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Plant Diversity in Highly Fragmented Forest Landscapes in Mexico and Chile: Implications for Conservation

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Aerial photograph illustrating clearcuttings and industrial plantations of *Pinus radiata* in the coastal range in south-central Chile. Photo: Cristian Echeverría

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Summary

Research addressed a range of issues relating to the regional determinants of species diversity, the effects of fragmentation and human disturbance on tree diversity at different spatial scales, changes of diversity along secondary succession after deforestation, and plausible future scenarios of species decline associated with continued habitat loss across a variety of ecological and socio-economic conditions in Latin America. This analysis was performed using different woody vegetation datasets in combination with various field measurements, remote sensing and GIS data. Regionally, climatic factors emerged as primary predictors of tree diversity. At finer scales, fragmentation and human disturbance better explained patterns of species diversity. These effects were, however, dependent on the time after fragmentation occurred. In the short term, habitat fragmentation was not likely to reduce the overall diversity of a fragment, but could have a slight positive effect on local diversity within fragments. Moreover, we detected a negative effect of human disturbance that far outweighed the effects of fragmentation at this scale. In the long term, however, fragmentation was found to significantly reduce the overall diversity of forest remnants.

Patterns of diversity along chronosequences of abandoned pastures and croplands were consistent across all study areas in Mexico and suggested that vegetation structure and community composition gradually come to mirror those of mature forests. However, species richness strongly depended upon the functional type under consideration.

Using ground-based floristic inventories and forest loss rates derived from satellite imagery, we estimated the percentage of species most likely to disappear, or at least become seriously threatened with extirpation, assuming continued habitat loss until 2025. Alarmingly, the predicted species decline in the Highlands of Chiapas was over 40% using estimated yearly deforestation rates of 4.8%.

Introduction

Identifying the factors driving patterns of species diversity has always fascinated ecologists. Some relevant issues that have emerged since the end of the 19th century are: (i) the description of diversity patterns; (ii) the underlying causes and processes that determine these patterns; (iii) the development of accurate estimators of species richness and diversity indices; and (iv) applied issues related to conservation, restoration and ecosystem management. Studies of diversity are complicated as this variable can be measured in a variety of ways and at different scales. The spatial scale at which biodiversity patterns are measured is directly related to the identification and understanding of underlying causal processes (Allen and Starr, 1982; Cushman and McGarigal, 2004).

The processes that have been suggested as determining patterns of diversity are varied and include phylogenetic, historical, biogeographic and environmental processes, as well as stochasticity (Brown and Lomolino, 1998; Rey-Benayas and Scheiner, 2002). At large spatial scales, factors relating to the flow of energy in the system (e.g. productivity and evapotranspiration) have emerged as primary predictors of species diversity (Wright *et al.*, 1993; Pausas and Austin, 2001; González-Espinosa *et al.*, 2004). At finer-grained scales, however, the type, history and frequency of disturbance, land use, and patch-specific characteristics such as soil type, topography and landscape pattern, as well as processes such as competition and dispersal, may be more relevant for explaining patterns of species diversity (Kerr and Packer, 1997; Lawton *et al.*, 1998; Ricklefs, 2004).

Increasing rates of biodiversity loss and its effects on essential ecosystem services (Heywood, 1995; Costanza *et al.*, 1997; Terborgh, 1999; Tilman, 1999; Bininda-Emonds *et al.*, 2000; Pimm and Raven, 2000; Gaston *et al.*, 2003; Lara *et al.*, 2003) have fuelled increasing concern about biodiversity conservation over the last decade (Ricketts *et al.*, 1999; Cincotta *et al.*, 2000; Myers *et al.*, 2000). Forest loss and fragmentation have been recognized as the main threat to biological diversity worldwide (CBD, 2005). An additional legacy of the extensive removal of native forest is the increased isolation and deterioration of remaining forest habitat owing to edge effects (Forman and Godron, 1986; Reed *et al.*, 1996; Franklin, 2001). Many theoretical and observational studies suggest that habitat fragmentation has a negative impact on the flora and fauna of remnant habitats and it is likely to affect a variety of population and community-level processes (Saunders *et al.*, 1991; Debinski and Holt, 2000). However, the ecological consequences of fragmentation may differ, depending on the peculiarities of particular taxonomic groups or species, the spatial configuration of the relevant landscape, and how it varies both temporally and spatially (Fahrig, 2003). In addition to forest loss and fragmentation, forest resources can be exploited and degraded by forest users to different degrees. These local disturbances alter the ecological processes operating in fragments and may have additive or interactive effects with fragmentation, affecting forest community structure and function (Debinski and Holt, 2000; Laurance and Cochrane, 2001).

This chapter synthesizes research undertaken to understand the mechanisms affecting plant diversity at multiple scales in a variety of highly fragmented forest landscapes in Latin America (Mexico and Chile). We address issues such as the regional determinants of species diversity, the effects of fragmentation and human disturbance on tree diversity at different spatial scales, changes of diversity along secondary succession after deforestation and plausible future scenarios of species decline associated with continuing habitat loss using a variety of case studies under different ecological and socio-economic conditions. We conclude by describing how this knowledge can be applied to the development and implementation of conservation policies.

Study Areas

The highly fragmented forest landscapes we studied were in the tropical mountainous regions of southern Mexico (the Highlands of Chiapas, Central Veracruz and Oaxaca) and temperate zone forests of southern Chile (Los Muermos-Ancud, Fig. 3.1). In Chiapas we also studied regional patterns of diversity for the entire state. Our study areas spanned a variety of biophysical and socio-economic situations that are described in Chapter 1.

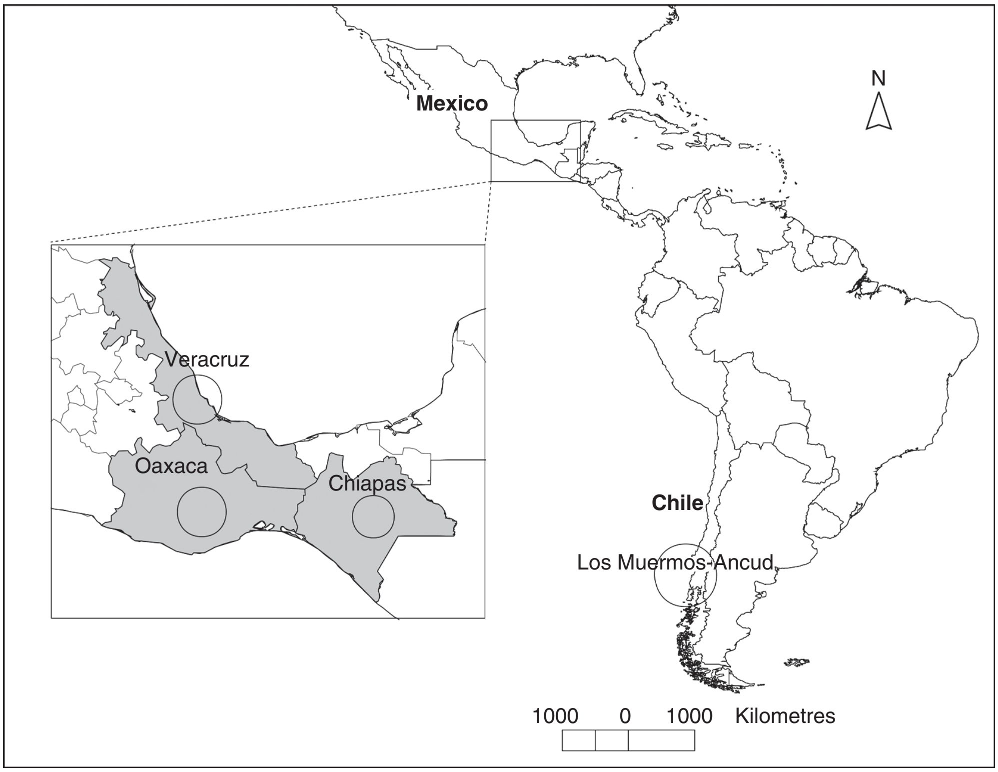

Fig. 3.1. Geographical location of the four study areas in Mexico and Chile.

Case Studies

Regional scale determinants of tree diversity in Chiapas, Mexico

Explaining the distribution of diversity along broad environmental gradients continues to challenge ecologists (Francis and Currie, 2003; Qian and Ricklefs, 2004). Spatial patterns of plant diversity have been related to regional macro-scale processes as well as to local processes. Here we investigate the relationship of tree species diversity and regional-scale environmental factors (e.g. several hundred thousand square kilometres; Mittelbach *et al.*, 2001; Qian and Ricklefs, 2004) in the state of Chiapas, Mexico.

Methods

We compiled a database with information from labels of herbarium sheets of all tree species collected over a period of 135 years (i.e. woody plants with dbh ≥ 3 cm and height ≥ 3 m) in Chiapas that are native to the state (González-Espinosa *et al.*, 2004). These data were spatially assigned to grid cells each of 5 minutes latitude × 5 minutes longitude. In each cell we calculated Simpson's index of diversity.

We used several climatic (*precipitation*, *temperature*, *actual evapotranspiration (AET)*, *seasonality*), edaphic (an index of *soil fertility/quality* was calculated based on the interpretation of physical and chemical properties of soil taxa as described in the legend of the map by FAO–UNESCO, 1974) and topographic heterogeneity variables to predict tree diversity (González-Espinosa *et al*., 2004).

Multiple regression models were fitted to independent explanatory variables to predict tree diversity as tests of hypotheses relating the variation of tree diversity with habitat favourableness, temporal heterogeneity or seasonality and spatial heterogeneity. We also tested whether the shape of the function between tree species diversity and *AET* was curvilinear unimodal with an interior maximum using the Mitchell-Olds and Shaw test (1987), with a null hypothesis of a non-intermediate maximum. We used regression quantiles (Cade *et al*., 1999) to estimate multiple rates of change (slopes) of tree diversity as a function of subsets of values (upper quantiles, 0.75–0.95) of those variables expected to be affected by known or unknown limiting factors.

Results

A model that accounted for 41.4% of the total variance in tree diversity showed positive effects of *AET* and *seasonality*, whereas *soil fertility/quality* had a negative effect. A curvilinear model described the relationship between tree diversity and *AET* well ($R^2 = 0.45$), and an intermediate maximum was detected (Fig. 3.2a). The data pattern also suggested an asymptotic relationship, which was confirmed with a two-part regression. Regression quantiles with the upper envelope of the data (0.85–0.90 quantiles) provided better estimates of the effect of *soil fertility/quality*. This analysis indicated that the statistical effect of *AET* is relatively independent of other environmental factors (i.e. it is – or its correlates are – an important limiting factor of tree diversity by itself). However, the effects of *soil fertility/quality* seem to be more dependent on the interactions with other limiting factors, and may be underestimated or obscured by multiple linear models. One such factor is rainfall. Minimum diversity at intermediate *rainfall* values hints at a bimodal model of tree diversity along a rainfall gradient, in opposition to the frequently described positive linear relationship (Fig. 3.2b).

Patch-level effects of forest fragmentation on tree diversity

Habitat fragmentation has serious implications for a variety of population and community processes over a range of temporal and spatial scales. Studies investigating these effects often draw analogies between forest fragments and oceanic islands (Harris, 1984; Laurance and Bierregaard, 1997; Rosenblatt *et al*., 1999; Ferraz *et al*., 2003; Hill and Curran, 2003). Their key assumptions are that loss in area, increasing edge effects and reduced connectivity decrease species diversity. We analysed the patch-level effects of fragmentation on tree diversity for the Highlands of Chiapas, Los Muermos-Ancud in southern Chile and Central Veracruz. We used Spearman's rank correlations to test univariate relationships between measures of tree diversity and different spatial

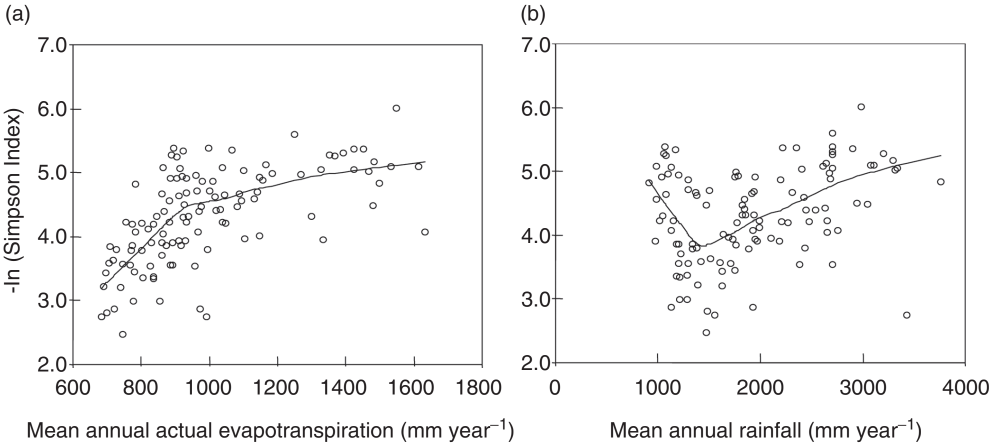

Fig. 3.2. Local weighted curve smoothing (LOWESS) for tree diversity (–ln SI, Simpson's index) as a function of: (a) mean annual actual evapotranspiration (mm year^{-1}); and (b) mean annual rainfall (mm year^{-1}) (after González-Espinosa *et al*., 2004).

metrics. These analyses were performed for: (i) all species; (ii) forest interior species that are characteristic of mature forest stands; and (iii) pioneer species that are characteristic of earlier successional stages.

Methods

In the Highlands of Chiapas, floristic inventories were carried out using 204 circular plots of 1000 m^2 each in different forest fragments; 168 of these plots were sampled from January 2003 to May 2004 (Cayuela *et al*., 2006a), and 36 were sampled in 1998 using the same sampling protocol (Galindo-Jaimes *et al*., 2002; L. Galindo-Jaimes, unpublished data). The abundance of all tree species with dbh ≥10 cm was recorded. The final database included 230 native tree species. Fragments with fewer than five plots were discarded prior to analysis, leaving 195 plots in 16 forest fragments.

In Los Muermos-Ancud, a total of 51 fragments were randomly sampled throughout the landscape (see Chapter 2). The selection of fragments with an age of at least 23 years with the same spatial attributes in 1976, 1985 and 1999 maximized our chances of recording the ecological impacts associated with fragmentation. Samples were also stratified by soil type. Owing to the different sizes of fragments, the number of sampling plots was weighted by the patch size (one plot in fragments less than 100 ha, two plots in fragments between 100 and 1000 ha, three plots in fragments >1000 ha). Sixty-three 20 m × 25 m plots were established in the core areas of 51 fragments. In fragments larger than 100 ha, these were evenly distributed at a minimum distance of 50 m from each other. Each plot was divided into 20 contiguous 5 m × 5 m subplots and, in each, shrub and tree species were identified and counted to estimate the number of individuals per species.

In Central Veracruz, 21 fragments were sampled: seven abandoned pastures (>12 years old) by means of eight 10 m × 10 m plots, four abandoned coffee plantations using ten 20 m × 20 m plots (10–20 years old), and ten montane cloud forest fragments using ten 10 m × 10 m plots. Fragment size ranged from 1.1 to 54 ha. In each plot, the abundance of all tree species with dbh ≥ 5 cm was recorded. A total of 153 tree species were recorded: 125 native species and 28 non-native species.

In all three study areas, we estimated, when feasible, a variety of diversity measures for each fragment. For α-diversity, total and mean plot species richness were calculated. For β-diversity, we calculated the mean Sørensen's index of dissimilarity between plots within each fragment (Magurran, 1988).

The predictors of diversity used were: (i) *area* (ha); (ii) *core area* (ha remaining after removing a 100 m edge); (iii) *total edge length* (km); and (iv) *proximity index* (ratio between the area and distance of all fragments whose edges are within a 1-km search radius of the focal fragment). Computation of spatial metrics was based on land-cover maps (Chapter 2).

Results

There were hardly any significant correlations between any of the diversity measures and fragment metrics in the Highlands of Chiapas and Central Veracruz (Table 3.1). The exception was the estimated number of tree species in a fragment in the Highlands of Chiapas, which was negatively related to the *proximity index*, indicating that the more isolated a fragment was, the higher the number of tree species it contained. For Los Muermos-Ancud, however, *area*, *core area*, *edge length* and *proximity index* were all negatively associated with mean pioneer species richness, and positively associated with forest interior species richness (Table 3.1).

Local effects of human disturbance and fragmentation on tree diversity

In addition to deforestation and fragmentation, forest patches can be degraded by selective logging, ground fires, the impacts of browsing by livestock and overhunting. These local disturbances alter the ecological processes operating in the fragments and may have additive or interactive effects with fragmentation on forest community structure and function (Cochrane *et al*., 1999; Nepstad *et al*., 1999; Gascon *et al*., 2000; Laurance and Cochrane, 2001). In the previous case study we analysed the patch-level effects of fragmentation on tree diversity. Here, we investigated the local effects of fragmentation and habitat disturbance. We focused our study in the Highlands of Chiapas, Mexico. The analysis was hierarchically structured so that the relative effects of climatic gradients on tree diversity could be separated from more subtle human-induced local effects (Cayuela *et al*., 2006a).

Methods

For the 195 plots described in the previous case study, we calculated 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).

Table 3.1. Spearman correlation coefficients (*R*) between forest fragment metrics and different tree diversity measures in the Highlands of Chiapas, Los Muermos-Ancud and Central Veracruz. Significance values are also provided (*P*). Total species richness was calculated using Clench accumulation curves (Colwell and Coddington, 1994). In Los Muermos-Ancud in Chile, all species (seedlings, juveniles and adults) sampled in a fragment were used to calculate total species richness. Sørensen's index was not calculated for pioneer and forest interior species because the matrices included too many zero values.

	Diversity measures	Area (ha)		Core area (ha)		Edge length (km)		Proximity index	
		R	*P*	*R*	*P*	*R*	*P*	*R*	*P*
The Highlands of Chiapas (n = 16)									
All species	Total species richness	–0.03	0.930	–0.08	0.784	0.00	0.990	–0.52	0.040
	Mean plot richness	–0.11	0.680	–0.11	0.672	–0.12	0.664	–0.41	0.120
	Sørensen index	0.38	0.146	0.06	0.818	0.42	0.110	0.03	0.917
Pioneer	Total species richness	–0.07	0.788	–0.21	0.433	–0.04	0.895	–0.41	0.117
	Mean plot richness	0.09	0.742	0.05	0.861	0.08	0.792	0.22	0.407
	Sørensen index	0.36	0.171	0.19	0.480	0.38	0.146	–0.07	0.805
Forest interior	Total species richness	0.05	0.865	0.16	0.560	0.00	0.991	–0.31	0.235
	Mean plot richness	–0.09	0.746	–0.11	0.672	–0.08	0.780	–0.39	0.132
	Sørensen index	0.14	0.605	0.11	0.684	0.09	0.738	0.19	0.480
Los Muermos-Ancud (n = 51)									
All species	Total species richness	0.11	0.421	0.08	0.571	0.10	0.467	0.08	0.584
	Mean plot richness	0.07	0.622	0.04	0.767	0.04	0.782	–0.02	0.897
	Sørensen index	–0.27	0.054	–0.25	0.075	–0.26	0.065	–0.25	0.075
Pioneer	Mean plot richness	–0.29	0.037	–0.34	0.014	–0.29	0.039	–0.46	0.001
Forest interior	Mean plot richness	0.44	0.001	0.39	0.004	0.41	0.003	0.44	0.001
Central Veracruz (n = 21)									
All species	Mean plot richness	–0.13	0.587	–0.11	0.627	–0.09	0.678	n.a.	n.a.
Pioneer	Mean plot richness	–0.34	0.127	–0.30	0.187	–0.25	0.280	n.a.	n.a.
Forest interior	Mean plot richness	0.39	0.085	0.33	0.139	0.34	0.126	n.a.	n.a.

We used Non-Metric Multidimensional Scaling (NMDS) to identify major community types in relation to climatic gradients (Cayuela *et al.*, 2006a). We then tested the effects of forest fragmentation and local disturbance on tree species diversity within each of these community types. The effect of fragmentation was measured as *proximity of a plot to the nearest forest edge* (m); this distance was divided by the maximum value in order to produce standardized values ranging between 0 and 1. Surrogates of human disturbance included *canopy closure*, measured as the proportion of forest cover in a 500 m-radius circle centred on each plot (ranges between 0 and 1), and a *degradation index* (DI), ranging between −1 and 1, which was calculated as the relative change in the Normalized Difference Vegetation Index (NDVI) between 1990 TM and 2000 ETM+ Landsat satellite images, respectively. Negative values of this index indicate forest disturbance, e.g. by selective logging of certain species, whereas positive values indicate recent forest recovery.

Effects within fragments were analysed by examining patterns in the deviations from the mean value for Fisher's alpha within each fragment. To do this we used linear mixed-effects models. These models include fixed effects (within-fragments) and additional random-effect terms (between-fragments) that are appropriate for representing clustered and therefore potentially correlated data (Pinheiro and Bates, 2000). In our case, the random variation arose from the grouping of plots within separated fragments.

Results

Using NMDS axes of floristic composition, five major community types were defined in relation to regional climatic gradients (Cayuela *et al.*, 2006a). We hypothesized that within-fragment variability was determined by the local effects of human activity. Thus, we explored in detail the effects of fragmentation and human disturbance within-fragments for those groups for which there was more than one forest fragment. These groups were montane cloud forest, pine–oak–liquidambar forest and pine–oak forest. All three vegetation types show clear differences regarding alpha tree diversity (ANOVA, $F = 35.42$, $P < 0.001$).

Linear mixed-effects models revealed notable differences in diversity between-fragments (random effect) for montane cloud and pine–oak–liquidambar forests ($P < 0.001$). There is also considerable variation in alpha diversity that is not linked to a random effect, but to variables related to fragmentation and local disturbance (Fig. 3.3). *Canopy closure* was, in all cases, highly correlated with the intercept ($r > 0.8$), suggesting that this variable 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), each consisting of one fragment, simple regressions resulted in non-significant relationships between tree diversity and the variables related to fragmentation and local disturbance ($P > 0.1$).

An analysis by guilds revealed that effects were more noticeable for forest interior species than for pioneer species (Fig. 3.3). 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.

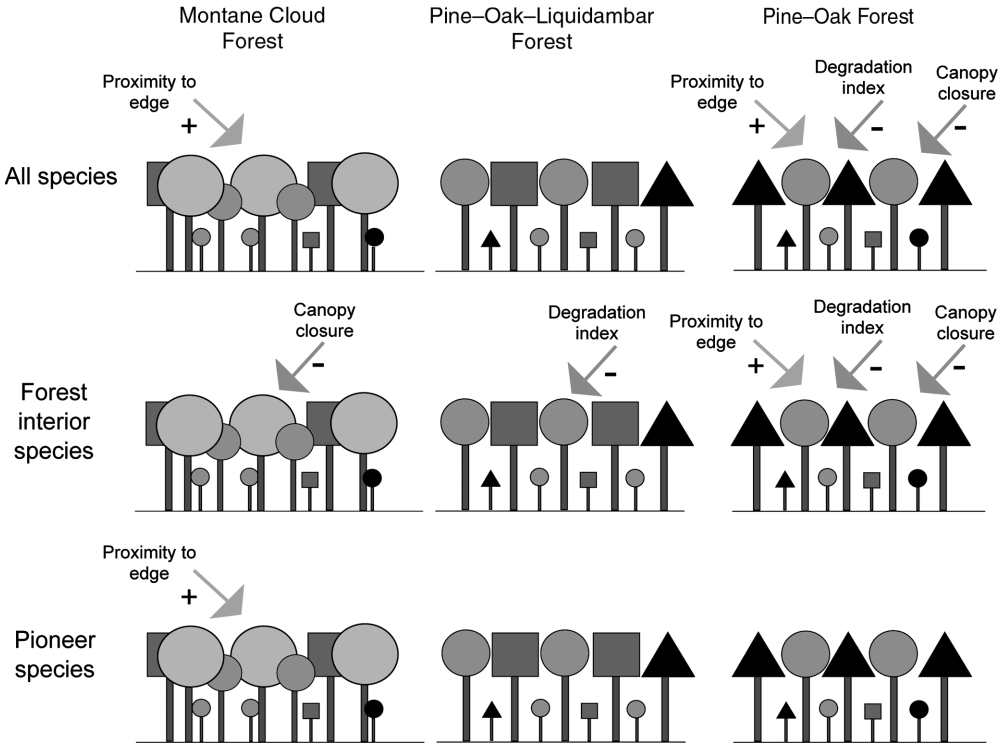

Fig. 3.3. Representation of within-fragment effects (fixed effects) of fragmentation and local disturbance on tree diversity for evergreen cloud forest, pine–oak–liquidambar forest and pine–oak forest considering all tree species (upper), late-successional species (middle) and pioneer species (bottom) (after Cayuela *et al*., 2006a).

Secondary succession and plant diversity

Montane forests of Central and South America have been subjected for centuries to a wide range of human disturbances. In Mexico, traditional land use drives secondary succession with impacts on forest composition, structure and regeneration through practices such as slash-and-burn agriculture, sparse logging, extraction of saplings and lopping of hardwoods for fuelwood, and sporadic cattle grazing (Ramírez-Marcial *et al*., 2001; González-Espinosa *et al*., 2006; Muñiz-Castro *et al*., 2006). Here, we investigate the importance of secondary succession for plant diversity conservation in the three study areas of Mexico.

Methods

In Central Veracruz, we selected 15 abandoned pastures from 0.25 to 80 years old that were adjacent to a forest fragment (Muñiz-Castro *et al*., 2006). To assess distance effects, in each old-field 100 m × 10 m parallel bands were located at 0–10 m and at 40–50 m from the forest edge. Four 10 m × 10 m plots were randomly located in each band to sample trees >5 cm dbh. At the centre of each 10 m × 10 m plot, one 4 m × 4 m plot was established to sample woody plants <5 cm dbh, and one 2 m × 2 m plot was sampled for seedlings <1.3 m height. We measured dbh and height and counted the number of individuals per species in all but the 2 m × 2 m plots, where only the number of individuals and basal diameter of tree species were measured. All plants in the plots were identified to species. Also, tree species were classified as forest interior and pioneer following species description in the *Flora de Veracruz* (Sosa and Gómez-Pompa, 1994). We used an analysis of covariance (ANCOVA) to test the effect of distance to forest edge (categorical variable) and age after abandonment (covariate) on plant diversity. A quadratic term of age was also included in the ANCOVA model since a non-linear quadratic relationship was expected between age and some of the response variables.

In Oaxaca, we studied three chronosequences developed in a montane cloud forest area at El Rincón Alto. Here we report an analysis of secondary succession, based on a subset of data of a study described in more detail in Chapter 7. The sampling plots were positioned in forests of approximately 15, 45, 75 and >100 years old, away from their edges. We sampled all plants with ≥ 3.5 cm dbh in ten 100 m^2 rectangular plots per stand. Plants were identified at species level in most of the cases, classified as lianas and climbing plants, shrubs and understorey trees (with less than 10 m height at adult stage), and canopy trees. We measured dbh and height of each sampled plant identified mostly at the species level. Analyses were based on correlation and ordination techniques.

In Chiapas, we used data on chronosequences following agricultural abandonment, obtained using different methods at 68 sites over a period of 10 years. Information on forest structure, diversity and composition of human-disturbed forests was collected at each site (sources of original data appear in González-Espinosa *et al.*, 2006).

Results

In Veracruz, a total of 164 woody species were recorded in the 15 abandoned pastures sampled: 71 species were trees, 49 shrubs and 44 vines. We recorded 63 tree, 40 shrub and 36 vine species at 0–10 m from the border, and 49 tree, 38 shrub and 29 vine species at the interior of the old-field. The age of the old-field significantly affected tree species richness and diversity along the chronosequence (Fig. 3.4). Richness of trees ≥ 5 cm dbh increased with time of pasture abandonment with a decrease towards the final stage of the chronosequence (Fig. 3.4a). Richness of saplings and seedlings increased linearly with age (Fig. 3.4b, c). Shrubs and lianas did not display any significant trend along the chronosequence. Richness at the two distances from the forest edge were similar for trees >5 cm dbh, shrubs and lianas. Only tree seedlings displayed higher richness and diversity values close to the edge (Fig. 3.4c). Interestingly, richness of late-successional species was higher close to the edge for trees <5 cm dbh ($F = 9.8$, $R^2 = 0.18$, $P = 0.020$, Fig. 3.4d), saplings ($F = 15.9$, $R^2 = 0.33$, $P < 0.001$, Fig. 3.4e) and seedlings ($F = 14.6$, $R^2 = 0.27$, $P = 0.002$, Fig. 3.4f). Pioneer species richness was similar between the two distances from the forest edge for trees, juveniles and seedlings.

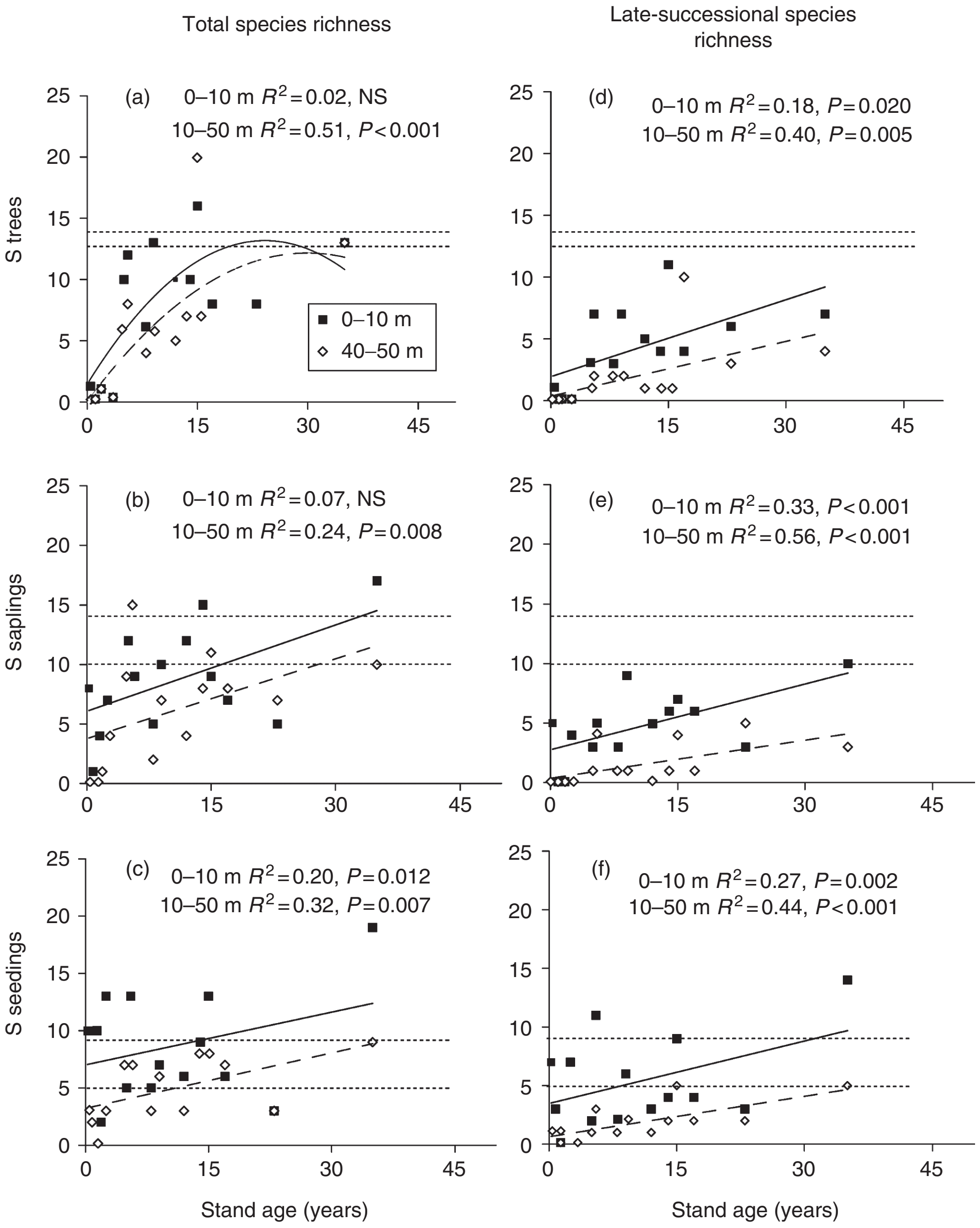

Fig. 3.4. Distance to the forest edge and age effects on tree species richness (S) along a chronosequence of abandoned pastures in Central Veracruz, Mexico. Data from mature forest (two sites) are shown for comparison (dotted lines). (a), (b) and (c) are total tree species; (d), (e) and (f) are late-successional tree species. Distances are 0–10 m (solid lines) and 40–50 m (dashed lines). The lines are derived from the minimal adequate model of ANCOVA; a quadratic term was used in the ANCOVA. When it is significant the relationship is represented by a unimodal curve, when it is non-significant the relationship is linear. Species richness was determined in 400 m^2 for trees, 64 m^2 for saplings and 16 m^2 for seedlings. NS, = not significant ($P>0.05$) (after Muñiz-Castro *et al*., 2006).

In Oaxaca, the analysis of changes in composition and structure in the three groups of plants along the three chronosequences identified 209 species of plants distributed in 128 genera and 69 families. Based on a previous structural analysis of the vegetation (Blanco-Macías, 2007), 45-year-old forests had basal area, average height values and a floristic composition similar to those of old-growth forests, but different from those of incipient secondary forests, which were abundant in shrubs and herbs that were absent in older forests. Lianas and climbing plants were the least diverse group. Liana species richness increased with forest age, at least during the first century of forest development (Table 3.2). In the 15-year-old incipient forests, we could not detect any plant in this group with ≥3.5 cm dbh. By contrast, shrubs and short trees peaked in species richness in 15-year-old stands and decreased in later successional stands, presumably as a result of shading and competition of canopy trees. The opposite trend was detected for canopy trees, by far the most diverse group. Species richness was low in 15-year-old stands, but had similar values at 45, 75 and >100 years after abandonment. Pearson correlation analysis in species richness in 0.01 ha sampling plots revealed that canopy tree richness was negatively correlated with that of shrubs and short trees ($r = -0.269$, $P = 0.003$), whereas no significant correlations were detected between canopy trees and liana species richness ($r = 0.023$, $P > 0.05$), or between lianas and shrubs and short trees ($r = 0.024$, $P > 0.05$). Overall these results suggest that secondary succession in tropical montane cloud forest areas involves relatively rapid changes in species richness, particularly during the first 45 years after abandonment. Species richness appears to depend not only on fallow time but also on species composition. In particular, a trade-off exists between the species richness of shrubs and short understorey trees and that of canopy trees, which was detected at both temporal (successional trends) and spatial (within plots) scales. This suggests that negative interactions among

Table 3.2. Species richness (and standard error) in 0.1 ha in four successional stages in three chronosequences for lianas and climbing plants, shrubs and understorey trees, and canopy trees in El Rincón Alto, Sierra Norte Oaxaca, Mexico (after Blanco-Macías, 2007).

Successional stage	Species richness	Range
Early successional forest (~15 years old)	0 ± 0.0 for lianas/climbing plants	0–0
	14 ± 1.0 for understorey trees	12–15
	17 ± 1.7 for canopy trees	15–20
Young successional forest (~45 years old)	1 ± 0.0 for lianas/climbing plants	1–1
	6 ± 1.2 for understorey trees	4–8
	23 ± 3.7 for canopy trees	19–30
Mature successional forest (~75 years old)	2 ± 1.0 for lianas/climbing plants	1–3
	6 ± 1.5 for understorey trees	4–9
	26 ± 0.7 for canopy trees	25–27
Old-growth forest (≥100 years old)	3 ± 1.5 for lianas/climbing plants	1–4
	7 ± 2.3 for understorey trees	3–11
	24 ± 2.4 for canopy trees	21–29

these groups, presumably mediated by competition, regulate the species composition during forest regeneration after disturbance.

The pattern of species richness change along a successional gradient following shifting agriculture in the Highlands of Chiapas is relatively well known (Table 3.3, González-Espinosa *et al.*, 1991, 2006). Under current land-use practices, agricultural land use may now last for many years based on the increased utilization of agrochemicals and pesticides. After abandonment, fallow fields may be replaced by induced grassland communities, depending on sheep and cattle stocking rates. Recruitment of both pine and oak individuals may occur in early open conditions, and they may become dominant in old-growth stages during the same successional series. Yet an almost complete floristic replacement has been recorded between the open and forested seral stages (González-Espinosa *et al.*, 1991). Canopy and understorey tree species may account for 20–30% of the total floristic richness of any given old-growth stand (not including epiphytes), but may be as low as 12–15% in severely disturbed forests (González-Espinosa *et al.*, 1995).

Future scenarios of species decline

Deforestation and habitat loss are widely expected to precipitate an extinction crisis among forest species (Tilman *et al.*, 1994; da Silva and Tabarelli, 2000; Brook *et al.*, 2006; Wright and Muller-Landau, 2006). These extinctions can be inferred by linking deforestation rates with estimates of regional diversity. Here, we use species–area accumulation curves to explore the likely impact

Table 3.3. Species richness (and standard error) in different successional stages in the Highlands of Chiapas, Mexico (after González-Espinosa *et al.*, 2006; N. Ramírez-Marcial, 2006, personal communication).

Successional stage (no. sites)	Mean species richness	Range
Old-field fallow (n = 22)	50 ± 3.6	30–85
Grassland (n = 4)	42 ± 1.7	30–57
Shrubland (n = 17)	76 ± 3.3	51–82
Early successional forest (n = 25)	47 ± 2.3 in the herb layer	30–50*
	30* in the shrub layer	25–35*
	27 ± 1.2 in the tree layer	20–35*
Mid-successional forest	20–30*	15–20[a]
		5–8[b]
Old-growth forest	35–45*	25–45[a,*]
		8–12[b,*]

[a] Understorey tree species only; regional-level richness based on available herbarium vouchers.

[b] Canopy tree species only; regional-level richness based on available herbarium vouchers.

*N. Ramírez-Marcial, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, México, 2006, personal observation.

of forest loss on tree species diversity in the Highlands of Chiapas, Central Veracruz, Oaxaca and Los Muermos-Ancud.

Methods

To investigate the potential effects of deforestation and fragmentation on the loss of tree diversity, we constructed species accumulation curves in the four study areas. As seen in Chapter 2, these are currently being subjected to different degrees of accelerated transformation as a result of human activities. Exponential (Fisher *et al.*, 1943) and power function models (Preston, 1962) were fitted to predict the potential loss of tree species linked to current estimated deforestation rates in each of the study areas.

Results

Based upon the forest extent in 2000 and given the estimated annual deforestation rates, we were able to predict the forest extent for 2025 (Table 3.4). Constructed non-asymptotic species–area accumulation curves predict the decline of species richness with the reduction of forest extent according to estimated ongoing deforestation rates (Fig. 3.5). For the 2025 scenario, the predicted decline of tree species ranged between <1% in Oaxaca and 41% in the Highlands of Chiapas (Table 3.4 and Fig. 3.5).

Discussion

The assessment of biodiversity in managed landscapes poses several methodological difficulties since: (i) diversity measures strongly depend on the spatial and temporal scale chosen, and unfortunately the scaling functions applicable to transfer results from one scale to another are not completely satisfactory (Waldhardt, 2003); (ii) it is often impractical to consider all the different ecological, historical and human-related factors that may contribute to patterns of species diversity (Lobo *et al.*, 2001); and (iii) field data are often scarce, particularly in tropical regions, owing to limited accessibility to forests (Stockwell and Peterson, 2003) and limited resources and capacity. However, for different regions and spatial scales we identified some common patterns relating to the environmental determinants of diversity and the effects of deforestation, forest fragmentation and human disturbance.

Regional determinants of plant diversity

There has been considerable research interest in the shape of the relationship and the possible mechanisms underlying the energy–species hypothesis at different spatial scales (Rosenzweig and Abramsky, 1993; Whittaker *et al.*, 2001). At the regional scale, the diversity–evapotranspiration relationship was found here to be significant in all multiple linear models. The proportion of total variance explained by either linear (36%) or quadratic (44%)

Table 3.4. Predicted effects of deforestation on species richness (S) decline in the four target areas. Only tree species were sampled for the Highlands of Chiapas, and all woody species were sampled for the other regions. The power model was not calculated for Central Veracruz owing to the small sample size.

						Exponential model			Power model		
Study region	Number of plots	Plot size (ha)	Forest area in 2000 (ha)	Deforestation rate (% year $^{-1}$)[a]	Predicted forest area in 2025 (ha)	2000 Log S	2025 Log S	Species loss (%)	2000 S	2025 S	Species loss (%)
Highlands of Chiapas	204	0.1	98,340	4.80[b]	19,850	4.01	3.78	41.18	5,144	3,314	35.58
Central Veracruz	21	0.1	69,493[c]	3.04	32,135	4.86	4.66	37.40	–	–	–
Sierra Norte, Oaxaca	89	0.01	4,098	0.13	3,948	2.67	2.66	0.01	249	247	0.01
Los Muermos-Ancud	54	0.05	202,167	0.78	166,223	2.40	2.38	4.20	145	140	3.21

[a] Deforestation rates were estimated for the period 1990–2000 in the Highlands of Chiapas, 1985–2000 in Los Muermos-Ancud, 1984–2000 in Central Veracruz and 1995–2000 in Sierra Norte, Oaxaca.

[b] For the Highlands of Chiapas we used a more conservative corrected deforestation rate (after Cayuela *et al*., 2006b) than that presented in Chapter 2.

[c] In Central Veracruz only montane cloud forest was considered.

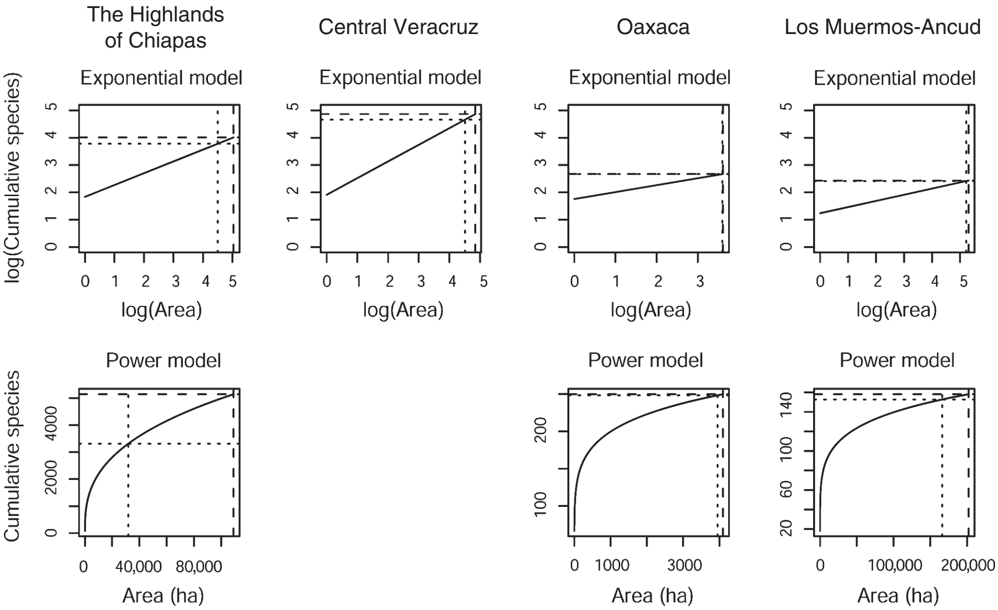

Fig. 3.5. Exponential and power models of species loss associated with deforestation for the Highlands of Chiapas, Central Veracruz, Sierra Norte in Oaxaca and Los Muermos-Ancud. Dashed lines refer to diversity in 2000, whereas dotted lines indicate the estimated loss of diversity in 2025 according to current deforestation rates.

models was higher than a previously reported median of 30% for plant diversity and energy-related factors at similar regional scales (González-Espinosa *et al.*, 2004). A more conservative interpretation of the data pattern (Fig. 3.2a) suggests a pronounced linear increase of tree diversity up to mid-range values of *AET* and a steady but slower increase up to a levelling off at higher values.

Mean annual precipitation showed an interior minimum (Fig. 3.2b). At high precipitation, higher plant diversity may occur owing to the following concatenated events: soil nutrients are depleted through weathering and leaching and growth rates and tree height are reduced; dominance in the canopy is then reduced; and diversity increases as a result of higher canopy richness and increased richness of the shade-tolerant understorey (Austin and Smith, 1989; González-Espinosa *et al.*, 2004).

Soil fertility/quality was found to be negatively related to tree diversity (González-Espinosa *et al.*, 2004). The effects of soil fertility/quality, however, seemed to be more dependent on the interactions with other limiting factors, and may be underestimated or obscured by multiple linear models. Other studies have highlighted different relationships (positive, negative, hump-shaped) between soil characteristics and plant diversity at meso- and landscape scales (Huston, 1980; Clinebell *et al.*, 1995; Clark *et al.*, 1999; Rey-Benayas and Scheiner, 2002). It therefore seems difficult to generalize the response of plant diversity to soil characteristics at the regional scale. We also found positive effects of climate seasonality but not of spatial heterogeneity as measured by elevation range and soil diversity.

Effects of fragmentation and human disturbance on tree diversity

At the patch level, there were significant differences between the study areas. Whereas in the Highlands of Chiapas and Central Veracruz the effects of fragmentation on tree diversity were not directly observable, in Los Muermos-Ancud correlations between mean species richness and fragment metrics were all significant for the forest interior (negative effect) and pioneer species (positive effect, Table 3.1). We attribute these differences to the historical patterns of deforestation. In the Chilean study area, the process of deforestation began during the 1850s and was driven largely by an expansion of agricultural land and Monterrey pine and eucalypt industrial plantations, particularly since the 1970s (Lara *et al.*, 2003). At present, most native forest fragments have been affected by logging for fuelwood and timber (Echeverría *et al.*, 2007). In the Highlands of Chiapas, forest loss was also associated with intensification of traditional agriculture and exploitation of forest resources, particularly since the 1990s (Cayuela *et al.*, 2006b). Because of the slow response of tree populations to recent disturbances, it is likely that the full impact of these changes will not become apparent for some time (Hanski and Ovaskainen, 2002; Helm *et al.*, 2006), thus explaining the current lack of a relationship between diversity measures and fragment metrics.

Lack of detection, however, does not necessarily mean that the effects of fragmentation are not important. Rather it indicates the limitations of statistical and conceptual models. One of these limitations is related to the scale at which species interact with their environment. Cushman and McGarigal (2004), for instance, 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 (Levey *et al.*, 2005). As a consequence, the fragment scale might not be appropriate for detecting the impacts of fragmentation and local disturbance. Our results in the Highlands of Chiapas support this hypothesis for tree diversity. We found that fragmentation and disturbance act simultaneously on tree diversity at a local scale, yet with opposite effects (Fig. 3.3). Whereas forest edges had a weak but positive effect on tree diversity (a review study by Ries *et al.*, 2004 largely corroborated this response), local disturbance was negatively related to it (Ramírez-Marcial *et al.*, 2001; Galindo-Jaimes *et al.*, 2002). Such a positive response of tree diversity to forest edges can be the result of traditional shifting cultivation, a common practice in many mountainous tropical regions of Central and South America. This creates a matrix dominated by semi-natural vegetation in various states of modification (Kappelle, 2006), which does not create dispersal barriers to most of 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. Under these circumstances, forest edges do not become hard boundaries between contrasting habitats but allow many species to disperse and flourish (Laurance *et al.*, 1998; Laurance and Cochrane, 2001; López-Barrera and Newton, 2005; López-Barrera *et al.*, 2006). Consequently, tree diversity increases near the forest edges (Fig. 3.3). This increase might occur owing to the increase of the more opportunistic pioneer species near these edges (Laurance *et al.*, 1998; Metzger, 2000; Hill and 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. Shade-tolerant, late-successional species have a lower chance of colonizing these sites, but mature trees growing near the forest edge can persist. Consequently these effects are likely to be neglected in the short term, but would be manifest after some decades, as seen in the temperate forests of southern Chile (Table 3.1). It may be significant therefore that fragmentation effects were only detected in the latter study, in which only fragments created at least 23 years ago were assessed.

Secondary succession and tree diversity

Disturbance, particularly deforestation, triggers secondary succession and hence a change in the community type. Consistencies in the patterns of diversity can be found along the chronosequences of abandoned pastures and croplands in all of the study areas. Overall, a longer time since abandonment produced a vegetation structure and community composition more similar to that of mature forests. However, species richness strongly depended upon the functional type under consideration. There are usually negative correlations between species richness of trees and other woody plants such as shrubs and geophytes. We found the largest number of woody species in early successional forests in the Highlands of Chiapas (Table 3.3). Similarly, richness and diversity values of tree species similar to those of the mature forest were achieved in earlier successional stages (*c.*20 years) in Central Veracruz (Fig. 3.4). This pattern could be explained by the shifting balance between late-successional (positive) and pioneer species (negative, and flat for juveniles) along this chronosequence resulting in a peak in species diversity at intermediate successional stages. At a distance closer to the forest border, there are higher richness and diversity of late-successional species (Muñiz-Castro *et al.*, 2006). As the forest matures, late-successional species outcompete pioneer species. Since biomass per unit area is a function of wood density and individual size, the biomass of the secondary forest will progressively become more similar to the biomass of the primary forest as long as the characteristic tall late-successional tree species with dense wood enter into the successional community by replacing light wood pioneer species (Brown and Lugo, 1992; Clark and Clark, 1996). Rapid recovery of species richness in smaller size classes has been reported in other tropical regions (Saldarriaga *et al*., 1988; Denslow and Guzmán, 2000).

Predicted species loss

Our models predicted the potential impact of deforestation on species diversity (Table 3.4 and Fig. 3.5). Based on ground-based floristic inventories and known forest deforestation rates derived from satellite imagery, and assuming that the drivers of deforestation will not change in the future, we calculated the percentage of species that are destined to disappear – or at least be seriously threatened with extinction – by a future year (2025). We can compare these values with the proportions of species projected to become extinct as a result of global habitat losses. Thomas *et al*. (2004) applied the species–area relationships to changes in global land use based on global rates of habitat loss. Projected conversion of humid tropical forest at an annual rate of 0.43% (Achard *et al*., 2002) from 1990 to 2050 predicted a value of 6.3% of species destined for extinction, a rate far lower than the rates estimated for the montane tropical forests of Central Veracruz and the Highlands of Chiapas. The amount of diversity decline differed considerably from one region to another. This might be due to differences in: (i) the regional species diversity, which determines the shape of the species–area accumulation curves; and (ii) the annual deforestation rate, which determines the amount of habitat that is lost. These two characteristics vary greatly in the forests in our study regions, and hence may explain the different predictions in Table 3.4 and Fig. 3.5. Alarmingly, the rate of species destined for extinction in the Highlands of Chiapas is above 40% owing to the extraordinarily high recent deforestation rates (see Chapter 2) and the high species diversity in the region. This predicted rate of species extinction is comparable to the rates of plant extinction projected for scenarios of maximum expected climate change in Amazonia (69%, an average of different area methods, Thomas *et al*., 2004). We note, however, that these models are still quite simplistic, since not all forest types are vanishing at the same rate, nor do they have the same diversity, and in addition the models are not spatially explicit (Cayuela *et al*., 2006a).

Implications for conservation

Forest fragmentation is most often a direct consequence of deforestation. A study by Fahrig (1997) indicated that the effects of habitat loss on population extinction far outweigh the effects of habitat fragmentation. Forest loss continues to be a major concern in most of our study areas, as indicated in Chapter 2. Therefore an obvious priority for conservation should be preventing further forest loss and fostering habitat preservation and restoration.

Many studies have focused their attention on what spatial pattern a landscape should adopt to enhance connectivity and reduce the adverse effects of fragmentation (Collinge, 1998; Hill and Curran, 2001; Butler *et al.*, 2004; Platt, 2004; Damschen *et al.*, 2006). This is impractical in many mountain regions of Central and South America, where land tenure, poverty and social issues would impede the implementation of effective regional conservation plans.

An important finding of this study is that the patch-level effects of fragmentation will only manifest some decades after this process starts taking place and, possibly, after a certain threshold of habitat loss is surpassed (Fahrig, 2001). It has been suggested that this threshold value is at about 20% of habitat, below which the effects of habitat fragmentation on population persistence may be more evident (Fahrig, 1997, 2001). According to Ewers and Didham (2006), actual empirical measurements of the landscape threshold suggest that a figure such as 20% is far too simplistic. In fact, the threshold for some species is as high as 95%, and varies widely from species to species. Matrix quality can also influence the effects of fragmentation, but unfortunately this variable is rarely included in research investigations (Fahrig, 2001). Ideally, conservation strategies should be aimed at mitigating the external influences on the natural system as much as at preserving the natural system itself (Saunders *et al.*, 1991).

Also of considerable relevance is the management of forest by local people. This study has stressed the negative effects that over-exploitation of forest resources has on tree diversity by triggering shifts in species composition along a successional gradient. However, if enough time is allowed without disturbance, and a source of colonists is available sufficiently nearby, the vegetation structure and community composition should begin to resemble that of mature forests. This provides a potential scenario for natural vegetation recovery.

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