, dentro de cinco tipos de comunidades forestales. Los efectos manifestados como diferencias entre fragmentos fueron analizados por medio de modelos lineales que relacionaban el área, área núcleo, ratio borde del fragmento/área y el índice de proximidad promedio con la diversidad local promedio del fragmento. Los efectos manifestados dentro de los fragmentos fueron analizados por medio de modelos lineales mixtos en donde la distancia al borde del fragmento, la apertura del dosel arbóreo y un índice de degradación representaban efectos fijos, y la agrupación de los inventarios dentro de los fragmentos forestales representaba un efecto aleatorio. Se utilizaron también curvas de acumulación especies-individuos para predecir la pérdida de especies de árboles cuando el número de individuos en un fragmento forestal es reducido a la mitad.

Los resultados sugieren que la variabilidad local contribuye más a estructurar las comunidades de plantas que la variabilidad a nivel de fragmento. No se detectaron efectos de la fragmentación *per se* (reducción del área y la conectividad entre fragmentos) en la diversidad de árboles. Los efectos observados dentro de los fragmentos confirmaron que la fragmentación y la perturbación actúan de manera sinérgica sobre la diversidad de árboles a escala local, si bien la perturbación tuvo un impacto negativo mucho mayor, en particular para las especies sucesionales tardías.

Con las curvas de acumulación especies-individuos predecimos una pérdida máxima de especies en bosques transicionales (12 especies) y bosques nublados (7-9 especies) y una pérdida mínima de especies en bosques de encino (3 especies).

Nuestros resultados apoyan la hipótesis de que muchas especies de árboles tienen la capacidad de superar, al menos a corto plazo, los problemas de la persistencia de sus poblaciones en paisajes fragmentados. La gestión forestal encaminada a preservar la diversidad local de árboles deberá centrarse en mitigar los efectos negativos de la perturbación local más que los de la fragmentación *per se*. Este estudio también plantea cuestiones generales sobre la capacidad predictiva de la teoría insular en aquellos estudios en donde las sinergias entre la fragmentación y la perturbación son evidentes.

Synergistic effects of landscape fragmentation and local disturbance on tree diversity in tropical montane forests

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Abstract

1. We hypothesised that forest fragmentation and local disturbance act synergistically to alter tree species diversity. This can challenge the predictive value of models based on island theory alone.
2. We analysed data on tree species occurrence from 195 field plots in 16 tropical montane forest fragments in the Highlands of Chiapas, Mexico. We evaluated the effects of forest fragmentation and local disturbance on all, pioneer and late successional tree species diversity within five community types. Effects manifested as differences between fragments were analysed by fitting linear models in which area, core area, edge/area ratio, and mean proximity index were related to mean plot diversity. Effects within fragments were analysed by means of linear mixed effects models in which distance to edge, canopy openness and a degradation index were used as predictor variables, and the intercept represented the random effect. Re-sampled species accumulation curves were used to predict the expected loss in species when the number of individual trees in a fragment is halved.
3. Our results suggest that plot-level variation was more important in structuring plant communities than fragment-level variation. Effects of fragmentation *per se* (i.e. reduction in area and connectivity between fragments) on tree diversity were not detectable. Within-fragment effects revealed that fragmentation and disturbance act synergistically on tree diversity at a local scale, with higher detrimental impact of local disturbance, particularly for late successional species.
4. We predicted a maximum loss of species in transitional forest (12 species lost) and evergreen cloud forest fragments (7-9 species lost), and a minimum in oak forest fragments (3 species lost).
5. *Synthesis and applications.* Our findings support the hypothesis that many tree species have the capacity to overcome the problems posed by fragmented landscapes in the short term. Forest management aiming to retain tree diversity should focus on mitigating the negative effects of local disturbance rather than those of fragmentation *per se*. This study also raised general questions regarding the predictive ability of island theory in setting fragmentation studies in which synergies between the effects of fragmentation and local disturbance are apparent.

Keywords: disturbance, fragmentation, island biogeography, linear mixed-effects models, species-accumulation curves, species loss, tree diversity.

1. Introduction

Past and current losses in forest cover associated with human activities occur in many regions of the world, particularly in tropical regions (Rudel & Roper 1997, Lamb *et al.* 2005). Extensive deforestation leads to forest islands within a fragmented landscape. In addition, forest fragments can be selectively logged, degraded by ground fires, and overhunted. These local disturbances alter the ecological processes operating in the fragments and may act additively or synergistically with fragmentation on forest community structure and function (Cochrane *et al.* 1999, Nepstad *et al.* 1999, Gascon *et al.* 2000, Laurance & Cochrane 2001).

Habitat fragmentation and disturbance have obvious implications for species diversity and can affect a variety of population and community processes over a range of temporal and spatial scales (Saunders *et al.* 1991, Debinski & Holt 2000, Fahrig 2003). However, separating the effects of each causal process can be challenging because: (1) the effects of 'habitat fragmentation' often co-vary with the effects of local 'human disturbance' (Villard *et al.* 1999, Caley *et al.* 2001, Haila 2002); and (2) different organisms and ecological systems experience the degree of fragmentation and disturbance in variable, even contradictory, ways (Haila 2002, Henle *et al.* 2004).

To link observations with underlying theory (MacArthur & Wilson 1967 and the extensive literature flowing from it), many studies on species diversity draw analogies between forest fragments and oceanic islands (Harris 1984, Laurance & Bierregaard 1997, Rosenblatt *et al.* 1999, Ferraz *et al.* 2003, Hill & Curran 2003). However, the *ceteris parabus* (all things being equal) assumption underlying island theory would seem to be rarely appropriate (Gotelli & Graves 1996), and case studies on forest fragmentation often have to face one or a combination of the following difficulties that challenge the predictive ability of this theory: (1) fragments exist within a complex vegetation matrix making isolation distance difficult to measure; (2) the degree of isolation varies across key processes, including dispersal and the extension of natural disturbances; (3) the time scale of human induced fragmentation is rarely long enough for tree

populations to reach equilibrium levels; (4) climate and soil usually vary at a landscape scale making direct comparisons between forest fragments difficult; (5) within fragment processes can be more important in their effects on species diversity than landscape scale processes; (6) too few individual fragments may be found/sampled on a given landscape to allow a statistically rigorous test of theory; and (7) current theories on the effects of fragmentation and disturbance on species have been developed mostly for animals, but may lack validity for long-lived plants.

In this study we evaluate the effects of fragmentation as a result of regional deforestation and the effects of more local, subtle habitat disturbances on tree species diversity in a tropical montane landscape. We define fragmentation effects *per se* as the reduction in area and connectivity of either historically or recently isolated areas of natural forest in a landscape. We define local synergistic effects as those effects associated with fragmentation *per se* that, while not reducing either the size or the connectivity of the fragments directly, can act within them to transform the remaining habitat in such a manner that species diversity may be changed. Thus an increase in edge effects, internal disturbance or canopy openness are all synergistic effects of anthropogenic fragmentation that are manifested within fragments. In practice it is difficult, if not impossible to cleanly separate these effects. However, we structure our data analysis in such a manner that the relative detectability of each of these sets of effects can be drawn out. This allowed us to interpret our case study as an empirical test of the practical utility of island theory in terrestrial systems.

The overall aim of the study was to illustrate the complex determinants of the biodiversity syndrome, including landscape and local process, and provide better insight on how to address the conservation of tropical montane forests. Our first goal was to estimate the relative importance of variables that are hypothesised to influence tree diversity at different scales. These were: (1) climatic gradients operating at a landscape scale; (2) fragmentation effects *per se* operating at the fragment scale (between-fragment

effects); and (3) synergistic effects of fragmentation and habitat disturbance operating at a local scale (within-fragment effects). Our second goal was to ascertain if there were differential responses of tree species guilds (late successional and pioneer species) to these factors. Our third goal was to predict the potential loss of species associated to continuous human disturbance, for which we used re-sampled species accumulation curves for the various forest fragments.

2. Methods

Study area

The study area covers the Central Highlands of Chiapas, Mexico (**Figure 7.1**). A detailed description can be found in **chapter 4**.

Tree species data and explanatory variables

We conducted inventories on 204 circular plots of 1000 m² each in different forest fragments (see **chapter 6**). The study fragments were well distributed over the broader landscape and provide a valuable description of the regional diversity (**Figure 7.1**). We discarded data collected from fragments with less than five plots in our analyses. This resulted in 195 plots allocated over 16 forest fragments (**Table 7.1**).

We used Fisher's alpha as a measure of plot diversity. Fisher's alpha is a good estimator of α -diversity because it is independent of the number of individual trees in a sample (Rosenzweig 1995) and assumes an underlying parametric model for the distribution of species abundances (Fisher *et al.* 1943). At the fragment level, the following fragment metrics were cal-

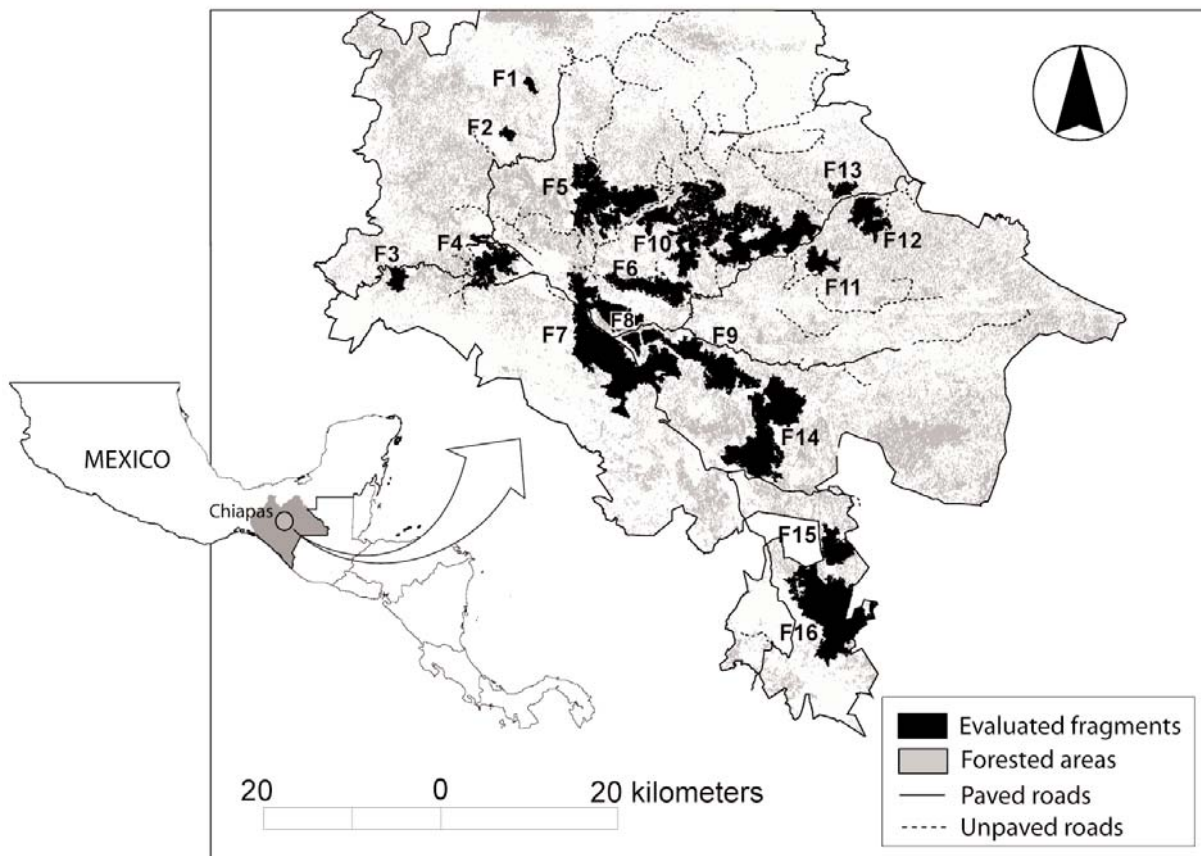


Figure 7.1. The state of Chiapas in southeastern Mexico and location of the studied forest fragments. The matrix surrounding forest fragments includes traditional shifting cropland, natural and induced pastureland, and developed areas. Forest extent was based on land cover classification of ETM+ Landsat imagery. Labels refer to fragment Id. In **Table 7.1**.

Table 7.1. Main features of the 16 forest fragments sampled in this study (Figure 1). Core area is measured at a distance of 100 m to the fragment edge.

Id	Fragment name	Number of plots	Observed species	Area (ha)	Core area (ha)
F1	Caridad del Ejido	10	54	71	15
F2	Epalchen	10	57	92	7
F3	Navenchauc	9	49	269	17
F4	Huitepec	18	39	1195	340
F5	Tzontehuitz	20	51	3032	656
F6	San Antonio	10	29	1182	303
F7	Santiago	10	55	5664	2028
F8	Mitziton	5	30	209	66
F9	Chilil	15	27	2207	623
F10	Bazom	26	14	5282	299
F11	Buena Vista	10	35	416	36
F12	Cholol	10	38	880	101
F13	Cruzton	6	36	278	5
F14	Yalcuc	18	44	3271	564
F15	San Juan las Tunas	7	12	721	120
F16	El Barreño	11	79	3382	614

culated: (a) area (ha); (b) core area (ha); (c) edge/area ratio; and (d) mean proximity index (ratio between the size and proximity of all patches whose edges are within 1 km of the focal patch). These indices were computed by FRAGSTATS version 3.3 (McGarigal *et al.* 2002).

At the plot level, the set of explanatory variables used included variables related to: (1) climate; (2) forest fragmentation; and (3) local human disturbance. (1) Climatic variables (monthly rainfall and monthly maximum and minimum temperature) were generated for 1x1 km cells using universal kriging (Golicher *et al.* 2006). After analysing the redundancy in closely correlated variables, we reduced the 36 initial climatic variables to two variables, namely mean monthly rainfall and maximum temperature during the dry season (from January to May). (2) The effects of fragmentation at this scale of analysis were measured as

distance to the nearest forest edge (m). This was divided by the maximum value in order to produce standardized values ranging between 0 and 1. (3) Surrogates of human disturbance included: canopy openness, measured as the proportion of forest cover in a 500 m-radius circle centred on each plot (ranges between 0 to 1); and a degradation index (DI) ranging between -1 and 1 that was calculated as the relative change in the Normalized Difference Vegetation Index (NDVI) between 1990 TM and 2000 ETM+ Landsat satellite images, respectively:

$$DI = \frac{NDVI(2000) - NDVI(1990)}{NDVI(1990)}$$

Negative values of the degradation index indicate forest disturbance, e.g. by selective logging of certain species, whereas positive values indicate recent forest recovery.

Data analyses

We used ordination techniques to relate the variability in tree species composition to environmental gradients and define major community types. We then tested the effects of forest fragmentation and local disturbance on tree species diversity within each of these community types. Effects manifested as differences between fragments were analysed by fitting simple linear models using the mean plot values of Fisher's alpha for each fragment. Effects within fragments were analysed by looking at patterns in the deviations from the mean value for alpha within each fragment. To do this we used linear mixed effects models that included fixed and random effects terms. These models are appropriate for representing clustered, and therefore potentially correlated data (Pinheiro & Bates 2000), as it is the case for plots within separated fragments. These models differed from the simple linear models which used fragments rather than plots as sampling units by assuming that the effects at the fragment level are essentially random. The fixed effects were interpreted as within fragment relationships, which occur over the set of fragments making up each forest type.

The overall analysis thus aimed to answer the following questions:

- (1) At what scale are the complex and potentially synergistic effects of forest fragmentation detectable?;
- (2) Does the detectability and strength of the relationships differ between forest types?;
- (3) Does the strength of these effects vary between fragments within each forest type?;
- (4) Is the response different between late successional and pioneer tree species?

We constructed as well species re-sampling curves for the different forest types. This allowed us to answer the question: How many species would we expect to lose for each forest type if the number of individuals in a fragment is halved? The answer assumed completely random associations between individuals and no selection for any particular species.

1. Community composition and environmental gradients

Canonical correspondence analysis (CCA) was used to identify key explanatory environmental variables of plot tree composition (**Appendix 7.1**). Analysis of the eigenvalues for constrained as opposed to unconstrained axes suggested that imposing constraints did not produce an optimum arrangement of species and sites in ordination space. We therefore used the unconstrained technique of non metric multidimensional scaling (NMDS) to look at the overall pattern of dispersion in species composition. We interpreted the ordination with respect to the major environmental variables identified in the CCA. NMDS was also used to group species and plots in order to identify major community types. Data were square root transformed and then submitted to Wisconsin double standardisation (Legendre & Gallagher 2001). We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among sites. Based on the NMDS plot, we generated smooth surfaces for elevation and the major climatic variables by fitting thin plate splines using general additive models and interpolating the fitted values on the unconstrained ordination diagram (Oksanen *et al.* 2005). CCA and NMDS were implemented by the R package 'vegan' (Oksanen *et al.* 2005).

2. Forest fragmentation, local disturbance and tree diversity

We used linear models to statistically test the effects of fragmentation per se on tree diversity. The fragment was used as the analytical unit and tree diversity was calculated as the mean of Fisher's alpha of all plots embedded within each fragment. The predictors of diversity used were area, core area, edge/area ratio, and mean proximity index.

Linear mixed effects models were fitted for each of the community types previously defined in the ordination analyses. For each community type we considered an additive multiple linear regression model in which all three covariables (distance to edge, canopy openness, degradation index) were used together and the random effect was modelled as the intercept.

All these analyses were also performed by guilds. Guilds divided species, based on their requirements for exposure to the sun for healthy regeneration, into late successional and pioneer species (modified after Hill & Curran 2001). Categorization was based on the results of detailed observations of seedling populations in the studied forest mosaic (N. Ramírez-Marcial & M. Martínez Icó, pers. comm.) as well as

on data from common-garden experiments (A. Camacho-Cruz, L. Galindo-Jaimes, M. González-Espinosa, J.M. Rey Benayas & M.A. Zavala, unpublished data).

3. Predicting species loss

To investigate the potential effects of local disturbance on the loss of tree diversity, we constructed spe-

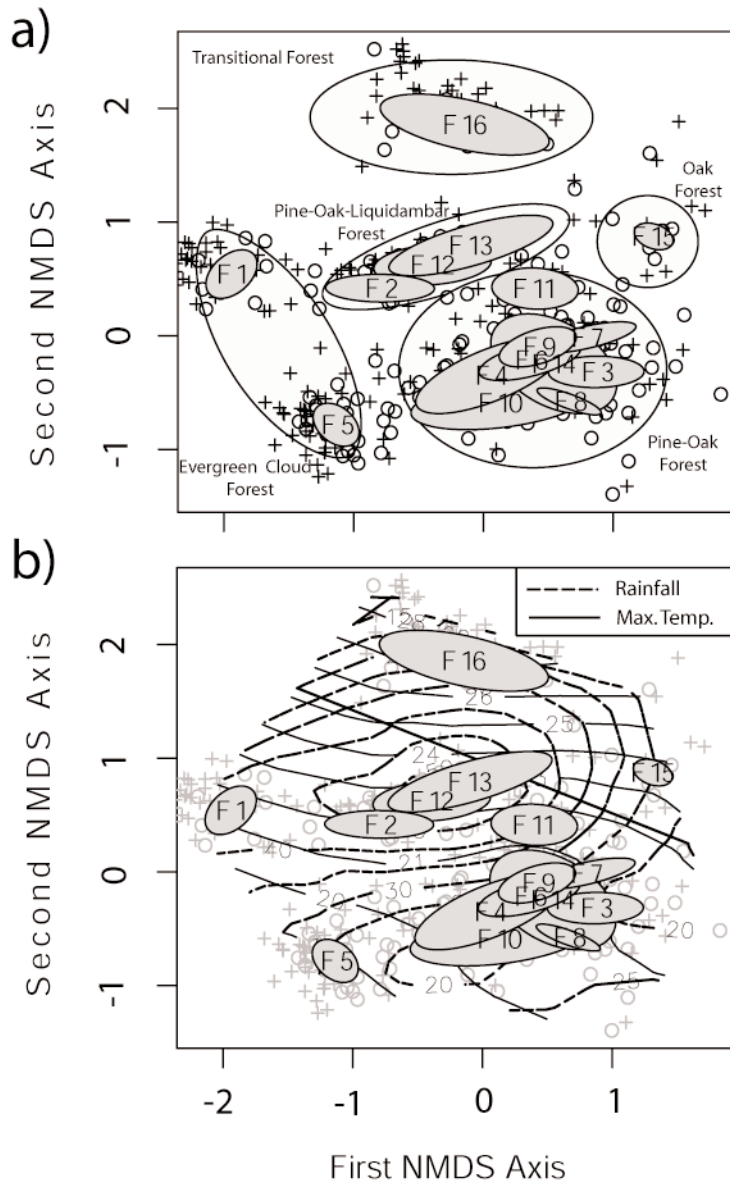


Figure 7.2. Non metric multidimensional scaling ordination of tree species composition in 204 plots showing (a) the identification of community types; and (b) the interpretation of the ordination axes with respect to major climatic variables. Labels refer to fragment Id in Table 1.

cies re-sampling curves (Gotelli & Colwell 2001) for the different forest fragments within each of the major NMDS community types. Rarefaction curves were used to avoid serial dependence between samples (O'Hara 2005). For 1000 re-sample sizes evenly spaced between 10% and 90% of the total number of individuals, s individuals were drawn from the sample without replacement and the number of species $S(s)$ in the sub-sample was counted. We calculated the number of species lost in each fragment by halving the number of individuals. We implemented the re-sampling technique using an R function described by O'Hara (2005).

3. Results

Community composition and environmental gradients

Five major groups were defined according to the NMDS ordination, namely evergreen cloud forest, pine-oak-liquidambar forest, pine-oak forest, oak forest, and transitional forest (**Figure 7.2a**). Floristic differences between these forest types were related to mean monthly rainfall and maximum temperature during the dry season (**Figure 7.2b**). This was supported by analyses of the variance (mean monthly rainfall: $F_{4,193} = 113.7$, $p < 0.0001$; max. temp. during the dry season: $F_{4,193} = 67.2$, $p < 0.0001$). **Table 7.2** summarises the major environmental features and the species that characterised each forest type.

Effects of forest fragmentation and local disturbance on tree diversity

At the fragment level, there was no significant correlation between mean Fisher's alpha and fragment size ($r = -0.11$, $p = 0.680$), core area ($r = -0.11$, $p = 0.672$), edge/area ratio ($r = -0.12$, $p = 0.664$), and mean proximity index ($r = -0.41$, $p = 0.120$). The results were also non significant for late successional and pioneer species (results not shown).

The five forest communities differed in alpha tree diversity (ANOVA $F_{4,193} = 35.42$, $p < 0.0001$, **Figure 7.3**). We explored in detail the effects of fragmentation and local disturbance within fragments in those

groups for which there were more than one fragment, namely evergreen cloud forest, pine-oak-liquidambar forest, and pine-oak forest. Linear mixed-effects models revealed differences in diversity between fragments (random effect) for evergreen cloud and pine-oak-liquidambar forests (**Table 7.3**). There is also considerable variation in alpha diversity that is not linked to the random effect but to variables related to fragmentation and local disturbance. Canopy openness was, in all cases, highly correlated with the intercept ($r > 0.8$), suggesting that this effect might be important in determining differences in diversity between fragments in addition to within fragments. For the two remaining forest types (oak and transitional forests), simple regressions resulted in no significant relationships between tree diversity and the variables related to fragmentation and local disturbance (results not shown).

An analysis by guilds revealed that effects were most noticeable for late successional species than for pioneer species (**Table 7.3**). This was particularly relevant in pine-oak forests, where no significant relationships between alpha diversity of pioneer species and any of the variables related to fragmentation and local disturbance were found.

Predicting species loss

One model for species loss assumes that smaller fragments hold fewer individuals. This assumption does not strictly apply to our studied fragments (**Figure 7.4**). Thus, the island biogeography hypothesis in its simplest form has to be investigated by random re-sampling from the collection of individuals for each fragment (rarefaction). A large number of randomly drawn samples of individuals of varying sizes was drawn from the sample of individuals from each fragment within each community type and the estimated number of species was plotted against the logarithm of the number of individuals. Visual analysis and a plot of the residuals suggested that a straight line relationship was appropriate in all 16 fragment cases (results not shown). The slope of these lines and the values of Fisher's alpha are shown in **Table 7.4**. Theory indicates that if the species-abundance relationship in a sample follows a

Table 7.2. Summary of main environmental features and tree species characterising the different forest types as resulting from interpretation of NMDS ordination. Nomenclature of species follows Breedlove (1986) and N. Ramírez-Marcial (pers. comm.).

Forest type	Environmental features	Characteristic species
Evergreen cloud forest	Elevation between 2,000 and 2,700 m. Permanent humid conditions due to high rainfall and/or fog interception.	<i>Persea americana</i> , <i>Clethra macrophylla</i> , <i>Cleyera theoides</i> , <i>Prunus brachybotrya</i> , <i>Parathesis leptopa</i> , the arborescent fern <i>Cyathea fulva</i>
Pine-oak-liquidambar forest	Elevation between 1,800-2,100 m, high rainfall and low seasonality	<i>Quercus crispipilis</i> , <i>Pinus oocarpa</i> , <i>Liquidambar styraciflua</i> , <i>Clethra suaveolens</i> , <i>Rapanea myricoides</i> , <i>Saurauia scabrida</i>
Pine-oak forest	Elevation between 2,100 and 2,600 m, exposed to highly seasonal conditions	<i>Quercus crassifolia</i> , <i>Q. laurina</i> , <i>Q. rugosa</i> , <i>Pinus ayacahuite</i> , <i>P. pseudostrobus</i> , <i>P. tecunumanii</i> , <i>Garrya laurifolia</i> , <i>Arbutus xalapensis</i> , <i>Alnus acuminata</i> , <i>Cornus disciflora</i> , <i>Oreopanax xalapense</i> , <i>Prunus serotina</i> , <i>Rapanea juergensenii</i>
Oak forest	Elevation between 1,900 and 2,100 m, dry climatic conditions	<i>Quercus segoviensis</i> , <i>Juniperus gamboana</i>
Transitional forest	Elevation below 1,700 m, warm temperatures and dry climatic conditions	<i>Ternstroemia oocarpa</i> , <i>Sebastiania cruenta</i> , <i>Eugenia capulioides</i> , <i>Parathesis belizensis</i> , <i>Xylosma flexuosum</i> , <i>Cupania dentata</i>

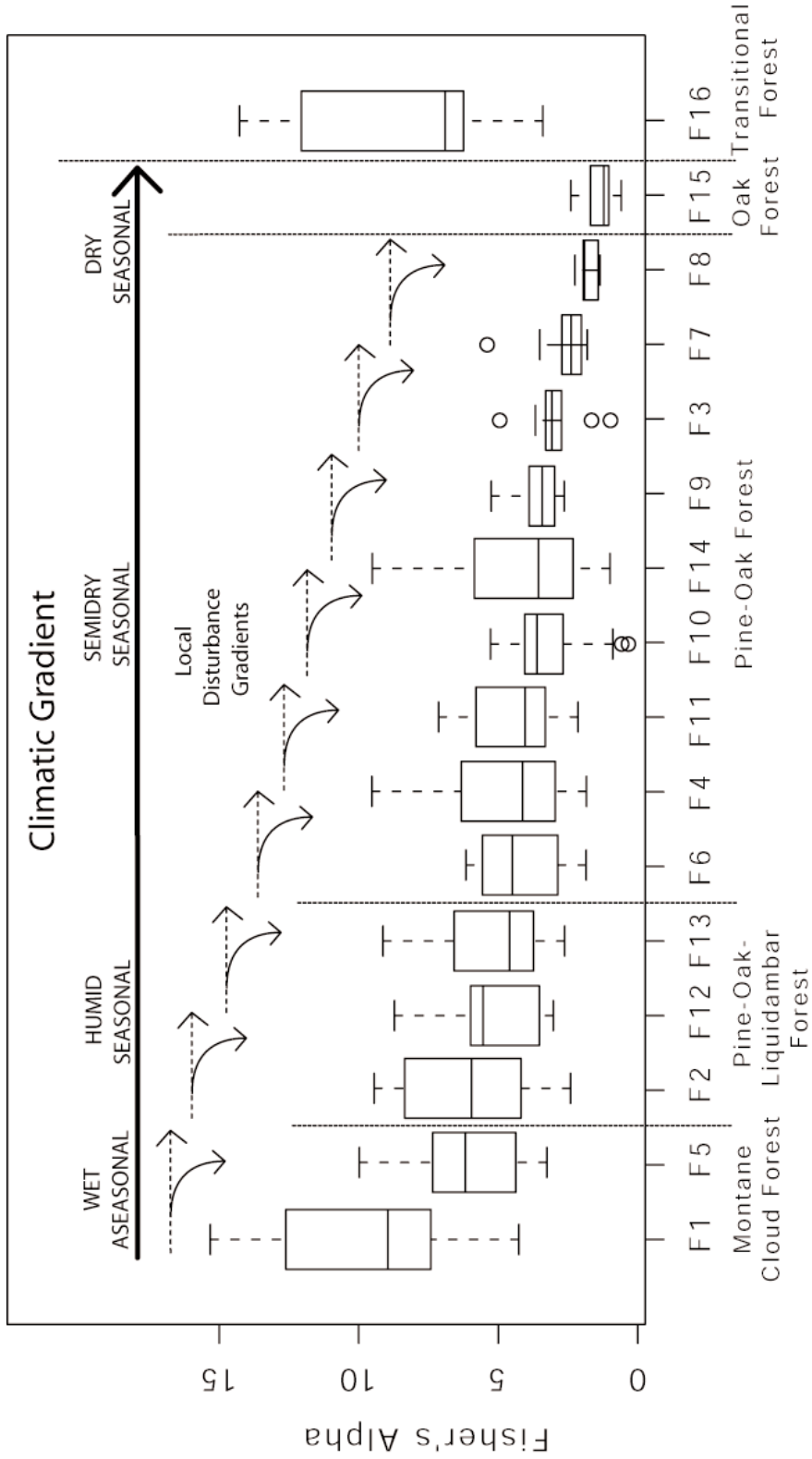


Figure 7.3. Box-plots of alpha tree diversity for each forest fragment grouped by forest type and ordered according to median value. The figure includes the authors' interpretation of the result with relation to regional climatic and local disturbance gradients.

Table 7.3. Fixed effects terms of linear mixed-effects models for evergreen cloud forest, pine-oak-liquidambar forest and pine-oak forest considering all tree species (left column), late successional species (central column) and pioneer species (right column). Plots grouped within fragments are assumed to be correlated; thus the models treat the intercept for each fragment as a random effect. Values of $p < 0.05$ are shown in bold.

Forest type	Explanatory variable	All species			Late successional			Pioneer					
		Value	Stand. Error	DF	p	Value	Stand. Error	DF	Value	Stand. Error	DF	p	
Evergreen	Intercept	17.07	4.27	25	<0.001	16.94	3.51	25	<0.001	-3.19	3.00	25	0.298
	Distance to edge	-10.9	4.42	25	0.021	-6.54	3.84	25	0.101	-5.82	1.72	25	0.002
Cloud Forest	Canopy openness	-9.85	5.06	25	0.063	-11.77	4.08	25	0.008	7.43	3.64	25	0.052
	Degradation index	7.46	6.07	25	0.231	3.32	5.26	25	0.534	3.97	2.41	25	0.111
Pine-Oak-Liquidambar Forest	Intercept	7.94	2.32	20	0.003	3.18	1.36	20	0.030	4.95	2.08	20	0.027
	Distance to edge	3.24	4.44	20	0.474	-1.42	2.60	20	0.589	5.80	3.98	20	0.161
	Canopy openness	-4.45	4.36	20	0.319	0.37	2.55	20	0.886	-4.36	3.90	20	0.277
	Degradation index	5.85	3.24	20	0.086	5.11	1.89	20	0.014	1.64	2.90	20	0.579
Pine-Oak Forest	Intercept	1.54	1.05	109	0.145	-0.02	1.16	109	0.986	1.73	0.61	109	0.005
	Distance to edge	-2.41	1.06	109	0.026	-3.08	1.17	109	0.010	-0.08	0.59	109	0.892
	Canopy openness	3.75	1.44	109	0.011	3.31	1.60	109	0.041	0.86	0.82	109	0.297
	Degradation index	2.43	1.20	109	0.045	2.70	1.32	109	0.043	0.27	0.66	109	0.682

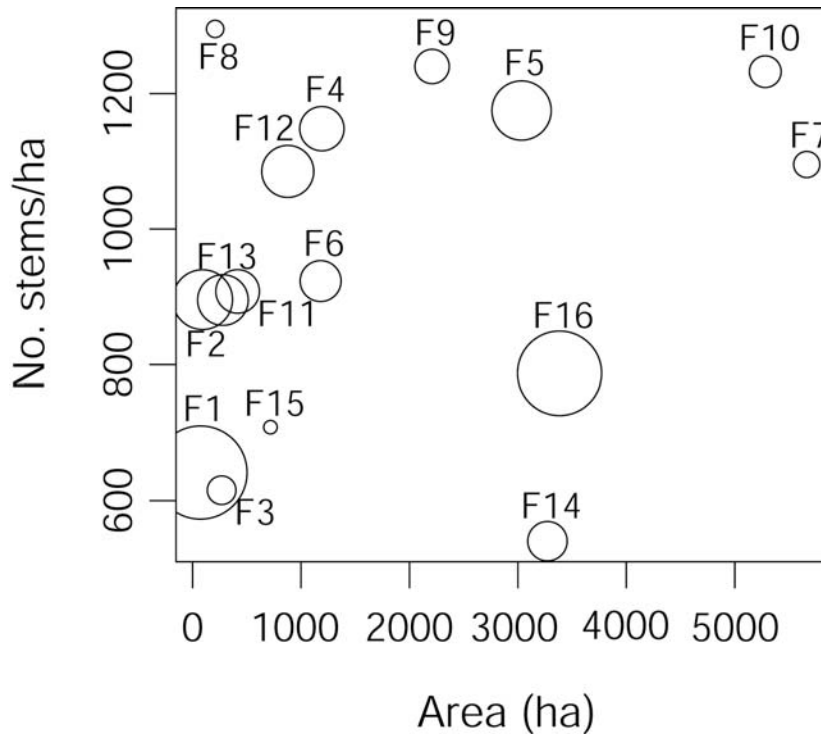


Figure 7.4. Relationship between the number of trees and the size of the forest fragment (ha) ($r = 0.27$, $p = 0.30$). The size of the dots represents mean plot values of Fisher's alpha.

log-series, then Fisher's alpha will equal this slope. This assumption was found to be true in most cases, and provides strong justification for using Fisher's alpha as the preferred diversity index for further analysis. The approximate number of species that would be lost when fragment size is halved under the *ceteris paribus* assumption of island theory ranges between 5 and 21% (Table 7.4). The maximum loss of species was predicted to occur in the transitional zone between pine-oak and lowland tropical deciduous forests (12 species lost), and the highly diverse evergreen cloud forest fragments (7-9 species lost). And the minimum in the oak forest fragments (3 species lost).

4. Discussion

The results of the analyses performed at the fragment level suggest that the effects of fragmentation *per se* on tree diversity are not directly observable. Given the slow response of tree populations to isolation of the remnant fragments, it is likely that the full

impact of these changes will not become apparent for some time (Hanski & Ovaskainen 2002, Helm *et al.* 2006). Lack of detection does not necessarily mean that these effects are not important. Rather it indicates statistical and conceptual model limitations. One of these limitations is related to the scale at which interactions of species with their environment take place. Cushman & McGarigal (2004) suggested that bird species interact most strongly with fine-scale habitat, within the range of their immediate perception. This is the scale at which predation, competition, and other interspecific interactions occur, and at which the organisms experience their environment. As a consequence, the fragment scale might not be appropriate for detecting the impacts of fragmentation and local disturbance. Our results for tree diversity support this hypothesis. We found that fragmentation and disturbance act synergistically on tree diversity at a local scale, yet with opposite effects. Edge effects had a weak but positive effect on tree diversity, whereas local disturbance was negatively related to it.

Table 7.4. Fisher's alpha, slope of the re-sampled species accumulation curves. Assuming random placement the model has been used to predict the number and percent of tree species that would be lost for each halving of the number of individuals in each fragment within each forest type.

Forest type	Fragment	Fisher's alpha	Log(slope)	Species lost	
				n	%
Evergreen cloud forest	F1	14.1	12.5	8.6	15.9
	F5	10.5	10.5	7.3	12.8
Pine-oak- liquidambar forest	F2	11.1	8.9	6.2	12.6
	F11	8.3	8.2	5.7	14.6
	F12	11.1	10.1	7.0	13.7
Pine-oak forest	F3	6.5	8.5	5.9	20.3
	F4	10.4	7.9	5.5	10.0
	F6	5.9	4.5	3.1	10.3
	F7	5.0	5.5	3.8	16.4
	F8	2.5	1.8	1.3	9.3
	F9	6.1	4.9	3.6	10.3
	F10	6.1	2.7	1.9	5.0
	F13	8.7	8.1	5.6	15.5
Oak forest	F14	9.5	9.3	6.5	14.8
	F15	2.2	3.6	2.5	20.8
Transitional forest	F16	21.1	17.3	12.0	15.2

In a recent study, Fahrig (2003) pointed out that the effects of fragmentation on diversity were ambiguous and could be as likely to be positive as negative. Apparently contradictory results are based on studies that differ in the spatial and temporal scale, degree of environmental variability (which is often not considered), history of human use, targeted organisms, and response variable (presence/absence, abundance, different diversity indices, etc.). In our study, we could not notice the effects of fragmentation at the fragment level, and found that it had a positive effect on tree diversity at the plot level. This might be because in the Highlands of Chiapas the form of habitat modification does not create barriers to the species, as opposed to the traditional concept of fragmentation which implies that high quality habitat remnants are isolated by a hostile environment to the organisms that thrive in the remnants. This is also the case of

many other mountainous tropical regions of Central and South America, where traditional shifting-cultivation land use has created a matrix still dominated by semi-natural vegetation in various states of modification. Under these circumstances, forest edges do not become hard frontiers between contrasting habitats but rather an opportunity that allow many species to disperse and flourish (Laurance *et al.* 1998, 2001, López-Barrera & Newton 2005). Consequently, tree diversity increases near the forest edges (**Table 7.3**). This increase might be thought of to occur due to the increase of the more opportunistic pioneer species near the forest edges (Laurance *et al.* 1998, Metzger 2000, Hill & Curran 2001, Kupfer *et al.* 2004). However, we found that the positive effect of forest edges on tree diversity affected both the pioneer and late successional species. The reason for this might be related to the time lag of tree species colonization

(Helm *et al.* 2006). After a gap is opened in the forest, pioneer species tend to colonize the forest edge. Late successional species have lower chances to colonize these sites, but mature trees growing near the forest edge can persist. Consequently these effects are likely to be neglected in the short term. Furthermore, categorization of species by dispersal traits (dispersal power, dispersal rate, agents of dispersal, etc.) and/or age ranges (e.g. by measuring saplings vs. trees) might lead to differential sensitivities to fragmentation (Henle *et al.* 2004). This information does not exist yet for the flora of our study area.

Human disturbance is typically considered to have a negative effect on biodiversity, but even so clear definitions of what is implied by changes in species composition are needed. Humans are capable of subtle manipulations (e.g. harvesting particular size classes of a particular species). Thus it can be difficult to know how much the correlates we found reflect controlling forces, and what the unmeasured role of humans might be. In addition, intense disturbance regimes may lead to a loss of biodiversity by triggering secondary succession processes (**Figure 7.3**). Oak and other broad-leaved species are preferentially logged. Under intense disturbance regimes there is a tendency for early succession stages to be dominated by pine species, particularly in drier areas (González-Espinosa *et al.* 1991, Ramírez-Marcial *et al.* 2001, Galindo-Jaimes *et al.* 2002). But if no disturbance occurs, oak and broad-leaved species tend to replace pines upon their death. This successional gradient is complex. The transitional forest found between pine-oak and lowland tropical deciduous forests seems to harbour higher tree diversity, perhaps due to biogeographical factors acting at a broader scale (Rey Benayas & Scheiner 2002).

Forest managers aiming to retain tree diversity within each of the major forest types should focus on mitigating the negative effects of local disturbance. A suggested option is to protect areas containing mature native forests (e.g. Cayuela *et al.* 2006b). As highlighted by our study, these areas can be near forest edges. Also, forest buffers of any kind would definitely have a positive effect on tree diversity.

Alternatively, active enrichment (seeding, planting) of young forest stands with late successional tree species might help accelerate succession (Martínez-Garz & Howe 2003) and decrease the risk of species loss in the region.

A limitation of this study is that our data represent a "snapshot" in the dynamic process of fragmentation. This makes difficult to understand where we stand and on a trajectory to what in such a dynamic process. Further simulation studies and investigations on the regional patterns of tree diversity seem to be needed in order to clarify these relationships. Our findings support the hypothesis that many tree species have the capacity to overcome the problems posed by fragmented landscapes in the short term. This study also emphasises the need to choose appropriate analytical tools to evaluate the effects of fragmentation and local disturbance at different spatial scales. We conclude that in the studied forests: (1) plot-level variation was more important in structuring plant communities than fragment-level variation; (2) fragmentation and local disturbance act synergistically on tree diversity at the plot level; (3) local habitat disturbance has a higher detrimental impact on diversity than does habitat fragmentation, particularly for pioneer tree species. These conclusions do not contradict the theory of island biogeography. Rather they suggest that a simple underlying theory is not sufficient to describe the complex processes acting in terrestrial systems or predict either their short or long term consequences.

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Appendix 7.1

Canonical Correspondence Analysis and environmental gradients

We used Canonical Correspondence Analysis (CCA) as an exploratory technique to identify key explanatory environmental variables. Variance inflation factors were calculated for each environmental variable as a diagnostic tool to identify non informative variables. We compared different models using Akaike's Information Criterion (AIC). The explored models were:

1. Major climatic variables;
2. Variables related to forest fragmentation (distance to edge, canopy openness) and local disturbance (degradation index).
3. Local spatial effects related to fragment identity, i.e. aggregation of a set of plots within a particular fragment;
4. Major climatic variables and variables related to forest fragmentation and disturbance;
5. Major climatic variables plus local spatial effects related to fragment identity;
6. Variables related to forest fragmentation and disturbance plus local spatial effects associated with fragment identity;
7. Major climatic variables, variables associated to forest fragmentation and disturbance, and local spatial effects related to fragment identity;

8. Spatial variables (latitude and longitude) in the form of a polynomial trend surface equation.

A difficulty arises for model selection using CCA: the likelihood function cannot be correctly calculated for constrained ordination methods. Thus they cannot have true AIC and deviance. However it is possible to extract similar statistics from the models that allows an informal analysis to be based on information criteria. This can be useful for exploratory investigation of structure in the data. Then, AIC values calculated for the CCA were used as a guide rather than an automated model selection tool. We ignored small differences in AIC but interpreted large differences as indicative of informative differences between models. We also assessed each model properties regarding the proportion of the total variability explained by the explanatory variables. **Table 7.1A** shows the summary parameters for the eight proposed models.

Major trends in species composition are clearly associated with climatic variables (model 1, **Figure 7.1A**). The eigenvalues associated to the unconstrained axes for this model (EV1 = 0.77, EV2 = 0.69) were higher than those associated with the constrained axes (EV1 = 0.70, EV2 = 0.45), suggesting the convenience of using unconstrained ordination such as NMDS. It is difficult to clearly link fragmentation and local disturbance with differences in species composition as model 2 explained a particularly low amount of variability. Interestingly, the model with the lowest

Table 7.1A. Summary of the CCA proposed models.

Models	D.f.	AIC	Explained variance (%)			
			Model	Axis 1	Axis 2	Axis 3
~Major climatic vars.	2	1426.4	7.2	4.4	2.8	-
~Human disturbance effects	3	1434.1	4.4	2.2	1.6	0.0
~Frag.id	15	1404.4	27.4	4.9	4.3	3.9
~Climatic vars. + Human disturbance effects	5	1425.1	10.6	4.5	3.1	1.5
~Climatic vars. + Frag.id	17	1404.2	29.0	5.0	4.3	3.9
~Human disturbance effects + Frag.id	18	1405.0	29.4	4.9	4.3	3.9
~Climatic vars. + Human disturbance effects + Frag.id	20	1404.8	30.9	5.0	4.3	3.9
~Polynomial trend surface equation	7	1414.0	17.3	4.8	3.9	3.1

AIC just uses the fragment identity as explanatory variable even though this model has a large number of parameters. This suggests that in a large number of fragments specific localised processes are involved in determining species composition above the other estimated explanatory variables. Variability in

species composition can be also modelled as by a large scale spatial trend (model 8). Sites close together in the landscape tend to be more similar in their species composition than those that are further away, but this model on its own has little predictive utility.

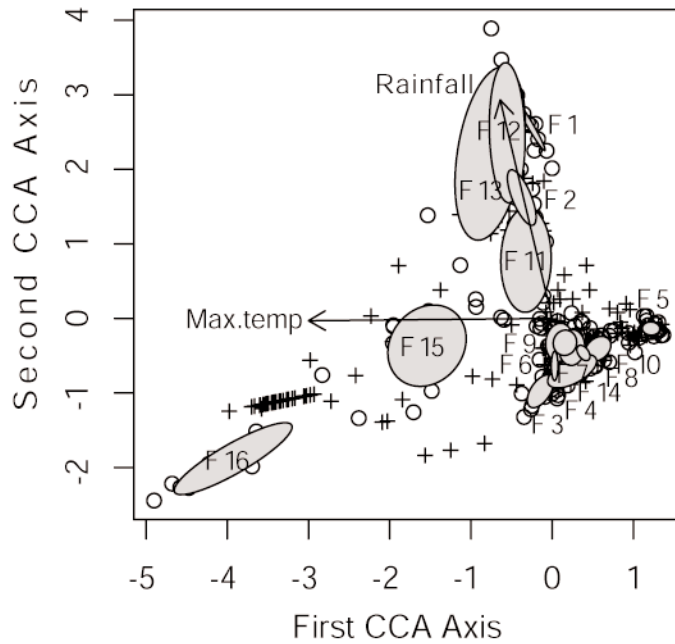


Figure 7.1A. Canonical correspondence analysis (CCA) showing the relationships between species (+), plots (o), and major climatic variables.