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Key attributes to the disturbance response of montane cloud forest trees: shade tolerance, dispersal mode and the capacity to form a seed bank

Francisco J. Díaz-Perea · Miguel Equihua · Víctor J. Jaramillo ·
Ignacio Méndez-Ramírez · Carlos Fragoso

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Abstract

• **Context** Understanding the biological mechanisms related to plant response to disturbance is essential for predicting the changes in the structure of plant communities resulting from disturbance.
• **Aims** The aims of this study are to identify the regeneration traits linked to the response to disturbance of tree species of a montane cloud forest in order to define regeneration types and to explore whether disturbance intensity acts to select specific regeneration types that can colonize disturbed plots.
• **Methods** A theoretical model was developed and evaluated using structural equation modeling to link two latent variables:

regeneration type and vulnerability to disturbance. We studied two plots that were subjected to different intensities of disturbance and one plot of mature forest.

• **Results** Shade tolerance, dispersal mode, and the capacity to form a seed bank were the traits that determine regeneration type. There was a trend for re-sprouting capacity to be associated with the regeneration types dominant in disturbed plots. Regeneration types were differentially distributed among the sites.

• **Conclusion** There was evidence that disturbance intensity has a filtering effect on the colonization of disturbed plots. Species vulnerability to disturbance depends on specific

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Contribution of the co-authors Francisco J. Díaz-Perea: designing the research, fieldwork, collecting data, statistical analysis, writing the manuscript
Miguel Equihua: overall design and supervising of the research
Víctor J. Jaramillo: collaboration in designing the research, internal reviews, reviewing the manuscript
Ignacio Méndez-Ramírez: advising for statistical analysis and reviewing the manuscript
Carlos Fragoso: collaboration in designing the research

F. J. Díaz-Perea · M. Equihua (✉)
Red de Ambiente y Sustentabilidad, Instituto de Ecología, A.C.,
91070 Xalapa, Veracruz, México
e-mail: miguel.equihua@inecol.mx

F. J. Díaz-Perea
e-mail: francisco.diaz04@cfe.gob.mx

F. J. Díaz-Perea
Gerencia de Protección Ambiental, Comisión Federal de
Electricidad, Boulevard Adolfo Ruiz Cortines 4156, piso 4, Col.
Jardines del Pedregal, 01900 Distrito Federal, México

V. J. Jaramillo
Centro de Investigaciones en Ecosistemas, Universidad Nacional
Autónoma de México, 58190 Morelia, Michoacán, México
e-mail: luque@oikos.unam.mx

I. Méndez-Ramírez
Departamento de Probabilidad y Estadística, Instituto de
Investigaciones en Matemáticas Aplicadas y en Sistemas,
Universidad Nacional Autónoma de México, 04510 Ciudad
Universitaria, Distrito Federal, México
e-mail: nacho@sigma.iimas.unam.mx

C. Fragoso
Red de Biodiversidad y Sistemática, Instituto de Ecología, A.C.,
Xalapa 91070, Veracruz, México
e-mail: carlos.fragoso@inecol.mx

combinations of regeneration traits. Structural equation modeling is useful for exploring plant response to disturbance using key parameters linked to plant persistence.

Keywords Functional classifications · Disturbance · Montane cloud forest · Regeneration type · Vulnerability to disturbance

1 Introduction

Plant species respond to disturbances differentially, some species are excluded from the community, others reduce their abundance and some others tolerate the disturbances. Therefore, predicting the changes in the structure of plant communities resulting from human disturbance is a major challenge in ecology. Addressing this challenge is made even more urgent by the increasing transformation of natural environments by human activities. A key step in addressing that challenge is to identify and to understand the biological mechanisms related to plant response to disturbance.

Disturbance, defined as irregularly occurring destruction of vegetation, is simultaneously the cause of mortality for some individuals and an opportunity for others to establish. Frequency and severity, among other attributes, are features of disturbance; severity is a measure of the damage caused to community by the disturbing force (Sousa 1984).

Vegetation recovery after disturbance is an intricate process; the directional changes in the plant community are known as secondary succession, a process that is influenced by stochasticity, species' biology, interactions with other species, and the interplay of biotic and abiotic components (Guariguata and Ostertag 2001). Bud, propagule, and sapling banks, as well as seed dispersal are sources of forest regeneration after a disturbance (Klimešová and Klimeš 2007).

Disturbances of varying severity create complex gradients of directional change in the environment, with the greatest disturbances causing the largest changes. Severity depends on: (1) the size of the area affected because it influences the magnitude of changes in the physical environment as well as the likelihood of propagules from neighboring locations colonizing the disturbed location, and (2) the damage to adult individuals and bud/sapling/seed banks, because it affects the recovery rate of the forest. With low-severity disturbance, resprouting species and the establishment of new individuals from the sapling/seed banks initiate a fast vegetation recovery (Guariguata and Ostertag 2001); by contrary, with severe disturbances, which eliminate all adult individuals and bud/sapling/seed/banks, vegetation recovery is slow, because colonization depends on propagule availability from nearby sources. Therefore, disturbance severity shapes plant colonization selecting for those species that can persist in a site after a disturbance of certain severity has occurred; the species

capacity to persist is a function of their vulnerability to disturbance.

Plant functional classifications can be applied to explore the plant response to disturbance. These offer a practical perspective to explain plant distribution along environmental and disturbance gradients (Lavorel and Garnier 2002; Suding et al. 2008). Functional classification is a way of grouping species that has been applied in plant ecology research since the mid-1980s. Using this approach, the complexity of varying species composition in plant communities is simplified because the species are grouped into functional units, named functional types. These are sets of plants that exhibit similar ecological functionality under given environmental conditions (Díaz et al. 1999). Functional types have also been defined as groups of plants that have similar effects on ecosystem processes (Walker et al. 1999) or groups with the same syndrome of traits (Rusch et al. 2003).

A trait-based response framework (Suding et al. 2008) is a good starting point for exploring plant response to disturbance. Under this approach, plant functional groups are defined using response traits and this knowledge can be used to generate scenarios about general patterns of reaction by plant communities to disturbance, e.g., the regeneration types that might colonize a disturbed plot.

Given the great number of factors involved in a plant's response to disturbance, we focus on only the critical processes that may help predict the changes in a plant community. We focus the analysis on plant regeneration processes that are important during the early phase of vegetation recovery when the factors that govern colonization are most important (Quesada et al. 2009). Thus, the analysis was based on parameters that determine the persistence of plants at different levels of ecological organization (Pausas and Lavorel 2003). These are: individual persistence, propagule persistence (population level), competitive capacity (community level), and dispersal capacity (landscape level). Defining plant functional type with these parameters opens up the possibility of understanding plant regeneration as an integral process.

Investigating the relationships among traits to define functional groups and determining how these traits are related to specific environmental conditions or ecosystem processes is a complex task that presents two challenges. It is necessary (a) to develop a consistent functional classification based on the plant traits associated with the process under study, and (b) to identify relationships between functional types and specific environmental conditions or ecosystem processes.

A promising approach for integrating various sources of ecological information around a conceptual proposition is structural equation modeling (SEM). This is a multivariate analysis strategy suitable for studying complex systems. It allows us to test the fit of data to a conceptual causal model that represents hypothetical relationships among multiple variables, and their interrelationships.

SEM includes several techniques: path analysis, confirmatory factor analysis and estimation of latent variables. The first has been used frequently in ecological research, whereas the other two have not, despite their potential (Iriondo et al. 2003). SEM has two main steps (Muller 1996): (a) model conceptualization and specification, and (b) data-model fit assessment and refinement. Model conceptualization involves developing a theoretical construct that relates observed or manifest variables to unobservable or latent variables. The premise is that observed variables—despite being imperfect indicators of certain underlying variables that are not susceptible to direct measurement—are valuable contributors to the estimation of the underlying variables (Shipley 2000). In addition, dependency relationships can be formulated among the latent variables. Data-model fit evaluates the match between the expected and observed variance/covariance structure between the observed variables and the theoretical model (Muller 1996). It is based on the idea that a hypothesis set as a whole is expected to produce a very specific correlation pattern. Path coefficients indicate the strength of the direct effect of one variable on another. To evaluate data-model fit, several indexes have been developed but the most frequently used is the chi-square statistic (Shipley 2000).

We use SEM to explore the response to disturbance of tree species of a montane cloud forest in Coatepec, Veracruz, Mexico. We studied two plots of secondary vegetation which were subjected to different intensities of human disturbance and one plot of mature forest. We were interested in: (a) identifying the regeneration traits linked to the response of montane cloud forest trees to disturbance, from which it is possible to define regeneration types, and (b) exploring whether disturbance intensity acts as a filter during the early phase of secondary succession, selecting for specific regeneration types that can colonize the disturbed plot.

A conceptual model based on latent variables was structured. The model articulates two propositions related to forest recovery: (1) regeneration types are groups of species with the same regeneration traits, each group representing a regeneration strategy, and (2) species' vulnerability to disturbance determines their distribution and abundance in sites with different disturbance histories. The model proposes that the vulnerability of species to disturbance depends on regeneration type (i.e., specific combinations of regeneration traits); therefore, regeneration types are expected to be differentially distributed among sites with different disturbance conditions.

1.1 Model conceptualization and specification

Our base model (Fig. 1) was articulated from the previous concepts. Regeneration type and vulnerability to disturbance are latent variables because they cannot be measured directly. Regeneration type was defined and estimated using traits key to plant regeneration processes, which are relatively easy to

measure (i.e. “soft” attributes, Lavorel and Garnier 2002): resprouting capacity, capacity to form seed and sapling banks, shade tolerance (indicator of light niche specialization), and seed dispersal mode. These are indicators of plant persistence that act on different scales of ecological organization: individual, population, community, and landscape (Pausas and Lavorel 2003).

Vulnerability to disturbance was structured based on species abundance within each plot. We assume that this latent variable indicates the species capacity to colonize and/or persist in disturbed plots, despite the changes in biophysical conditions and the damage to propagule availability caused by the intensity of disturbance. In this way, species vulnerability has a major influence on both composition and species abundance in each plot.

Both latent variables were linked through a structural relationship: regeneration type influences vulnerability to disturbance and the latter is a dependent variable in the model. If disturbance intensity acts as a filter, we expect to find a differential distribution of species in the plots depending on its vulnerability to disturbance. Also, since species vulnerability depends on regeneration type, we anticipate a different composition of regeneration types in the plots. Additionally, the model identifies regeneration traits related to vulnerability to disturbance.

2 Methods

2.1 Study area

The study area is called La Cortadura, a municipal forest reserve in Coatepec, Veracruz, Mexico (2,000–2,200 m a.s.l.). It is a forest of 107 ha, located in the upper basin of the Antigua River. Montane cloud forest is the dominant vegetation in this region (Muñoz-Villers and López-Blanco 2007). In Mexico, montane cloud forest is a diverse and fragile ecosystem in which floristic elements from Nearctic and Neotropical origin converge. It is commonly distributed in foggy areas in transitional regions between tropical and temperate climates. These forests are valued for the environmental goods and services they provide, which are mainly hydrological services that are protected in exchange for economic compensation, but they are also a biodiversity hotspot (Toledo-Aceves et al. 2011). In the region, montane cloud forest cover has decreased by more than 200 km² from 1990 to 2003, through forest conversion to cropland or pastures (Muñoz-Villers and López-Blanco 2007).

La Cortadura's topography is characterized by steep slopes (20–45 %). Montane cloud forest and secondary vegetation (known as Acahual in Mexican Spanish, and Alder forest) are the dominant vegetation types (Muñoz-Villers and López-Blanco 2007). Secondary vegetation is present in areas

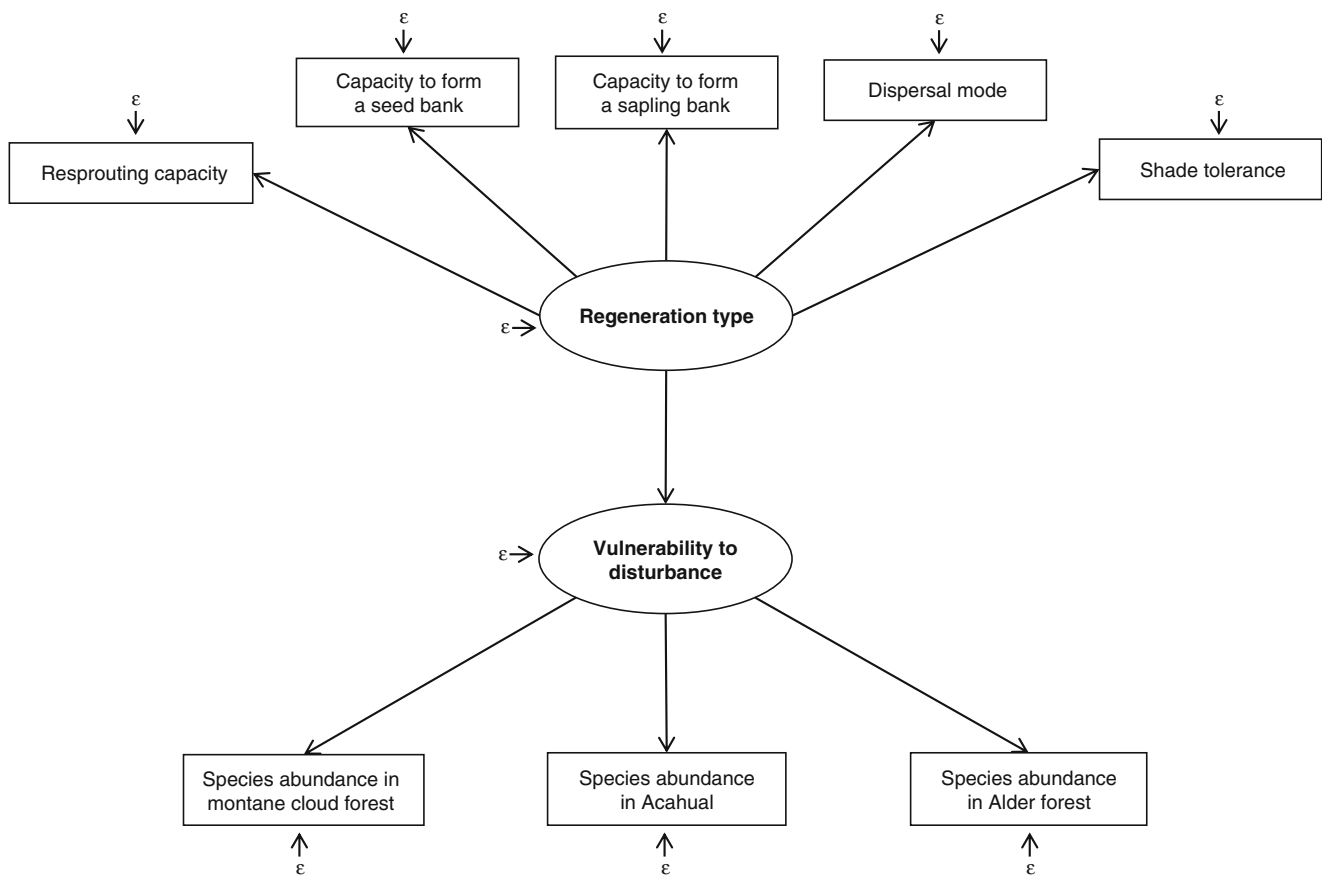


Fig. 1 Base model with regeneration type and vulnerability to disturbance as latent variables; the former was structured with regeneration indicators (observed variables). Vulnerability to disturbance was structured with species abundance under different conditions of disturbance–conservation and is a dependent variable. The diagram shows the measurement error of indicators

originally covered by montane cloud forest that were clear cut for crops and animal husbandry. Acahual vegetation covers more than 5 ha, it has grown on land previously used for agriculture that was abandoned 20 years ago. The Alder forest covers 12 ha, and it has grown in an area that was originally used for agricultural activities. It was accidentally burned 19 years ago according to local farmers. We assumed that the burned land was the most severely disturbed area because fire could eliminate most seed and seedling banks (Kennard et al. 2002). The Acahual represents a less severely disturbed community, since the seed bank was not totally eliminated and this plot was the smallest disturbed area; thereby, there was a possibility of the vegetation recovering from the seeds dispersed from nearby forest and the seed bank.

2.2 Vegetation sampling and data analysis

The vegetation was sampled using a point-centered quarter method (Mueller-Dombois and Ellenberg 1974). In each plot, we set four 50-m-long parallel lines toward the center of the patch, at a distance greater than 50 m from the edge. Each line was separated from the next by at least 50 m. Along each line, at 10-m intervals, we set up a cross which delimited four

quadrants and recorded the two trees nearest to the central point in each quadrant, from the upper and lower strata. For the upper stratum, we included individuals with a diameter at breast height (dbh) > 10 cm in montane cloud forest and Alder forest, while trees larger than 5 cm dbh were included for the Acahual. For the lower stratum we recorded individuals with a dbh of 5–10 cm in montane cloud forest and Alder forest, and of 3–5 cm for Acahual trees. We recorded species identity, distance to the central point (in meter), height (in meter), dbh (in centimeter), and crown radius (in meter). Two 50-m × 1-m transects were used to record saplings (i.e. individuals less than 0.5 m in height) in each plot.

Species richness was analyzed by graphing the species accumulation curve for each plot and using four non-parametric estimators (Chao 2, Jackknife 1, Jackknife 2, and Bootstrap) run in the Vegan package 2.0–5 for R (Oksanen et al. 2013). The sampling effort for the species accumulation curves was the number of points on each line (20 in each plot).

From the field vegetation data, we calculated basal area, as well as the density and average height for the upper and lower strata of each plot. Also, for each species we calculated the relative basal area in 100 m², this parameter is an estimator of species abundance (*A*) in each plot. From these values, we

defined an ordinal scale with four levels in order to get ordinal and categorical variables to use in SEM. The levels were: species with $A > 10\%$; species with A between 1 and 10 %; species with $A > 0$ and \leq than 1 %; and absent species (Table 1).

2.3 Evaluation of plant regeneration indicators

Regeneration indicators were evaluated based on the attributes shown in Table 1, each measured on a binary or ordinal scale. We obtained information from several sources including floras, biological, ecological, and vegetation reports and species descriptions. With such information, along with field observations and expert advice, we determined the category for each regeneration indicator and transformed those data into an ordinal or binary scale for statistical analysis.

Dispersal mode was associated with fruit type, thus fleshy fruits were considered to be animal dispersed; wind dispersal

was assumed from the presence of aerial dispersal structures. The capacity of a species to form a sapling bank was determined based on the literature, direct observations and seed size: species with larger seeds germinate faster and tend to form sapling banks (Martínez-Ramos and García-Orth 2007). The ecological, biological, and vegetation literature was used to classify species as shade tolerant or intolerant.

2.4 Model fit

The model fit was implemented using a student version of LISREL 8.8 for Windows (Jöreskog and Sörbom 2008). Since the model was based on ordinal and categorical variables, we used weighted least squares as the fitting method, which takes into account the non-normal nature of such variables (Vile et al. 2006). Similarly, correlation among observed variables was calculated using a polychoric technique.

Table 1 Scales used for indicators of latent variables, traits, or observed variables associated with indicator and information source

Indicator	Scale	Trait or observed variable	Information source
Species abundance in Montane cloud forest	Absent=0; $0 < A \leq 1\%$ =1; $1\% < A \leq 10\%$ =2; $A > 10\%$ =3	Abundance	Field records
Species abundance in Acahual	Absent=0; $0 < A \leq 1\%$ =1; $1\% < A \leq 10\%$ =2; $A > 10\%$ =3	Abundance	Field records
Species abundance in Alder forest	Absent=0; $0 < A \leq 1\%$ =1; $1\% < A \leq 10\%$ =2; $A > 10\%$ =3	Abundance	Field records
Resprouting capacity	Present=1; absent=0	Phenomenological	Literature; field observation; expert consultation
Dispersal mode	Baro-synzoocorous=0 Animal dispersed=1 Wind dispersed=2	Fruit consistency; presence of appendix	Literature, field observations
Capacity to form a seed bank	Present=1; absent=0	Seed size, shape seed	Literature
Capacity to form a sapling bank	Present=1; absent=0	Phenomenological	Literature, field observations
Shade tolerance	Intolerant=1; tolerant=0	Seed size	Literature
Composite indicators			
Dispersal mode—shade tolerance	Baro-synzoocorous – Shade tolerant=0; Animal dispersed – Shade tolerant=1; Animal dispersed – Shade intolerant=2; Wind dispersed – Shade intolerant=3		
Capacity to form a seed bank— capacity to form a sapling bank	Seed bank=0; Sapling bank=1; Seed and Sapling bank=2		

A relative abundance of species

We used four indexes to evaluate data-model fit: the chi-square statistic and relative chi-square, root mean square error of approximation (RMSEA), and the expected cross-validation index (ECVI).

Chi-square is an overall measure of data-model fit. It evaluates the match between the theoretical model and the empirical data. The null hypothesis states there is no difference between them; we regarded a significant goodness-of-fit chi-square with $P < 0.05$ as indicative of a lack of fit between the model and the data. The relative chi-square (chi-square value divided by degrees of freedom) is an unbiased index: a value of two or less represents good fit (Mueller 1996). RMSEA assesses closeness of fit; good models have a $RMSEA < 0.05$. The ECVI is an index for validating the model, and reflects the discrepancy between model-implied and observed covariance matrices; thus, a lower value of ECVI suggests a better fit.

The Latent Variable Scores and Observational Residuals module (LISREL) was used to obtain the scores of latent variables. Finally, we identified regeneration types; these are groups of species defined by the combination of regeneration traits and represent functional types (sensu Rusch et al. 2003), each with a specific regeneration trait syndrome. We ordered the regeneration types based on the scores of the latent variable regeneration type.

3 Results

3.1 General vegetation description

In total, 28 tree species were recorded: 21 in montane cloud forest, 19 in the Acahual, and 11 in the Alder forest. The number of rare species (those that occurred only once or twice) was higher in Acahual (11 species), than in the Alder forest (seven) or in montane cloud forest (six). We recorded seven unique species in montane cloud forest, two in the Acahual, and only one in the Alder forest. The species accumulation curves did not reach a defined asymptote for any of the plots. From the estimators used, the range of species richness obtained was 13–14 species for Alder forest; 23–26 for the Acahual, and 23–24 for montane cloud forest. According to these estimates, we recorded more than 75 % of the species present in each vegetation type.

In montane cloud forest, *Quercus ocoteifolia* was the dominant species followed by *Quercus corrugata* and *Turpinia occidentalis* (Table 2). In the Acahual, dominance was shared by *Clethra macrophylla* and *Alchornea latifolia*. As expected, *Alnus jorullensis* was dominant in the Alder forest; followed by *Miconia glaberrima* and *Solanum nigricans* (Table 2).

Tree height was similar for the montane cloud forest and Alder forest in both the upper and lower strata; and was more than twice as high as the upper stratum of the Acahual (Table 3). Basal area was much greater in montane cloud

Table 2 Relative abundance of montane cloud forest (MCF) species, Acahual and Alder forest. For each species, A was calculated by multiplying the average basal area by its relative density in an area of 100 m²

Species	MCF	Acahual	Alder forest
<i>Alchornea latifolia</i> Sw.	4.24	20.14	1.46
<i>Alnus jorullensis</i> Kunth	0.00	5.06	86.49
<i>Buddleja cordata</i> Kunth	0.00	2.66	0.19
<i>Calyptanthus schlechtendalia</i> (O. Berg) Kuntze	1.26	0.00	0.00
<i>Cinnamomum effusum</i> (Meisn.) Kosterm	0.54	0.00	0.00
<i>Clethra macrophylla</i> M. Martens & Galeotti	2.94	34.57	0.94
<i>Dicksonia sellowiana</i> Hook.	0.9	2.61	0.00
<i>Hedyosmum mexicanum</i> C. Cordem.	0.66	5.22	0.00
<i>Icacorea compressa</i> (Kunth) Standl.	5.16	5.9	0.00
<i>Ilex tolucana</i> Hemsl.	3.96	0.00	0.00
<i>Lippia myriocephala</i> Schltdl. & Cham.	0.00	5.15	0.22
<i>Magnolia schiedeana</i> Schltdl.	0.57	0.00	0.00
<i>Miconia chrysoneura</i> Triana	0.00	0.09	0.00
<i>Miconia glaberrima</i> (Schltdl.) Naudin	0.68	5.46	5.45
<i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch.	0.64	0.00	0.00
<i>Parathesis melanosticta</i> (Schltdl.) Hemsl.	0.03	0.73	0.21
<i>Phyllonoma laticuspis</i> (Turcz) Engl.	0.16	0.27	0.00
<i>Prunus tetradenia</i> Koehne	1.85	0.00	0.00
<i>Psychotria</i> spp.	0.00	0.19	0.00
<i>Quercus corrugata</i> Hook.	6.28	0.71	2.28
<i>Quercus ocoteifolia</i> A. Camus	58.81	1.82	0.00
<i>Sambucus canadensis</i> L.	0.00	0.00	0.15
<i>Solanum nigricans</i> M. Martens & Galeotti	0.43	5.42	2.7
<i>Ternstroemia sylvatica</i> Schltdl. & Cham.	2.97	0.00	0.00
<i>Turpinia occidentalis</i> (Sw.) G. Don	6.03	0.26	0.00
<i>Viburnum tiliifolium</i> (Oerst) Hemsl.	0.66	3.31	0.00
<i>Zanthoxylum melanostictum</i> Schltdl. & Cham.	1.21	0.45	0.00
Rubiaceae	0.00	0.00	0.13

forest than in the other two vegetation types, but tree density was highest in the Acahual.

3.2 Plant regeneration indicators

We searched for information on regeneration indicators for all species recorded, but found complete information for only 20 of them (Table 4 and Appendix).

Animal, baro-synzocorous, and wind-dispersed species were present in our sample. Most species had baro-synzocorous or animal-dispersed fruits (70 %), many of them were distributed in montane cloud forest. Wind-dispersed propagules were common for dominant species in the disturbed plots (Acahual and Alder forest).

Regarding propagule persistence, most of the montane cloud forest species formed sapling banks, while a seed bank

Table 3 Structural parameters of vegetation types in La Cortadura, Veracruz, Mexico

Structural parameter	Vegetation types		
	MCF ^a	Acahual	Alder forest
Average density (trees/100 m ²)			
Upper stratum	3.0 (2.5–3.9)	18.2 (15.2–22.1)	5.5 (4.4–7.2)
Lower stratum	7.2 (5.4–10.2)	18.6 (15.1–23.5)	9.6 (7.5–12.6)
Average height (m)			
Upper stratum	19.2±1.5	8.2±0.7	19.4±1.2
Lower stratum	5.7±0.5	4.1±0.3	5.4±0.5
Average basal area (cm ²)	38.4±4.5	10.9±1.5	15.7±3.4

^a Montane cloud forest (MCF); $\alpha=0.05$

was common for species from the disturbed plots. No information was found regarding whether the seed banks were persistent, but in most species the seeds did not have the characteristics associated with a persistent seed bank (i.e., spherical shape and small size; *A. jorullensis* has small seeds but does not form seed bank according to literature, see Appendix). Based on the absence of these traits and considering the study in cloud forest tree species of Manatlán (Saldaña-Acosta et al. 2008), we assumed that smaller seeds (for example those of *M. glaberrima*) form a transitory seed bank.

Montane cloud forest species were generally shade tolerant, while species in disturbed areas were shade intolerant.

3.3 Model evaluation

There was a high correlation between most indicators related to the two latent variables regeneration type and vulnerability to disturbance (Table 5). The pairs of indicators with the highest correlation values were: capacity to form a seed bank—capacity to form a sapling bank and dispersal

Table 4 Indicator values for each species. Capacity to form a seed bank: present (1), absent (0); Capacity to form a sapling bank: present (1), absent (0); Dispersal mode: baro-synzoocorous (0), animal (1), wind (2); Shade tolerance: intolerant (1), tolerant (0); Resprouting capacity: present (1), absent (0)

Species	Vegetation type	Capacity to form a seed bank	Capacity to form a sapling bank	Dispersal mode	Shade tolerance	Resprouting capacity
<i>Alchornea latifolia</i> Sw.	MCF, A, Af	1	1	1	1	1
<i>Alnus jorullensis</i> Kunth	A, Af	0	1	2	1	1
<i>Buddleja cordata</i> Kunth	A, Af	1	0	2	1	1
<i>Calyptanthes schlechtendaliana</i> (O. Berg) Kuntze	MCF	1	1	2	1	1
<i>Cinnamomum effusum</i> (Meisn.) Kosterm	MCF	1	1	0	0	0
<i>Clethra macrophylla</i> M. Martens & Galeotti	MCF, A, Af	1	0	2	1	0
<i>Hedyosmum mexicanum</i> C. Cordem.	MCF, A	1	0	1	0	0
<i>Ilex toluhana</i> Hemsl.	MCF	1	1	1	0	0
<i>Lippia myriocephala</i> Schltdl. & Cham.	A, Af	1	0	2	1	0
<i>Magnolia schiedeana</i> Schltdl.	MCF	0	1	0	0	0
<i>Micomia glaberrima</i> (Schltdl.) Naudin	MCF, A, Af	1	1	1	1	1
<i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch.	MCF	0	1	1	0	0
<i>Prunus tetradenia</i> Koehne	MCF	0	1	1	0	0
<i>Quercus corrugata</i> Hook.	MCF, A, Af	0	1	0	0	1
<i>Quercus ocoteifolia</i> A. Camus	MCF, A	0	1	0	0	1
<i>Sambucus canadensis</i> L.	Af	1	0	1	1	1
<i>Solanum nigricans</i> M. Martens & Galeotti	MCF, A, Af	1	0	2	1	0
<i>Ternstroemia sylvatica</i> Schltdl. & Cham.	MCF	0	1	1	0	0
<i>Turpinia occidentalis</i> (Sw.) G. Don	MCF, A	0	1	1	0	1
<i>Zanthoxylum melanostictum</i> Schltdl. & Cham.	MCF, A	1	0	1	0	0

MCF montane cloud forest; A Acahual; Af Alder forest

Table 5 Correlation among indicators calculated with polychoric correlation

	Resprouting capacity	Capacity to form a seed bank	Capacity to form a sapling bank	Dispersal mode	Shade tolerance	Species abundance in MCF	Species abundance in Acahual	Species abundance in Alder forest
Resprouting capacity	1							
Capacity to form a seed bank	−0.130	1						
Capacity to form a sapling bank	0.388	−0.991	1					
Dispersal mode	0.021	0.558	−0.708	1				
Shade tolerance	0.581	0.771	−0.587	0.996	1			
Species abundance in MCF	−0.014	−0.381	0.577	−0.484	−0.654	1		
Species abundance in Acahual	0.331	0.443	−0.507	0.444	0.706	0.004	1	
Species abundance in Alder forest	0.624	0.193	−0.205	0.463	0.853	−0.506	0.666	1

MCF Montane cloud forest

mode—shade tolerance. In turn, re-sprouting capacity had the lowest correlation values. The high correlations between most indicators suggest that there were common underlying factors, as assumed when conceiving the latent variables in our theoretical model.

There was no match between the base model and the empirical data; re-sprouting capacity did not fit, although a large proportion of species had this trait (45 %). Thus we structured and evaluated some alternative models; we removed or combined some indicator variables of regeneration type based on the high correlation between the indicators. We applied a backward stepwise approach trying to preserve as many of the indicator variables as possible. Re-sprouting capacity was later analyzed relating it to regeneration types identified with the fit model.

In model A, we only removed re-sprouting capacity. In model B, we removed re-sprouting capacity and combined: capacity to form a seed bank—capacity to form a sapling bank and dispersal mode—shade tolerance. In model C, re-sprouting capacity was removed, shade tolerance and dispersal mode were not modified and we combined the capacity to form a seed bank—capacity to form a sapling bank. In model D, re-sprouting capacity was removed, capacity to form a seed bank and capacity to form a sapling bank were not modified and shade tolerance and dispersal mode were combined. In model E, re-sprouting capacity and the capacity to form a sapling bank were removed, capacity to form a seed bank was not modified and shade tolerance and dispersal mode were combined.

We accepted model E which had a satisfactory fit. In model A, there was not match between it and empirical data; meanwhile in models B, C, D, the *t* values for some path coefficients were not significant.

In model E, the indicators for regeneration type were capacity to form a seed bank and an indicator combining shade tolerance during establishment and seed dispersal mode

(Fig. 2). Capacity to form a sapling bank was not included; however, most of the information provided by this variable was indirectly considered because it is negatively correlated with the capacity to form a seed bank. The chi-squared value of 2.81 ($P=0.42$), with 3 *df*, the relative chi-square of 0.94 and the *RMSEA* value <0.001 , were indicative of the good fit of the empirical data in the proposed model. Also, this model had the lowest *ECVI* (1.42) and thus had a higher predictive validity than the others.

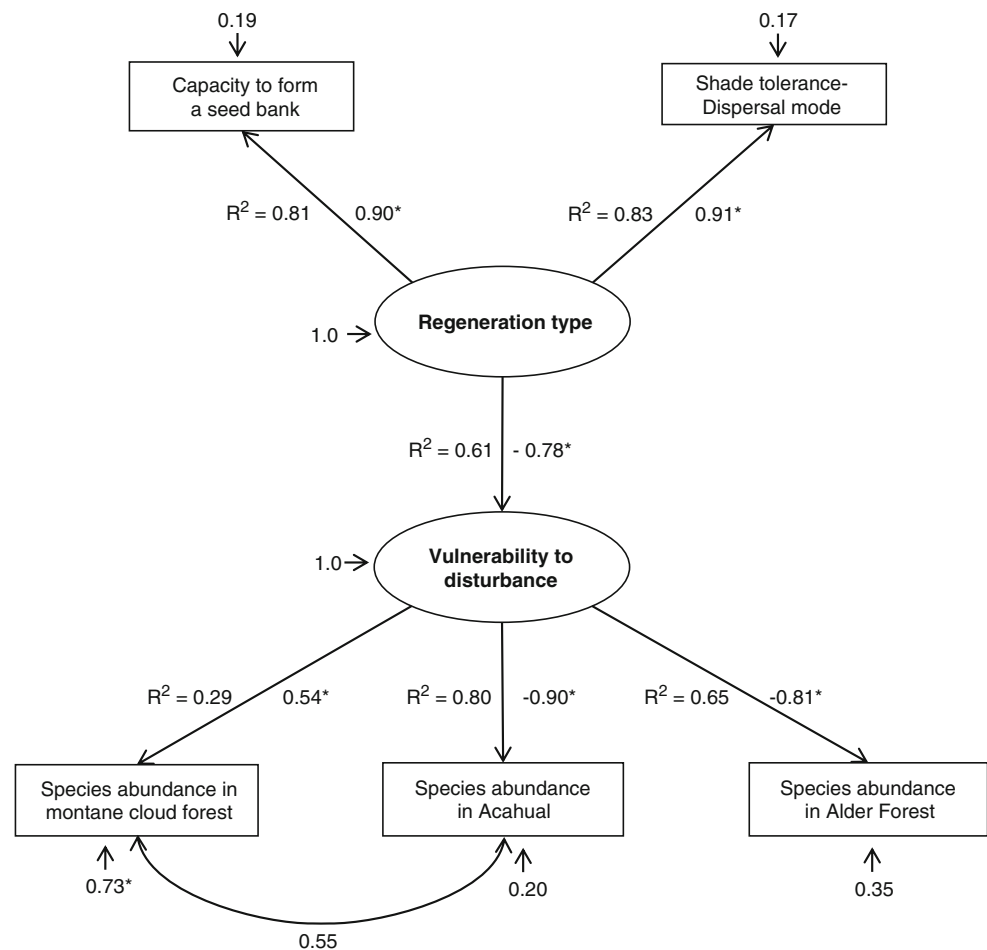
The measurement error of the indicators was non-significant according to the *t* values, except for montane cloud forest. Also, covariation between the measurement error of montane cloud forest species abundance and Acahual species abundance was evident; this relationship was not meaningful because most of the measurement errors of the indicators were not significant.

All of the path coefficients that relate indicators to regeneration type and vulnerability to disturbance had a significant *t* value ($P<0.01$), suggesting that these variables are appropriate indicators of the latent variables proposed (Fig. 2).

According to the R^2 values, regeneration type explained a high proportion of the indicators' variability (81 % for capacity to form a seed bank and 83 % for shade tolerance—dispersal mode). Vulnerability to disturbance explained between 29 and 80 % of species abundance variability of the plots studied. On the other hand, 61 % of the vulnerability to disturbance variability was explained by regeneration type (see R^2 values in Fig. 2).

We identified seven regeneration types based on trait combinations (Table 6). Only four regeneration types were represented in the Alder forest, while six regeneration types were represented in the Acahual and montane cloud forest. Based on regeneration type scores, the arrangement of trait syndromes was as follows: at one extreme there were three regeneration types (I, II, and III) which share shade intolerance as their common attribute; in particular, types I and II

Fig. 2 Standardized solution of the model accepted. Goodness-of-fit statistics are: chi-square: 2.81; $df=3$; $P=0.42$; root mean square error of approximation (RMSEA) <0.0001 . Path coefficients between indicators and latent variables are standardized; all were statistically significant ($P<0.01$). *Short arrows* represent the measurement error, which was only significant for montane cloud forest. The *double-headed arrow* represents the covariance between measurement errors



have wind-dispersed seeds and types I and III form a seed bank. Most of the species falling into these types had high abundance values in disturbed areas (*A. jorullensis*, *C. macrophylla*, *S. nigricans*, see Table 2); but *Calyptanthus schlechtendaliana*, one of the species in this group, occurred in disturbed areas in montane cloud forest (for example gaps caused by tree falls). Regeneration types IV, VI and VII are interspersed at the opposite location on the regeneration type axis: they are shade tolerant, may have baro-synzoocorous or animal-dispersed seeds and types VI and VII do not form a seed bank. These types included species found only in mature forest or that have high abundance values on this land cover type, such as *Magnolia schiedeana*, *Prunus tetradenia*, *Q. ocoteifolia*, and *T. occidentalis* (Table 2).

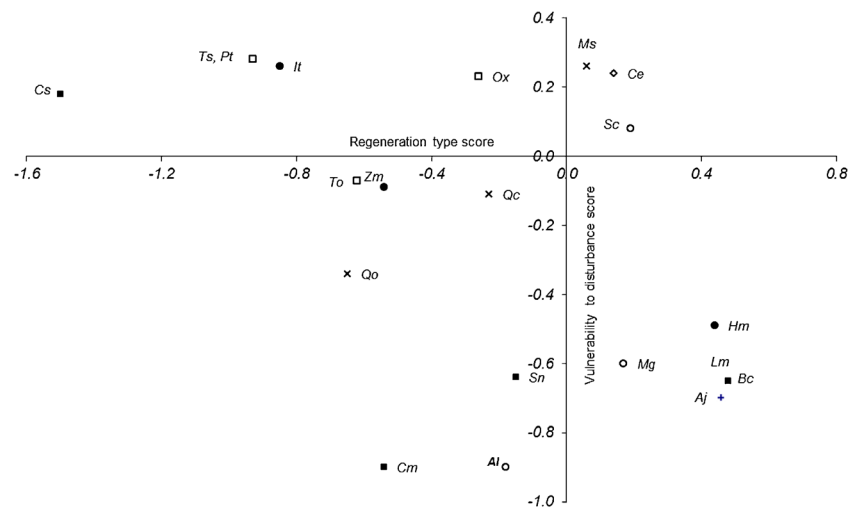
Regeneration type had a significant structural effect on vulnerability to disturbance (path coefficient -0.78). This correlation is evidence that vulnerability to disturbance depends on regeneration type and ultimately on regeneration traits, specifically: capacity to form a seed bank, dispersal mode and shade tolerance. The distribution of species (labeled

with the regeneration type to which they belong) in the space defined by these latent variables revealed that types IV to VII had the highest values of vulnerability to disturbance while types I to III had lower values (Fig. 3).

The regeneration types were distributed differentially among vegetation types. In the Alder forest, the most severely disturbed area, 95 % of the trees belonged to types I to III, which had the lowest values of vulnerability to disturbance. In the Acahual, the less severely disturbed area, dominance of types I to III was lower (60 % of the trees belonged to these types); in this plot there was an important representation of types IV, VI, and VII (10 % of trees are of these types). In montane cloud forest, the mature forest, types IV to VII—which had highest values of vulnerability to disturbance—were dominant (57 % of trees belonged to these types); in this community, the proportion of types I to III was low (23 % of trees are of these types). These patterns of regeneration type distribution are consistent with our hypothesis that disturbance intensity acts as a filter during the early phase of secondary succession, selecting for specific regeneration types that can colonize the disturbed plot.

Table 6 Scores for the latent variables vulnerability to disturbance and regeneration type, species groups of regeneration types and a description of the trait syndrome

Regeneration type	Species	Vulnerability to disturbance score	Regeneration type score	Trait syndrome
I	<i>Clethra macrophylla</i> M.Martens & Galeotti	-0.9	-0.54	Shade intolerant; wind dispersed; form a seed bank; some species form a sapling bank
	<i>Calyptanthes schlehtendalana</i> (O. Berg) Kuntze	0.18	-1.5	
	<i>Solanum nigricans</i> M. Martens & Galeotti	-0.64	-0.15	
	<i>Buddleja cordata</i> Kunth	-0.65	0.48	
	<i>Lippia myriocephala</i> Schltdl. & Cham.	-0.65	0.48	
II	<i>Alnus jorullensis</i> Kunth	-0.7	0.46	Shade intolerant; wind dispersed; do not form a seed bank but do form a sapling bank
III	<i>Alchornea latifolia</i> Sw.	-0.9	-0.18	Shade intolerant; animal dispersed; form a seed bank; some species form a sapling bank
	<i>Miconia glaberrima</i> (Schltdl.) Naudin	-0.6	0.17	
	<i>Sambucus canadensis</i> L.	0.08	0.19	
IV	<i>Zanthoxylum melanostictum</i> Schltdl. & Cham.	-0.09	-0.54	Shade tolerant; animal dispersed; form a seed bank; some species form a sapling bank
	<i>Ilex tolucana</i> Hemsl.	0.26	-0.85	
	<i>Hedyosmum mexicanum</i> C. Cordem.	-0.49	0.44	
V	<i>Cinnamomum effusum</i> (Meisn.) Kosterm	0.24	0.14	Shade tolerant; baro-synzoocorous dispersal; form a seed and a sapling bank
VI	<i>Turpinia occidentalis</i> (Sw.) G.Don	-0.07	-0.62	Shade tolerant; animal dispersed; form a sapling bank, but not a seed bank
	<i>Ternstroemia sylvatica</i> Schltdl. & Cham.	0.28	-0.93	
	<i>Prunus tetradenia</i> Koehne	0.28	-0.93	
	<i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch.	0.23	-0.26	
VII	<i>Quercus ocoteifolia</i> A. Camus	-0.34	-0.65	Shade tolerant; baro-synzoocorous dispersal; form a sapling bank. but not a seed bank
	<i>Quercus corrugata</i> Hook.	-0.11	-0.23	
	<i>Magnolia schiedeana</i> Schltdl.	0.26	0.06	

**Fig. 3** Distribution of species labeled with the regeneration type they belong to in the space formed by the regeneration type (independent variable) and vulnerability to disturbance (dependent variable) scores. Regeneration types dominant on disturbed plots are in the lower and right quadrant of the graph (i.e., they have a low vulnerability to disturbance value and a high regeneration type value); the opposite occurs for regeneration types dominant in montane cloud forest. Black square, regeneration type I; plus sign, regeneration type II; white circle, regeneration type III; black circle, regeneration type IV; white diamond, regeneration type

V: white square, regeneration type VI; multiplication sign, regeneration type VII. *Alnus jorullensis* (Aj), *Clethra macrophylla* (Cm), *Calyptanthes schlehtendalana* (Cs), *Solanum nigricans* (Sn), *Buddleja cordata* (Bc), *Lippia myriocephala* (Lm), *Alchornea latifolia* (Al), *Miconia glaberrima* (Mg), *Sambucus canadensis* (Sc), *Zanthoxylum melanostictum* (Zm), *Ilex tolucana* (It), *Hedyosmum mexicanum* (Hm), *Turpinia occidentalis* (To), *Ternstroemia sylvatica* (Ts), *Prunus tetradenia* (Pt), *Oreopanax xalapensis* (Ox), *Cinnamomum effusum* (Ce), *Quercus ocoteifolia* (Qo), *Quercus corrugata* (Qc), *Magnolia schiedeana* (Ms)

Finally, re-sprouting capacity was mostly linked to regeneration types I to III (66 % of species in these types had this trait); while this trait was present in only 27 % of the species which belonged to regeneration types IV to VII. To test the significance of these differences, we applied a nonparametric ANOVA by calculating the Fisher and Yates exact probability. Although the difference was not significant at the level we specified in advance (the value found was 0.08), there was a trend for this trait to be associated with the regeneration types dominant in disturbed plots.

4 Discussion

The evaluation of the theoretical models revealed that three variables, namely shade tolerance, dispersal mode, and the capacity to form a seed bank, are indicators of the latent variable regeneration type (path coefficients greater than 0.9, see Fig. 2); this variable represents the regeneration strategies of montane cloud forest trees. The order of species along the regeneration type axes (see Fig. 3) had an arrangement similar to that observed in other studies where it has been suggested that there is a dominant axis of niche differentiation identified by a trade-off between survival under shade stress and maximum growth rate in full sun (Hubbell and Foster 1992). The ends of this axis are occupied by different trait syndromes: at one end the colonizer (pioneer) functional group and at the other the competitive (stress tolerant) functional group (Fernandez-Palacios and Arévalo 1998, Kitajima and Poorter 2008). In our study, the combination of the traits shade tolerance, dispersal mode, and the capacity to form a seed bank define the regeneration trait syndromes of montane cloud forest trees. Types I to III have the profile of colonizer and the trait syndrome for these types is shade-intolerant species, generally with wind-dispersed seeds and that form a seed bank. Types IV to VII have the profile of a competitive functional group, with a trait syndrome that includes shade tolerance, either baro-synzocorous or animal-dispersed seeds and some with no seed bank. The expression of regeneration traits as a syndrome can be understood by remembering that traits are not filtered out by environmental forces independently of each other since selective pressures act on whole organisms; thus, plant traits tend to be linked in recurrent patterns (Díaz et al. 1999).

The syndromes of regeneration traits identified in this study could be partially explained by seed size. This trait is correlated with the capacity to form a seed bank and with shade tolerance (see Table 1). Seed size has received a great deal of attention in the literature since the negative relationship between seed number and seed size represents a trade-off for individual plants (Harper et al. 1970). Seeds are usually abundant and small in species colonizing disturbed sites (Bazzaz et al. 2000). In contrast, large seeds may represent advantages

for saplings growing under shady conditions; their greater initial reserves provide the opportunity to survive longer (Leishman and Westoby 1994). This could be related to the ability to form a sapling bank in some of these species. Divergence in seed size is also correlated with differences in propagule persistence: seed banks are dominated by small seeds in many ecosystems, while large seeds are rare (Leishman et al. 2000).

The strong correlation between the latent variables regeneration type and vulnerability to disturbance indicates that species vulnerability to disturbance depends on specific combinations of regeneration traits (here conceptualized as regeneration type). This relationship showed that the colonizer group (regeneration types I to II) was not very vulnerable to disturbance, whereas the competitive group (regeneration types IV to VII) was highly vulnerable to disturbance (see Fig. 3).

The contrast in the composition of regeneration types in disturbed areas compared to the conserved site (montane cloud forest) indicated that regeneration types were not randomly distributed among the sites. These results are consistent with the hypothesis that disturbance intensity has a filtering effect on the colonization of disturbed plots, it acts on regeneration syndromes and would explain the differences in the abundance of regeneration types among sites. These results are also in line with the idea that disturbance history is a key element in the interpretation of vegetation responses to land use (Lavorel et al. 2005; Suding et al. 2008).

In general, these results are concurrent with the reports from regeneration in other montane cloud forests. Saldaña-Acosta et al. (2008) suggested that cloud forest tree species of Manantlán possess a set of traits that are linked to key aspects of the establishment phase of their life cycles: most species from advanced regeneration phases have persistent sapling bank as regeneration strategy, in contrast, other species are large-canopy trees, with their saplings being scarce or absent in the understory. Similar results have been reported for regeneration of laurel-forest of the Canary Islands; in this place, it was suggested the existence of three ecological groups derived from different regeneration pattern (Fernández-Palacios and Arévalo 1998): pioneer (these species produce easily dispersed seed that are viable in a seed bank); climax (these species have sapling bank growing under closed canopies), and remnant species (these species form sapling bank too but vegetative reproduction was very important).

In these studies, the regeneration patterns reported are basically supported in a single regeneration mechanism. We proposed an integral approach based on the different combinations of regeneration mechanisms for temporal and spatial species persistence in disturbed ecosystems.

We propose that montane cloud forest includes several regeneration types that provide potential responses to disturbances of varying intensity (types with different vulnerability

to disturbance) or to changing environmental conditions. Also, some types include several species with the same combination of regeneration traits (for example, *Q. ocoteifolia* and the other two species in type VII, see Table 6) that can respond in similar ways to specific environmental conditions, which represent functional equivalents. The results suggest that regeneration types and functional equivalents provide the montane cloud forest with a buffering capacity against perturbations and environmental variability.

When a disturbance occurs, the time needed for vegetation recovery depends on the severity of the disturbance and the regeneration types available in the surroundings (Fernández-Palacios and Arévalo 1998). In severely disturbed sites where a large area is affected and all of the adults and seed/sapling banks are eliminated, we hypothesize that shade intolerant (i.e., those species able to establish in open sites) and wind-dispersed regeneration types are sources for secondary succession (Martínez-Ramos and García-Orth 2007). Under this scenario, vegetation recovery is possible via wind-dispersed propagules of types I and II from the surrounding areas. Type III could participate in vegetation recovery at open sites because it is shade intolerant; however, it is unlikely to colonize severely disturbed sites because the seeds are dispersed by animals. We would expect this regeneration type to be involved in forest recovery in sites where the seed/sapling banks are not completely destroyed or where some trees remain. Types IV to VII are shade tolerant, baro-synzoocorous or animal dispersed and most of them have the capacity to form sapling banks. We would expect these types to colonize slightly disturbed sites which occur over a small area, where only a few trees were eliminated and with seed/sapling banks affected only to a small degree. This agrees with studies which report that montane cloud forest recovery on slightly disturbed sites occurs from the sapling bank (e.g., Sosa and Puig 1987).

Re-sprouting capacity (individual tolerance to disturbance) and the capacity to form a sapling bank were not good indicators of regeneration type. The lack of fit of re-sprouting capacity to our base model was striking because re-sprouting is an efficient means by which many plants can persist and plays a crucial role in plant regeneration after disturbance in many ecosystems (Klimešová and Klimeš 2007). The lack of fit can be attributed to the low correlation between most traits related to processes associated with sexual reproduction and re-sprouting capacity, which is linked to adult plants (Table 5). This result does not mean that re-sprouting capacity is unimportant to vegetation recovery; it only means that this trait is not a good indicator of the latent variable regeneration type. The trend detected for re-sprouting capacity to be associated with regeneration types that thrive in disturbed areas is therefore interesting (regeneration types I to III). In this regard, it has been suggested that re-sprouting is a common response to the

least severe disturbance regimes and disturbance regimes of high severity (Bellingham and Sparrow 2000); however, re-sprouting patterns are poorly documented.

To deal with disturbance, plants face the trade-off of investing to recover the same individuals through re-sprouting or investing in the production of new individuals that colonize the same or another site (Bond and Midgley 2001). In matched species comparisons resprouters have been reported to generally produce fewer seeds, have smaller seed banks, slower growth and maturation rates (from seeds), and almost always have fewer seedlings and poorer seedling survival than nonsprouters (Bond and Midgley 2001).

Based on our findings, we support the view that re-sprouting represents a mechanism for plant regeneration which increases the persistence probability of the regeneration types that can deal with critical environmental conditions, such as those that occur in severely disturbed sites.

5 Conclusions

This study shows that the use of latent variables to develop and evaluate a complex model based on functional classifications is useful for exploring the vulnerability of trees to disturbance using a small set of parameters linked to plant persistence. The use of functional classifications is a feasible and useful approach for dealing with the complexity associated with high diversity ecosystems, such as montane cloud forest. We find evidence that (1) disturbance intensity has a filtering effect on the tree colonization of disturbed plots; also (2) species vulnerability to disturbance depends on specific combinations of regeneration traits. The approach used in this study can help predict changes in the composition of plant regeneration types resulting from the impact of human activities and to generate an understanding of the main patterns of response to disturbance of plant communities; knowledge that could be used for devising forest management and restoration programs.

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Appendix

Table 7 Tree regeneration traits of montane cloud forest, Coatepec, Veracruz, México

Species	Vegetative Spreading	Resprouting capacity	Capacity to form a seed bank	Capacity to form a sapling bank	Dispersal mode	Shade tolerance/Habitat	Seed and/or fruit features
<i>Alchornea latifolia</i> Sw (Francis 1993)	a	a	a	fr ^a	A	Saplings need light to grow; secondary and primary vegetation/fast growth/ respond to big disturbances	Bilocular capsule with two seeds. Seed 6 mm diameter, slightly compressed laterally covered with a fleshy aril. Dry seed weight: 0.042 g
<i>Alnus jorullensis</i> Kunth (Benítez et al. 2004; Ludlow-Wiechers 1978; Nee 1981; Nieto and Rodríguez s/f)	a,b	a	a	a	W	Secondary vegetation pioneer	Seeds winged. Cone-shaped fruit 1.5 cm diameter. Each fruit has 80–100 seeds. Seed weight: 0.002 g
<i>Buddleja cordata</i> H.B.K. subsp. <i>Cordata</i> (Alvarez-Aquino et al. 2005 and Rzedowski and Rzedowski 1985)	a	fr ^a	a	a	W	Pioneer	Ovoid-ellipsoid fruit. 2.5 to 6 mm in length, 1.5 to 4 mm diameter. Septicidal dehiscence.
<i>Calypttranthes Schlechtendalliana</i> O. Berg (Sánchez-Vindas 1990)		fr ^a		fr ^a	w	Shade intolerant; secondary	Globose fruit, black-purple when mature. 5–9 mm long, 1.5 mm diameter, only one seed per fruit
<i>Cinnamomum effusum</i> (Meisn.) Kosterm (Muñiz-Castro 2008; Van der Werff H and Lorea 1997)			a	a	Bs	Shade tolerant	Drupe bluish black, nearly ellipsoidal. 9–13 mm long
<i>Clethra macrophylla</i> M. Martens & Galeotti (Benítez et al. 2004; Ramírez 1998; Rzedowski and Rzedowski 1985)	a,b		a	a	W	Secondary vegetation, late succession	Fruit capsule, reddish-brown in color, 3–4 mm diameter,
<i>Hedyosmum mexicanum</i> C. Corderm. (Ludlow-Wiechers 1978; Nash 1976; Quintana 1993; Williams-Linera 1993)			a	a	A	Shade tolerant	2.5–3 mm long, with long adpressed
<i>Ilex tolucana</i> Hensl. (Alvarez-Aquino et al. 2005); Gentry and Standley (1974); Santiago et al. 2002; Williams-Linera (1993)			a	a	A	Shade tolerant	Fruit a fleshy drupe, small and elliptic
<i>Lippia myriocephala</i> Schltdl. & Cham. (Muñiz-Castro et al. 2006)		a			W	Secondary vegetation	Subglobose fruit, red or orange, 4–6 mm long, seeds have a bony cover, four seeds per fruit
<i>Magnolia schiedeana</i> Schltdl. (Muñiz-Castro 2006; Sosa and Puig 1987)	a			a	Bs	Shade tolerant	Fruit dry <10 mm
<i>Miconia glaberrima</i> (Schltdl.) Naudin (Almeda 1993; Ramírez et al. 1998; Santiago et al. 2002)	a	fr ^a	a	a	A	Intermediate succession	Fruit multi-follicle, green when immature and grayish-brown when mature. 4–8 cm long, each follicle with dorsal dehiscence. Seed 5–7 mm long abundant endosperm
<i>Oreopanax xalapensis</i> (Kunth) Decne. & Planch (Pennington and Sarukhán 2005; Quintana and González 1993; Ramírez et al. 1998; Santiago et al. 2002; Sosa 1979; Williams-Linera 1993)			a	a	A	Shade tolerant Intermediate succession	Blue berry, 4–5 mm diameter, ovoid seeds 0.75–1 mm
<i>Prunus tetradenia</i> Koelne (Santiago et al. 2002)			fr ⁺	fr ⁺	A	Shade tolerant	Fruit a fleshy berry, up to 6 mm diameter, four or five seeds per fruit. Ovoid seed, side Compressed 5 mm long
<i>Quercus corrugata</i> Hook. (Francis 1993; Muñiz-Castro et al. 2006; Nash 1976)	+		fr ⁺	fr ⁺	Bs	Mature forest	Acorn, 30–50 mm long
<i>Quercus ocoteifolia</i> A. Camus (Muñiz-Castro 2008; Standley 1922)	fr ^a		fr ^a	fr ^a	Bs	Shade tolerant	Ovoid acorn, 8 mm diameter, 10 mm long
<i>Sambucus canadensis</i> L. (Nash 1976)	a	a	a	a	A	Open sites	Fruit a berry, purple-black in color, 5–8 mm diameter. Fruit are eaten by birds

Table 7 (continued)

Species	Vegetative Spreading	Resprouting capacity	Capacity to form a seed bank	Capacity to form a sapling bank	Dispersal mode	Shade tolerance/Habitat	Seed and/or fruit features
<i>Solanum nigricans</i> M. Martens & Galeotti (Gentry and Standley 1974; Ramirez et al. 1998; Rzedowski and Rzedowski 1985)			^a		W	Early secondary vegetation	Globose fruit, color black 1 to 1.5 mm diameter. Compressed seeds (2 to 3 per fruit) 3.5–5 mm long
<i>Ternstroemia syhvatiza</i> Schltdl. & Cham. (Muñiz-Castro 2008 and Rzedowski and Rzedowski 1985)				^a	A	Shade tolerant	Conical fruit, not-dehiscent, 1.5 mm long and 8–10 mm wide. Seeds 10 mm long and 6 mm wide surrounded by an aril with fleshy hairs
<i>Turpinia occidentalis</i> (Sw.) G. Don (Carranza 2004; Dalling et al. 1998; Santiago et al. 2002)		^{fr} ^a		^{fr} ^a	A	Shade tolerant	Fruit a berry subglobose to obovate with three loculi. Several seeds per loculus. Seeds irregular, ovate, 4–5 mm long
<i>Zanthoxylum melanostictum</i> Schltdl. & Cham. (Dalling et al. 1998 and Quintana and González 1993)			^{fr} ^a		A	Shade tolerant mature forest	

fr confirmed in the field, *W* wind, *A* animal, *Bs* baro-synzoochorous

^a Present

^b By root cutting

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