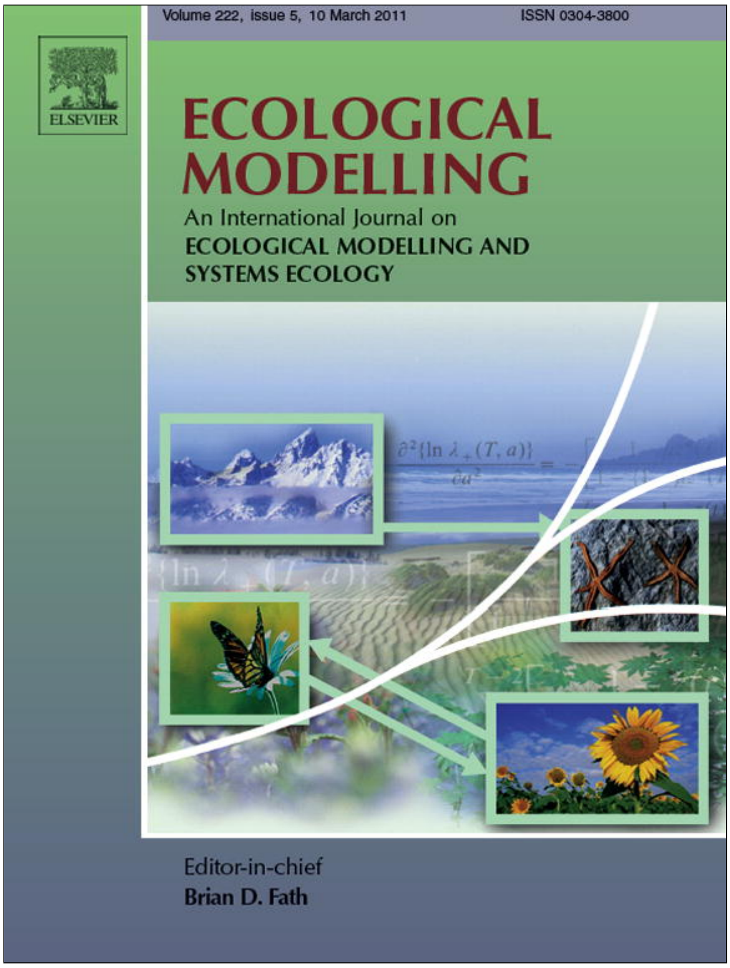
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Simulating the potential for ecological restoration of dryland forests in Mexico under different disturbance regimes

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ABSTRACT

Examining the potential for ecological restoration is important in areas where anthropogenic disturbance has degraded forest landscapes. However, the conditions under which restoration of degraded tropical dry forests (TDF) might be achieved in practice have not been determined in detail. In this study, we used LANDIS-II, a spatially explicit model of forest dynamics, to assess the potential for passive restoration of TDF through natural regeneration. The model was applied to two Mexican landscapes under six different disturbance regimes, focusing on the impact of fire and cattle grazing on forest cover, structure and composition. Model results identified two main findings. First, tropical dry forests are more resilient to anthropogenic disturbance than expected. Results suggested that under both a scenario of small, infrequent fires and a scenario of large, frequent fires, forest area can increase relatively rapidly. However, forest structure and composition differed markedly between these scenarios. After 400 years, the landscape becomes increasingly occupied by relatively shade-tolerant species under small, infrequent fires, but only species with both relatively high shade tolerance and high fire tolerance can thrive under conditions with large, frequent fires. Second, we demonstrated that different forms of disturbance can interact in unexpected ways. Our projections revealed that when grazing acts in combination with fire, forest cover, structure and composition vary dramatically depending on the frequency and extent of the fires. Results indicated that grazing and fire have a synergistic effect causing a reduction in forest cover greater than the sum of their individual effects. This suggests that passive landscape-scale restoration of TDF is achievable in both Mexican study areas only if grazing is reduced, and fires are carefully managed to reduce their frequency and intensity.

1. Introduction

The tropical dryland forests (TDF) of Mexico are recognised as a global conservation priority, being centres of species richness and endemism, as well as providing a range of benefits to local communities (Gordon and Newton, 2006a,b; Miles et al., 2006). However, in recent decades these forests have been degraded and fragmented at an alarming rate. At the national scale, a recent study reported an annual TDF deforestation rate of 1.6% (177,000 ha) during 1976–1993, and 0.5% (44,416 ha) during the following decade (Challenger and Dirzo, 2009). This study also indicated that only 26% of the original TDF cover remained as intact forest by 2002 and that the remaining areas were characterised by different degrees of human disturbance. The development of effective restoration programs of TDF is therefore an urgent priority (Trejo and Dirzo, 2000; Quesada et al., 2009). Ecological restoration of TDF can potentially occur naturally through the processes of dispersal, migration, colonization and succession if the causes of ecological degradation can be removed or controlled (Kennard, 2002; Lamb et al., 2005). Such 'passive' restoration is probably the most common forest restoration approach implemented in tropical regions (Lamb et al., 2005). However, if disturbances have severely altered the composition, structure and dynamics of TDF, the capacity for natural recovery may be dramatically reduced or eliminated altogether (Lamb and Gilmour, 2003).

Among anthropogenic disturbances, fire and grazing by livestock have caused the most serious degradation of TDF in Mexico. For example, Maass (1995) reported that cattle ranching has expanded rapidly during the past 50 years, and is now considered to be the main cause of TDF degradation. Roman-Cuesta et al. (2007) reported that in recent decades fire has become one of the most important threats to the conservation of TDF. In 1998, Mexico experienced fires which burned the largest area of forest ever affected in a single season (Cedeño, 2001). In addition, during the period

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2003–2007, ecoregions in Mexico with TDF had an intermediate to high density of detected fires compared with other ecoregions in the country (Manson et al., 2009).

Information on the rate of ecological recovery under different disturbance scenarios is required to evaluate the feasibility of passive restoration efforts (Vieira and Scariot, 2006). Ideally such information should be spatially explicit, given that forest restoration should be undertaken at the landscape scale in order to address the problem of forest fragmentation and to restore connectivity (Mansourian et al., 2005). Although a number of studies have analysed TDF recovery after disturbance (Guariguata and Ostertag, 2001; Vieira and Scariot, 2006; Griscom et al., 2009), very little information is available regarding the processes of recovery of TDF at the landscape scale.

This study addresses the information needs for ecological restoration of TDF by applying a spatially explicit model (LANDIS-II), which was designed to simulate the dynamics of forested landscapes through the incorporation of ecological processes, including succession, disturbances and seed dispersal over long time domains (Scheller et al., 2007). The LANDIS-II model is an elaboration of the LANDIS family of landscape disturbance and forest succession models. Although the architecture has changed since the initial version and new features have been added, LANDIS-II retains many principles from earlier versions that have been widely tested and applied in different parts of the world (He and Mladenoff, 1999; Wang et al., 2006; Swanson, 2009). However, we are not aware of any previous attempt to apply LANDIS-II, or any other spatially explicit model of forest dynamics, to tropical dry forest landscapes.

The aim of this investigation was to test the following hypotheses; (1) ecological disturbances (grazing and fire) at landscape level can have synergistic effects in altering the cover, structure and composition of TDF; (2) expansion of TDF cover in degraded landscapes could be achieved without complete prevention of anthropogenic disturbance. In particular, we explored the application of LANDIS-II for modelling TDF dynamics in two Mexican case studies, to examine the individual and combined impacts of fire and grazing on forest cover, structure and composition at the landscape scale. The overall objective was to use this modelling approach to identify restoration approaches with broad applicability and to examine the conditions under which passive restoration of degraded TDF might be optimized in practice.

2. Methods

Research was undertaken in two study areas dominated by TDF, namely the Tablon, Chiapas, and the Central Veracruz, Mexico (Fig. 1). Both study areas are global conservation priorities, being identified as global biodiversity hotspots (Myers et al., 2000), and in recent decades both have been degraded at a high rate owing to the effects of human disturbances (Challenger and Dirzo, 2009). Both study areas cover similar areas, but they differ in the percentage of forest cover. According to CONABIO (2006) both areas have a high degree of marginalisation, and an average of 23 inhabitants km^{-2} and 14 inhabitants km^{-2} respectively were recorded in 2000 in Central Veracruz and Tablon.

2.1. Study areas

2.1.1. Tablon, Chiapas

The Tablon study area covers 24,735 ha and is situated between 675 and 1537 m altitude in the municipalities of Villaflores and Jiquipilas, state of Chiapas (16°11′38″ and 16°22′29″N, and 93°31′57″ and 93°44′31″W). The climate is defined as warm sub-humid, with an average annual rainfall between 1200 and 2800 mm concentrated from late May to early November (Aguilar-Jiménez, 2008). According to the land cover map produced for this study (see Section 2.2 for a description), 88.6% of the entire Tablon area is covered by forests and 9.9% by pasture; 0.9% is represented by arable land and 0.6% by urban areas. The natural vegetation of Tablon forms a gradient of forest types ranging from low-stature deciduous tropical forest in the lower elevations of the study area, through dry oak and pine-oak with increasing elevation, and with pine forests on the highest ridges. Owing to its steep topography and sandy soils, Tablon is susceptible to severe soil erosion if the natural vegetation is removed by subsistence agriculture and extensive cattle ranching.

Tablon falls within the La Sepultura Biosphere Reserve, which was designated in 1995 for its high number of endemic species, high biodiversity value and species richness. It is also an important water catchment for the region. Government bodies and NGOs are actively promoting more sustainable forms of land use in the region (Lillo et al., 1999).

2.1.2. Central Veracruz

The Central Veracruz study area, with an area of 29,468 ha, is situated between 10 and 507 m altitude in the state of Veracruz, Mexico (19°07′45″ and 19°21′18″N, and 96°21′33″ and 96°41′12″W). The climate is defined as warm sub-humid (minimum and maximum average temperatures are 20 °C and 31 °C, respectively) with rainfall of 800–1500 mm, occurring primarily from June to September followed by an extended dry season. Areas on the eastern side of Central Veracruz have a warm-humid climate, whereas those on the western side are characterized by a warm-dry climate. Soil types are predominantly Feozems, Litosols and Vertisols (INIFAP and CONABIO, 1995; CONABIO, 1999). According to the land cover map produced for this study area (see Section 2.2 for a description), 43% of the entire Central Veracruz area is represented by pasture, 23% by shrubland (locally know as acahual), 21% by arable land, 5.5% by tree plantation, and 3% by urban areas and only 4.4% covered by undisturbed forest. The original vegetation was predominantly tropical dry forest (Rzedowski, 1990). None of the remaining forest fragments are under protection. The primary land use is cattle ranching, which is generally undertaken on a relatively small scale by private landowners. For common land tenants (know as ejidatarios), the main activities are cultivation of maize and sugar cane.

2.2. Input data

2.2.1. Spatial layers

The LANDIS-II model is designed to accept raster imagery as a spatially explicit input to simulate landscape dynamics, as described below.

In Tablon, input raster data included a Digital Elevation Model (DEM) and QuickBird satellite imagery, from which a series of secondary maps were derived. The DEM (50 m cell-size) was derived from the 30 m resolution national DEM (INEGI, 2003), resampled to a 50 m grid using regularized spline with tension (Mitasova and Mitas, 1993). A direct beam solar radiation map (50 m cell-size) was calculated using the formulae proposed by Rigollier et al. (2000) and implemented in the GRASS module r.sun (Neteler and Mitasova, 2008). An ecoregion map was produced from the combination of the DEM with the beam solar radiation map (Table 1).

Three QuickBird scenes acquired in November–December 2004 were obtained as a mosaic to cover the study area. These data consisted of a panchromatic band (0.61 m spatial resolution) and four multispectral bands (2.44 m resolution) covering the visible blue to near infrared wavelengths (450–900 nm). A basic land cover map (50 m cell-size) (Fig. 2), which identified forest, pasture, roads, urban areas and permanent agricultural areas was derived from the QuickBird imagery. The production of the basic land cover map

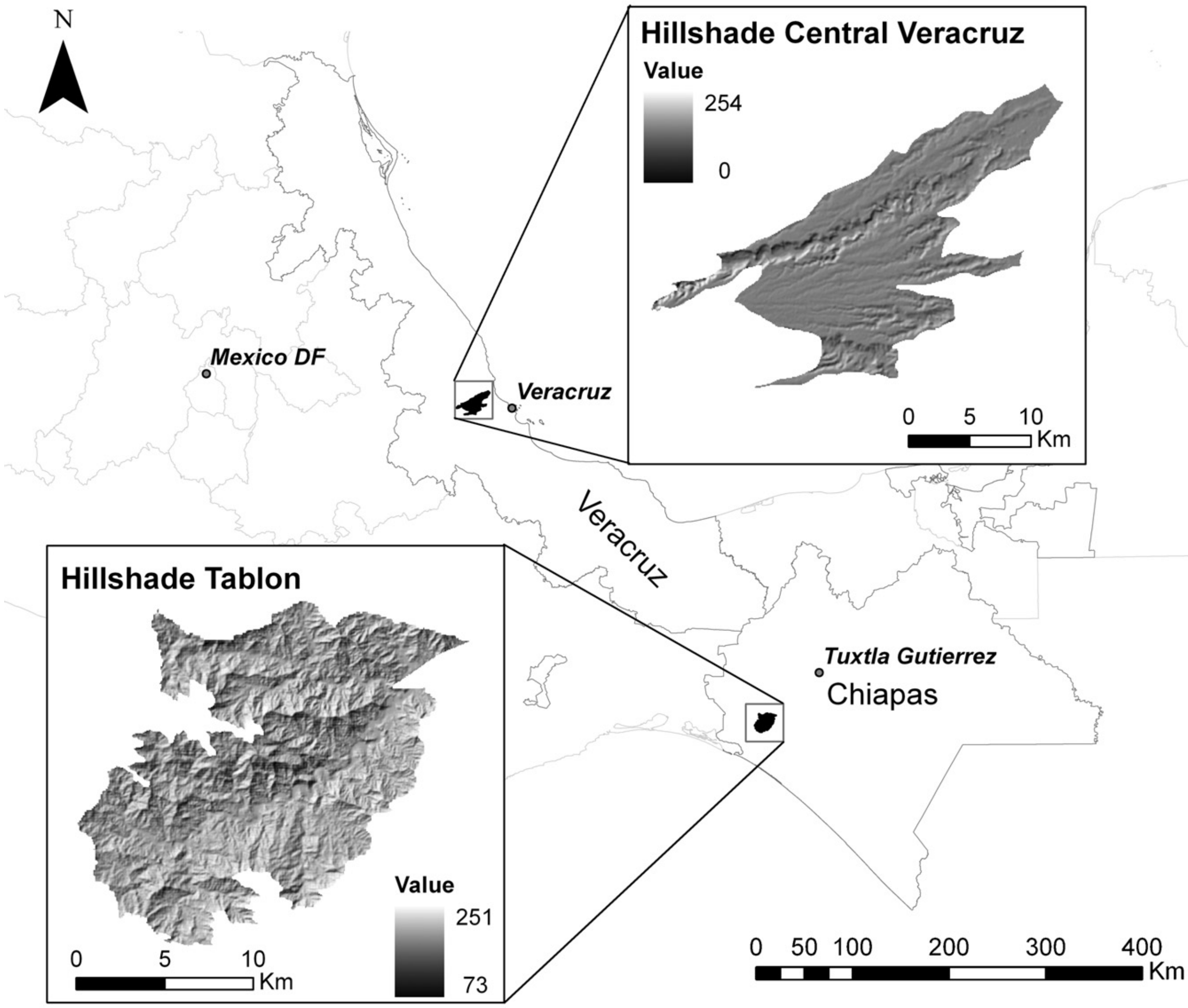

Fig. 1. Overview map showing the locations of the study areas within Mexico and close-up maps of the study areas (Central Veracruz and Tablon), with overlaid shading of topography.

Table 1
Details of the *ecoregions* map in Tablon and Central Veracruz.

Active	Code	TAB DEM; beam solar radiation	VER DEM; soil type
Yes	1	675–900 m, 139–4149.5 W m^{-2}	10–109.4 m, Vertisol
Yes	2	900–1100 m, 139–4149.5 W m^{-2}	109.5–208.8 m, Vertisol
Yes	3	1100–1300 m, 139–4149.5 W m^{-2}	10–109.4 m, Feozem
Yes	4	1300–1537 m, 139–4149.5 W m^{-2}	109.5–208.8 m, Feozem
Yes	5	675–900 m, 4149.5–5319 W m^{-2}	208.9–308.2 m, Vertisol
Yes	6	900–1100 m, 4149.5–5319 W m^{-2}	208.9–308.2 m, Feozem
Yes	7	1100–1300 m, 4149.5–5319 W m^{-2}	308.3–407.6 m, Vertisol
Yes	8	1300–1537 m, 4149.5–5319 W m^{-2}	308.3–407.6 m, Feozem
Yes	9	675–900 m, 5319–7241 W m^{-2}	208.9–308.2 m, Litosol
Yes	10	900–1100 m, 5319–7241 W m^{-2}	308.3–407.6 m, Litosol
Yes	11	1100–1300 m, 5319–7241 W m^{-2}	407.7–507 m, Litosol
Yes	12	1300–1537 m, 5319–7241 W m^{-2}	407.7–507 m, Vertisol
Yes	13	cattle pasture, 139–4149.5 W m^{-2}	109.5–208.8 m, Litosol
Yes	14	Cattle pasture, 4149.5–5319 W m^{-2}	
Yes	15	Cattle pasture, 5319–7241 W m^{-2}	
No	100	Roads, urban, agricultural areas	Roads, urban, agricultural areas, plantations

See Section 2.2 for details.

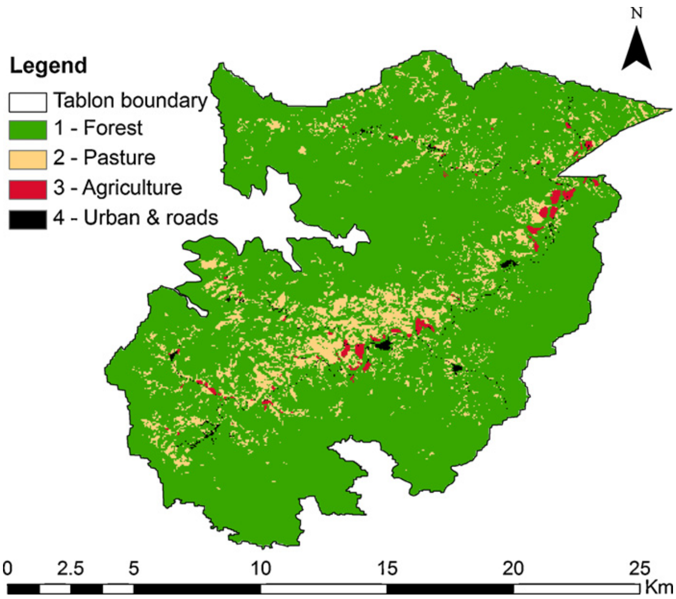

Fig. 2. Land cover map for the Tablon study area produced from QuickBird imagery classification (see Section 2.2 for details). The forest cover type includes 28 forest types, not displayed here.

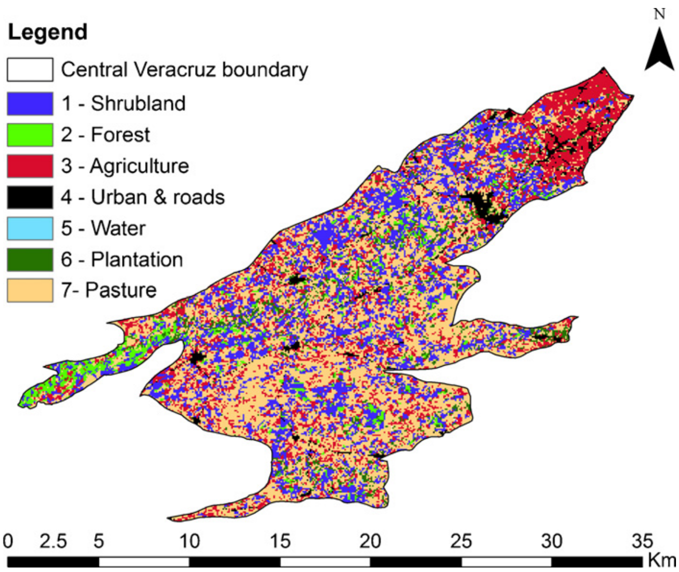

Fig. 3. Land cover map for the Central Veracruz study area produced from SPOT 4 imagery classification (see Section 2.2 for details). The forest cover type includes 15 forest types, not displayed here.

involved a combination of supervised classification of the multispectral mosaic to separate forest from pasture with the manual digitizing of roads, urban areas and permanent agricultural areas on the panchromatic mosaic. A forest stand type map (50 m cell-size) was derived from the QuickBird imagery and ecoregion map. The production of the forest stand type map involved performing an unsupervised classification of the forest component of the QuickBird imagery into twenty forest classes which were split by ecoregions into a 28 forest stand type layer. This layer was validated by manual comparison against the panchromatic mosaic and the field survey data describing species and stem diameter distributions.

In Central Veracruz, input raster data included a DEM and SPOT satellite imagery which were used to obtain a series of secondary maps. The DEM (cell-size 80 m) was derived from Shuttle Radar Topography Mission (SRTM) data with a resolution of three arc seconds per pixel (Farr et al., 2007). A soil type map (cell-size 80 m) was extracted from the national edaphology map (INIFAP and CONABIO, 1995). An ecoregion map was produced from the combination of the DEM with soil type map (Table 1).

Three SPOT high-resolution visible and infrared (HRVIR) multispectral images (20 m resolution) from December 2007 and January 2008 were utilized to cover the study area. A land cover map (80 m cell-size) (Fig. 3), which identified shrubland, forest, agriculture, urban and roads, water, plantation and pasture was derived from the SPOT imagery. The production of the land cover map involved a segmentation of the SPOT imagery using the software eCognition Professional 5.0 (©2009 Definiens Inc., USA), followed by a supervised classification of the generated polygons with an average of 1 training area per 150 ha. Validation was conducted by using field visits and visual inspection of high resolution Google Earth images (©2008 Google Inc., CA, USA). A forest stand type map (80 m cell-size) was derived from the land cover map and the field survey data (see Section 2.2.2). The production of this layer involved the classification of each polygon labelled as forest in the land cover map into 15 forest stand types, based on four types of forest structure (ranging from small to large crown size trees), and four types of composition (with up to 7, 12, 17 and 22 of the most abundant species). Interpretation of Google Earth images in combination with GARP (Genetic Algorithm for Rule-set Production) models (Stockwell and Peters, 1999) was utilized to assign each polygon to a stand type. For the purpose of this study the shrubland cover type was also considered as a forest stand type.

2.2.2. Field survey data

36 circular plots (0.1 ha each) were established along an altitudinal gradient in Tablon, and 100 survey plots (0.1 ha each) were established within ten TDF fragments in Central Veracruz (Williams-Linera and Lorea, 2009). In each plot, tree species were identified and diameter at breast height (dbh) of each tree > 5 cm was measured. Dbh values were converted into ages by consulting a group of local experts, composed of staff of the Instituto de Ecología, A.C. (INECOL), El Colegio de la Frontera Sur (ECOSUR), the Comisión Nacional Forestal (CONAFOR), the Universidad Veracruzana, and the director of La Sepultura Biosphere Reserve. The group of local experts concluded that a linear regression between dbh values and ages could be applied based on their extensive experience of field surveys of the tree species occurring in each of the study areas. Although more complex models were discussed, a simpler approach was preferred owing to the lack of reliable annual tree ring counts, and to the fact that the LANDIS-II model does not depend on age–growth relationships, but proceeds by age cohorts. Therefore any systematic error in ageing of the trees that might have been introduced at this point would have only affected the initial age structure of the forest stands, which would be expected to become less evident with time as new recruits established.

2.3. Model overview

The LANDIS model is described in more detail elsewhere (He and Mladenoff, 1999; Mladenoff, 2004) <http://www.landis-ii.org>. In essence, LANDIS-II uses a cell-based data format; within each cell it tracks the presence/absence of tree species age cohorts at a time step specified by the user. Vegetation patches can aggregate and disaggregate in response to spatial patterns of stochastic rules of disturbance and succession. Tree species succession is a competitive process governed by species life history parameters, and the probability of species establishment on different ecoregions (or landtypes). Tree succession interacts with several spatial processes (i.e. seeding, wind and fire disturbances, and harvesting). As disturbance in LANDIS-II is stochastic, calibration is required to ensure the output is fitted to the ecological characteristics of the simulated area (Franklin et al., 2001).

2.4. Model parameterisation

2.4.1. Ecoregions

In LANDIS-II the landscape is stratified into ecoregions, which are ecologically homogenous sub-areas characterized by the same habitat suitability (establishment probability) for each species to be modelled. Ecoregions can be active or non-active depending on whether they represent areas where forests can grow or not.

In Tablon, one non-active and fifteen active ecoregions were considered; active ecoregions covered 24,354 ha, non-active 381 ha (Table 1). The species establishment probabilities for each ecoregion were derived from the outputs of Generalized Additive Models (GAM) (Guisan et al., 2002; Hastie, 2008) as interpreted by local experts (Appendix A, see online material). Input to the models included species occurrence data, obtained from the MOBOT Tropicos® data base (©2010 Missouri Botanical Garden, USA), and climate data extracted from the Worldclim database (Hijmans et al., 2005).

In Central Veracruz, one non-active and thirteen active ecoregions were considered; active ecoregions covered 20,788 ha, and non-active 8,680 ha (Table 1). The species establishment probabilities for each ecoregion were derived from the outputs of GARP models (Stockwell and Peters, 1999), which were produced by using the software DesktopGarp (©2002 University of Kansas Center for Research, Inc., USA) and interpreted by local experts (Appendix A, see online material).

2.4.2. Initial communities

The inputs required by LANDIS-II include information about the initial distribution, composition and age structure of forest stands. In both study areas, to populate each cell of the landscape with species and age cohort we combined the forest cover map (see Section 2.2.1) with the field survey data describing species and age distributions (see Section 2.2.2).

2.4.3. Species attributes

For each species, LANDIS-II requires information about longevity, age of sexual maturity, shade and fire tolerance class, effective and maximum seed dispersal distance, vegetative reproduction probability, minimum and maximum age of vegetative reproduction, and post-fire regeneration. The field surveys conducted in both study areas revealed high tree species richness; 97 trees species were recorded in Central Veracruz, and 53 in Tablon. However, because of computer resource limitations, only a subset composed of the most abundant species recorded was modelled. In Central Veracruz, species attributes were extracted for the 22 most abundant species (i.e. species with >14 sampled individuals in the field survey). The subset was characterized by a range of shade and fire tolerances (Table 2). In Tablon, none of the 23 most abundant species (i.e. species with >5 sampled individuals in the field survey) had high shade tolerance. Two relatively infrequent species (*Sapindus saponaria* and *Gyrocarpus mocinnoi*) were therefore included in the model, to ensure that the full range of shade tolerance was included, giving a total of 25 species included in the model (Table 3).

In both study areas species attributes were extracted from the literature (Bullock, 1995; Gentry, 1995; Lillo et al., 1999; Medina Ortega, 2000; Castillo-Campos and Medina-Abreo, 2002; Rodriguez-Trejo and Fule, 2003; Kalacska et al., 2004; CABI, 2005; Pennington and Sarukhán, 2005; Vieira and Scariot, 2006; Tejedor-Garavito, 2007; Corlett, 2009; Griscom et al., 2009; Powers et al., 2009) and by consulting the local experts.

2.4.4. Disturbance regimes

To parameterize the fire module of LANDIS-II, fire characteristics (event sizes, ignition probability, expected fire rotation period, expected average burned area, fuel accumulation, fire damage

Table 2
Details of the *species characteristics* in Central Veracruz.

Species	Species abbr.	Long	Mat	ShT	FiT	EffD	MaxD	VP	MinVP	MaxVP	P-FR
Acacia cochliacantha	Acaccoch	50	2	1	5	5	100	1	2	50	Resprout
Brosimum alicastrum (GT)[a]	Brosalic	150	20	5	1	5	10,000	1	3	60	Resprout
Bursera cinerea	Burscine	80	5	4	1	5	10,000	0	0	0	None
Bursera fagaroides (GT)[a]	Bursfaga	80	5	4	3	5	10,000	0	0	0	None
Bursera graveolens	Bursgrav	80	5	4	2	5	10,000	0	0	0	None
Bursera simaruba	Burssima	80	5	3	3	5	10,000	1	2	50	Resprout
Calyptranthes schiedeana	Calyschi	60	15	5	2	5	10,000	0	0	0	None
Cochlospermum vitifolium	Ceibaesc	60	15	3	5	3	100	1	1	30	Resprout
Ceiba aesculifolia (VI)[a]	Cochviti	40	10	3	2	5	100	1	2	30	Resprout
Comocladia engleriana	Comoengl	70	25	3	2	200	1000	1	7	60	Resprout
Eugenia hypargyrea	Eugehypa	40	5	5	1	5	100	0	0	0	None
Guazuma ulmifolia	Guazulmi	40	3	1	5	5	100	1	2	40	Resprout
Heliocarpus donnell-smithii	Helidonn	50	10	1	3	100	100	1	3	25	Resprout
Ipomoea wolkottiana	Ipomwolc	60	10	1	3	11	100	1	2	20	Resprout
Leucaena lanceolata (CI)[a]	Leuclanc	20	2	1	2	5	100	0	0	0	Serotiny
Luehea candida	Luehcand	70	20	3	2	20	100	1	3	60	Resprout
Lysiloma microphyllum (CI)[a]	Lysimicr	70	15	1	2	5	100	1	3	60	Resprout
Savia sessiliflora	Savisess	30	5	5	1	5	100	0	0	0	None
Senna atomaria (SI)[a]	Sennatom	30	5	1	4	5	100	1	2	10	Resprout
Stemmadenia pubescens	Stempube	30	5	3	1	5	1000	0	0	0	None
Tabebuia chrysantha	Tabechry	120	15	3	3	20	100	1	2	50	Resprout
Thouinidium decandrum	Thoudeca	70	10	1	4	20	100	1	3	60	Resprout

Long, longevity (years); Mat, age of maturity (years); ShT, shade tolerance class (1–5, with 1 for the most shade intolerant and 5 for the most shade tolerant); FiT, fire tolerance class (1–5, with 1 for the least tolerant and 5 for the most tolerant); EffSD, effective seeding distance (m); MaxSD, maximum seeding distance (m); VRP, vegetative reproduction probability; MinVRP, minimum age of vegetative reproduction (years); MaxVRP, maximum age of vegetative reproduction (years); P-FiR, post-fire regeneration (form of reproduction that the species adopts after fire events). T = shade tolerant species able to establish immediately after disturbance; I = species only able to establish during the short period of reduced competition immediately after the disturbance; C = species in which only mature individuals can produce juveniles after disturbance; D = species with sufficient dispersal; G = individuals vulnerable to closely spaced disturbances; R = shade tolerant species that can establish only some time after a disturbance; S = species with a seed pool that survive the disturbance; V = species in which individuals survive the disturbance but revert to a juvenile state.

[a] Species selected in the data analyses and their functional group (in parentheses) according to Table 1 of Noble and Gitay (1996).

Table 3
Details of the *species characteristics* in Tablon.

Species	Species abbr.	Long	Mat	ShT	FiT	EffD	MaxD	VP	MinVP	MaxVP	P-FiR
Acacia cornigera	Acaccorn	30	3	1	4	50	10,000	1	1	15	Resprout
Acacia pennatula	Acacpenn	40	3	1	4	100	10,000	1	1	20	Resprout
Bursera bipinnata	Bursbipi	50	5	3	3	25	10,000	1	3	25	Resprout
Bursera excelsa	Bursexce	50	5	3	3	20	10,000	1	3	25	Resprout
Bursera simaruba (DT)[a]	Burssima	80	3	3	4	20	10,000	1	3	30	Resprout
Byrsonimia crassifolia	Byrscras	30	5	1	5	10	15,000	1	3	15	Resprout
Diphysa robiniodes	Diphrobi	40	8	2	3	20	100	1	3	40	Resprout
Erythrina chiapasana	Erytchia	40	5	2	3	10	100	1	3	20	Resprout
Erythrina folkersii (GI)[a]	Erytfolk	40	6	1	3	10	100	1	3	25	Resprout
Eysenhardtia adenostylis	Eyseaden	30	4	2	1	20	100	1	1	30	Resprout
Guazuma ulmifolia	Guazulmi	30	3	1	5	100	1000	1	2	25	Resprout
Gyrocarpus mocinnoi (ST)[a]	Gyromoci	30	4	5	4	10	100	0	0	0	None
Heliocarpus reticulatus	Helireti	40	10	1	1	20	100	0	0	0	None
Leucaena diversifolia	Leucdive	25	3	1	2	10	10	1	1	20	Resprout
Lonchocarpus rugosus	Loncrugo	45	10	2	3	20	15,000	1	5	25	Resprout
Pinus maximinoi	Pinumaxi	100	20	1	4	20	100	0	0	0	None
Pinus oocarpa (VI)[a]	Pinuooca	100	7	1	5	20	100	0	0	0	Serotiny
Quercus acutifolia	Queracut	120	20	2	4	20	10,000	1	5	60	Resprout
Quercus castanea (GI)[a]	Quercast	80	15	2	2	10	10,000	1	5	40	Resprout
Quercus conspersa	Quercons	120	20	2	4	20	10,000	1	5	60	Resprout
Quercus elliptica	Querelli	200	20	2	5	100	10,000	1	1	80	Resprout
Quercus penducularis	Querpedu	200	15	2	5	100	10,000	1	1	80	Resprout
Quercus segoviensis	Quersego	200	20	2	4	100	10,000	1	1	80	Resprout
Sapindus saponaria (CT)[a]	Sapisapo	80	15	4	1	10	10	0	0	0	None
Ternstroemia tepesapote	Terntepe	40	5	1	3	100	10,000	1	1	30	Resprout

See caption of Table 2 for abbreviations.
[a] Species selected in the data analyses and their functional group (in parentheses).

classes) (Appendix B, see online material) were derived from the literature (Fule and Covington, 1997; Minnich et al., 2000; Negrete Paz et al., 2004; Roman-Cuesta and Martinez-Vilalta, 2006; Evett et al., 2007; Roman-Cuesta et al., 2007; Drury and Veblen, 2008; Rodriguez Trejo, 2008). In addition, data were extracted from the MODIS-Terra/Aqua database from 2004 to 2008, as described in Ressl et al. (2009), supported by local expert knowledge. The fire module does not automatically generate a desired average annual burned area; rather, the module needs to be calibrated to achieve the desired average annual burned area. Calibration is typically carried out by adjusting the fire ignition probabilities (He and Mladenoff, 1999; Franklin et al., 2001). In this study, fire ignition probabilities were adjusted to achieve an expected average annual burned area close to 4.3% and 4.1% of the total burnable area for Tablon and Central Veracruz respectively, under a scenario of Large, Frequent Fires (LFF), and an expected average annual burned area close to 0.7% of the total burnable area for both study areas, under a scenario of Small, Infrequent Fires (SIF). Ten to fifteen calibration runs (using a fixed random number seed) for each of the two fire scenarios were performed to reach the best-calibrated scenarios. The mean observed return interval (i.e. the average time it takes to burn an area equivalent to the size of the area of analysis) was 22 and 25 years in Tablon and Central Veracruz respectively under LFF, and 141 and 154 years in Tablon and Central Veracruz respectively under SIF.

In the harvest module of LANDIS-II (Gustafson et al., 2000), which was used to simulate grazing disturbances, grazing parameters (management area map, stand map, stand ranking method in each management area, site selection method for grazing, species list for cohort removal, cohort removed, and target percentage of the management unit to be grazed) (Appendix C, see online material) were extracted from available literature (Pinto Ruiz et al., 2001; Stern et al., 2002; Aguilar-Jiménez, 2008) and by consulting the local experts. The mean annual damaged area under a grazing scenario (five replicates) ranged between 1.68% and 1.75% of the total active ecoregions area (24,354 ha) in Tablon; and between 6.23% and 6.26% of the total active ecoregions area (20,788 ha) in Central Veracruz.

2.5. Scenarios

Timmermann et al. (1999) and Conde (2003) suggested that under a realistic future scenario of increasing greenhouse-gas concentrations, more frequent El Niño Southern Oscillation (ENSO) conditions (Magaña, 1999) may occur in Mexico, which may be associated with large, intense, frequent fires. Livestock grazing is projected to increase in developing countries as the demand for meat products rises with the growth of the human population (Goodland and Anhang, 2009; Thornton and Gerber, 2010). Consequently, to explore disturbance regimes that could potentially occur in the future, six different scenarios were simulated: (i) no disturbance (NO-DIST); (ii) grazing without fire (GRAZ), (iii) small, low intensity, infrequent fires without grazing (SIF), (iv) small, low intensity, infrequent fires with grazing (SIF-GRAZ); (iv) large, intense, frequent fires without grazing (LFF) and (vi) large, intense, frequent fires with grazing (LFF-GRAZ). The Base Fire (v2.1) and Base Harvest (v1.2) extensions of LANDIS-II were used to generate the fire and grazing scenarios.

LANDIS-II simulations were conducted over a 400 year timespan that represents twice the longevity of the species with the longest lifespan, and approximately six times the mean longevity of all of the species modelled. 400 years was therefore considered adequate to allow fire and grazing to manifest their principal effects on forest succession. We chose 50 m in Tablon and 80 m in Central Veracruz as the cell-size for simulations based on the resolution of the elevation map available at each study areas. Five replicated simulations (with varying random number seed) were performed for each best-calibrated disturbance scenario to explore the variability of model predictions. The time steps were set at 10 years for tree succession, 5 years for fire disturbance and 1 year for grazing. The list of ages for each species was therefore grouped into age cohorts as follows: aged 1–10 years (10), 21–30 years (20), 31–40 years (30), etc.

2.6. Data analyses

The Age Cohort Statistics v1.0 extension of LANDIS-II was used to produce outputs of (i) maximum age across all species in each cell (50 m in Tablon and 80 m in Central Veracruz, (ii) total number of species in each cell, and (iii) presence of selected species in each cell, under each of the six scenarios that this study considered. A list of species were selected on the basis of their post-fire regeneration, shade and fire tolerance using Noble and Gitay (1996) functional groups (Tables 2 and 3).

The LANDIS-II outputs consist of raster maps, each corresponding to a time step specified by the user (10 years in this study). Given the low stochastic variability in the scenarios design (the five replicates of each disturbance scenario displayed a range of error of ±3% in both study areas; see see Appendix B), only the output maps of the best-calibrated scenarios (with fixed random number seed) were considered to analyse forest structure and composition. To facilitate the interpretation of results for the 400 year simulation, maximum age data were grouped into five classes based on the oldest tree cohort across all species for each pixel: (i) aged 0–10 years, (ii) 11–30 years, (iii) 31–60 years, (iv) 61–100 years and (v) >100 years; whereas species number data were grouped into six classes: (i) 1–2 species, (ii) 3–4 species, (iii) 5–6 species, (iv) 7–8 species, (v) 9–10 species and (vi) >10 species.

Statistical analyses were performed using SPSS 16.0 for Windows (© 1989–2007, SPSS Inc., USA). Descriptive statistics were used to calculate the median, minimum/maximum, standard deviations (S.D.) and standard errors (S.E.) of percent cover of trees and selected species. Mann–Whitney tests were used to compare percentage cover values for the best-calibrated model runs over the 400 year simulations under the six different scenarios.

3. Results

3.1. Forest cover

Forest cover (defined here as percent cover of trees > 10 years) increased quite rapidly under NO-DIST scenario from 89.9% to 97.6% in Tablon and 6.26% to 99.6% in Central Veracruz after only 50 years. Under LFF, SIF, GRAZ and SIF-GRAZ scenarios, forest cover still increased, but values were lower than the NO-DIST scenario after 50 years, with values reaching between 90.1% and 96.2% in Tablon; and 50.8% and 99.5% in Central Veracruz. Under LFF-GRAZ scenario the forest cover decreased after 50 years to 86.3% in Tablon, but slightly increased to 9.62% in Central Veracruz (Figs. 4 and 5). In both study areas, the median forest cover was the lowest under LFF-GRAZ, which statistically differed from the median forest cover value of all of the other scenarios except under SIF-GRAZ in Tablon. When only the fire and grazing disturbance scenarios are considered, the median forest cover was the highest under the SIF scenario in Tablon and under the GRAZ scenario in Veracruz (Table 4).

3.2. Forest structure

Simulation results indicated that tree size class structure differed under the six scenarios in both study areas (Figs. 4 and 5). In Tablon initial landscape, trees between 31 and 60 years occupied the highest percentage cover (53.9%). Over the simulation period different age classes occupied the highest percentage cover at different times. Over 400 years, the highest percentage cover of the landscape was occupied by: (i) trees > 100 years old under NO-DIST, SIF, GRAZ and SIF-GRAZ scenario after 100 years (73.9%, 46.5%, 72.3%, and 41.1%, respectively); and (ii) trees between 31 and 60 years old under LFF and LFF-GRAZ scenarios after 50 years (45.0% and 35.1%, respectively) (Fig. 4). The median percentage cover of trees older than 60 years was the lowest under LFF-GRAZ scenario (31.8%), and statistically differed from the median % cover values under NO-DIST, LFF and SIF scenarios ($P < 0.05$ in each case; Mann–Whitney test). When only the fire and grazing disturbance scenarios are considered, the median percentage cover of trees older than 60 years was the highest under the SIF scenario (53.0%), which differed statistically from the median percentage cover value under the LFF-GRAZ scenario ($P < 0.05$; Mann–Whitney test).

In Central Veracruz initial landscape, trees between 0 and 10 years old occupied the highest percentage cover (33.0%). Over the simulation period, the highest percentage cover of the landscape was occupied by: (i) trees > 100 years under the NO-DIST scenario after 400 years (87%), (ii) trees aged between 0 and 10 years under LFF and LFF-GRAZ scenarios after 50 years (42.1% and 84.4%, respectively), (iii) trees between 31 and 60 years under the SIF scenario after 50 years (47.0%), and under the GRAZ and SIF-GRAZ scenarios after 150 years (64.7% and 55.5%, respectively) (Fig. 5). Similar results to Tablon were obtained when median percentage cover of trees older than 60 years was compared. Values were the lowest under the LFF-GRAZ scenario (0.05%), which differed statistically from the median percentage cover values under all of the fire and grazing scenarios ($P < 0.05$ in each case; Mann–Whitney test). When only the fire and grazing disturbance scenarios are considered, the median percentage cover of trees older than 60 years was the highest under the SIF scenario (64.6%), which differed statistically from the median percentage cover values under the LFF, SIF, LFF-GRAZ and SIF-GRAZ scenarios ($P < 0.05$ in each case; Mann–Whitney test).

3.3. Forest composition

Simulation results show that modelled species richness (25 modelled species out of 53 sampled species in Tablon, and 22 modelled species out of 97 recorded species in Central Veracruz) differed under the six scenarios in both study areas (Figs. 6 and 7). In Tablon, the majority of the initial landscape (44.4%) was occupied by 5–6 species. During the simulation, the highest percentage cover of the landscape was occupied by areas with: (i) 3–4 species under NO-DIST, SIF and SIF-GRAZ scenarios after 100 years (52.0%, 41.9%, and 40.4%, respectively); (ii) 1–2 species under the LFF and GRAZ scenarios after 150 years (37.9% and 51.0%, respectively) and under the LFF-GRAZ scenario after 200 years (34.9%) (Fig. 6). The median percentage area with ≥5 species was the highest under the SIF scenario (47.8%), which differed statistically from the median percentage cover values under the NO-DIST and GRAZ scenarios ($P < 0.05$ in each case; Mann–Whitney test). When only the fire and grazing disturbance scenarios were considered, the median percentage area with ≥5 species was the lowest under the GRAZ scenario (30.4%), which differed statistically from the median percentage cover values under the LFF, SIF and LFF-GRAZ scenarios ($P < 0.05$ in each case; Mann–Whitney test).

In Central Veracruz, the majority of the initial landscape (33.0%) was occupied by 1–2 species. Over the simulation period, the highest percentage cover of the landscape was occupied by areas with: (i) 3–4 species under the NO-DIST, GRAZ and SIF-GRAZ scenarios after 400 years (80.4%, 70.1% and 51.7%, respectively), and SIF after 350 years (54.4%); (ii) 1–2 species under the LFF scenario after 100 years (91.2%) and under the LFF-GRAZ scenario after 150 years (89.7%) (Fig. 7). Similar to Tablon, the median percentage area with ≥5 species was the highest under the SIF scenario (31.5%), which differed statistically from the median percentage cover values under all of the fire and grazing scenarios ($P < 0.05$ in each case; Mann–Whitney test). When only the fire and grazing disturbance scenarios were considered, the median percentage area with ≥5 species was the lowest under the LFF scenario (0.14%), which differed statistically from the median percentage cover values under the SIF, GRAZ and SIF-GRAZ scenarios ($P < 0.05$ in each case; Mann–Whitney test).

Simulation results also indicated that the different disturbance regimes influenced the proportion of the landscape occupied by the selected species (Figs. 8 and 9 and Table 5). For example in

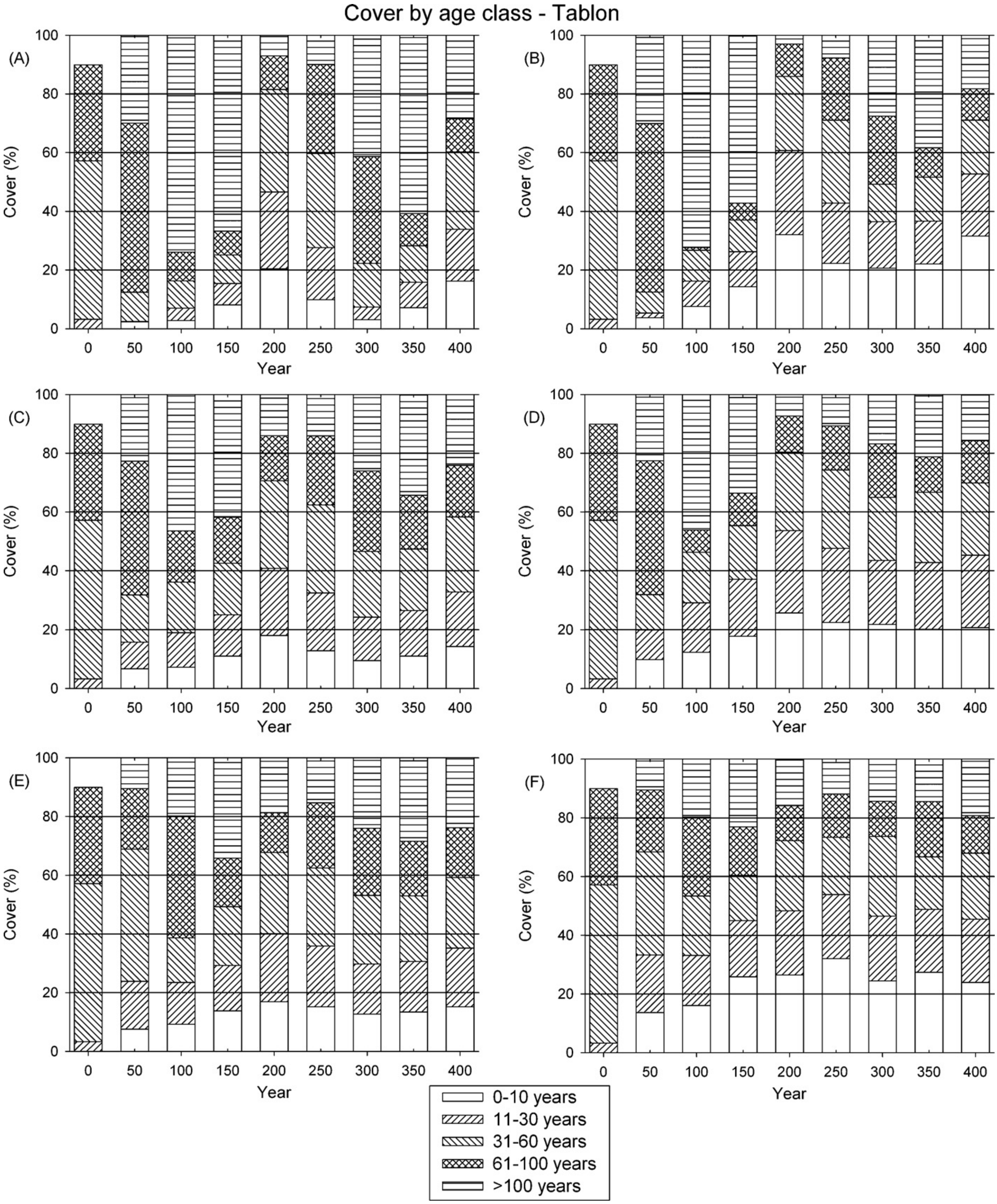

Fig. 4. Relative cover (%) of simulated landscape occupied by each age class under the six scenarios in Tablon. Each 0.25 ha cell could contain up to 25 species. (A) NO-DIST scenario, (B) GRAZ scenario, (C), SIF scenario (D), SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

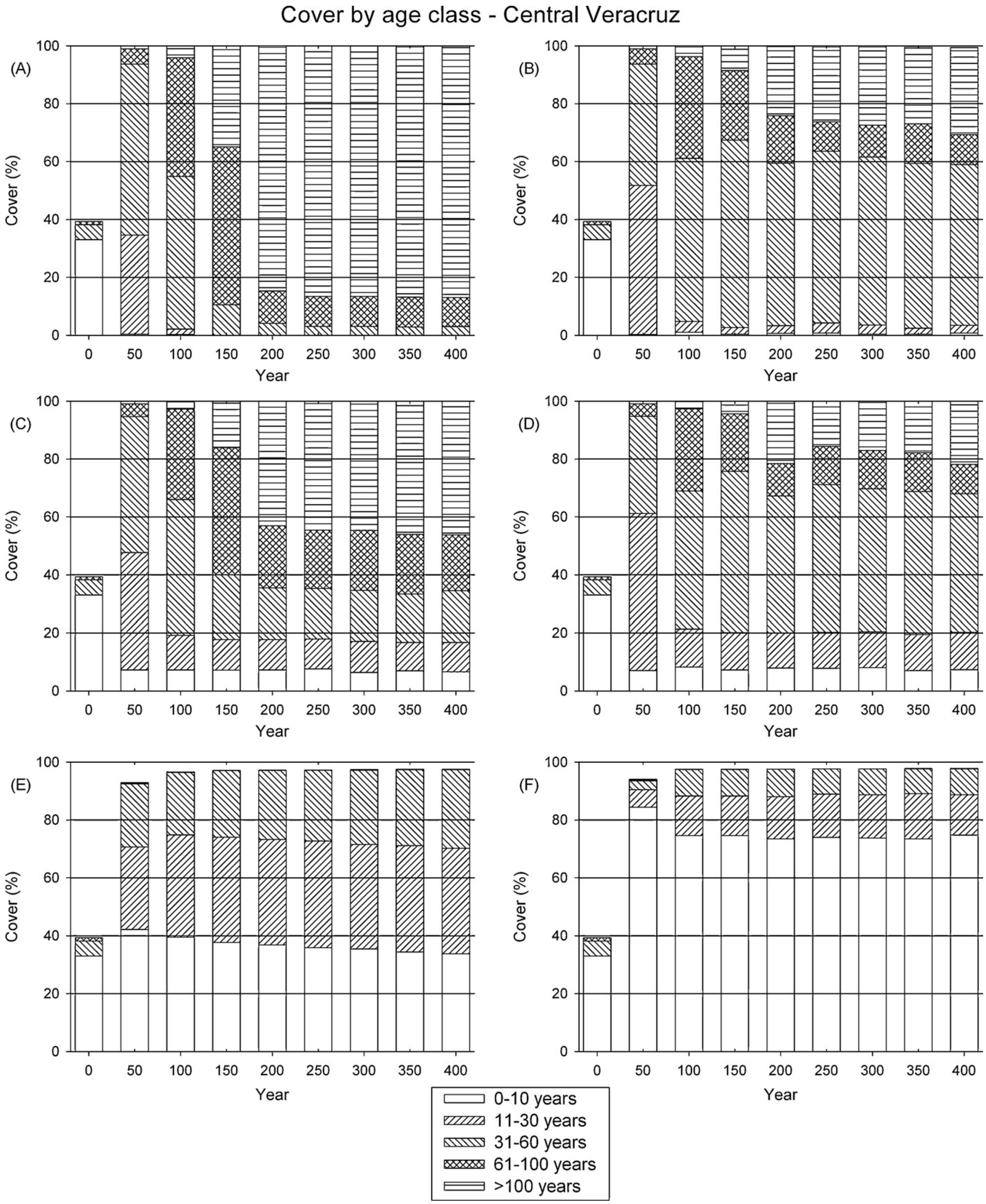

Fig. 5. Relative cover (%) of simulated landscape occupied by each age class under the six scenarios in Central Veracruz. Each 0.64 ha cell could contain up to 22 species. (A) NO-DIST scenario, (B) GRAZ scenario, (C) SIF scenario, (D) SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

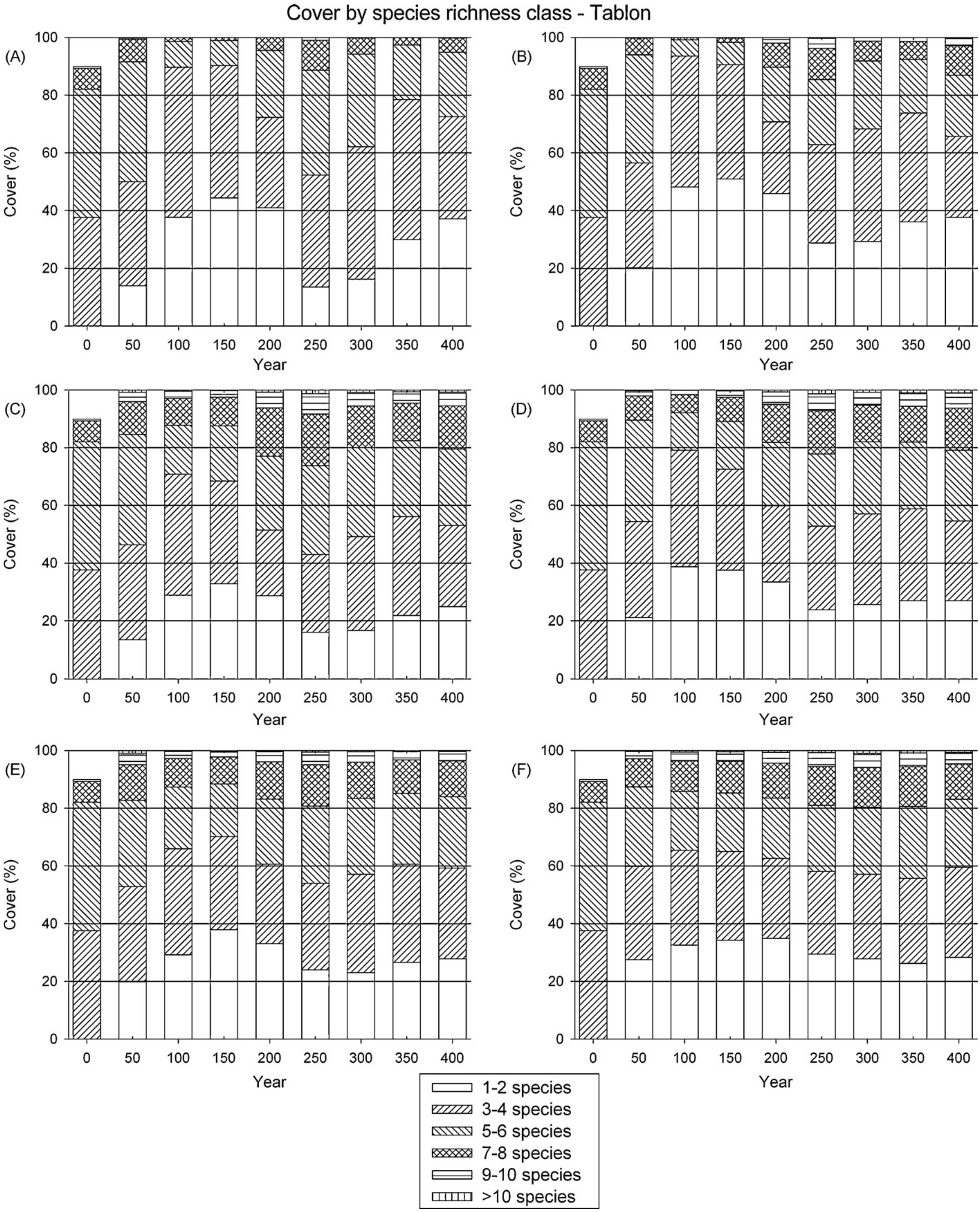

Fig. 6. Relative cover (%) of simulated landscape occupied by each species richness class under the six scenarios in Tablon. Species richness classes refer to the 25 species that were modelled (out of 53 recorded species). (A) NO-DIST scenario, (B) GRAZ scenario, (C) SIF scenario, (D) SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

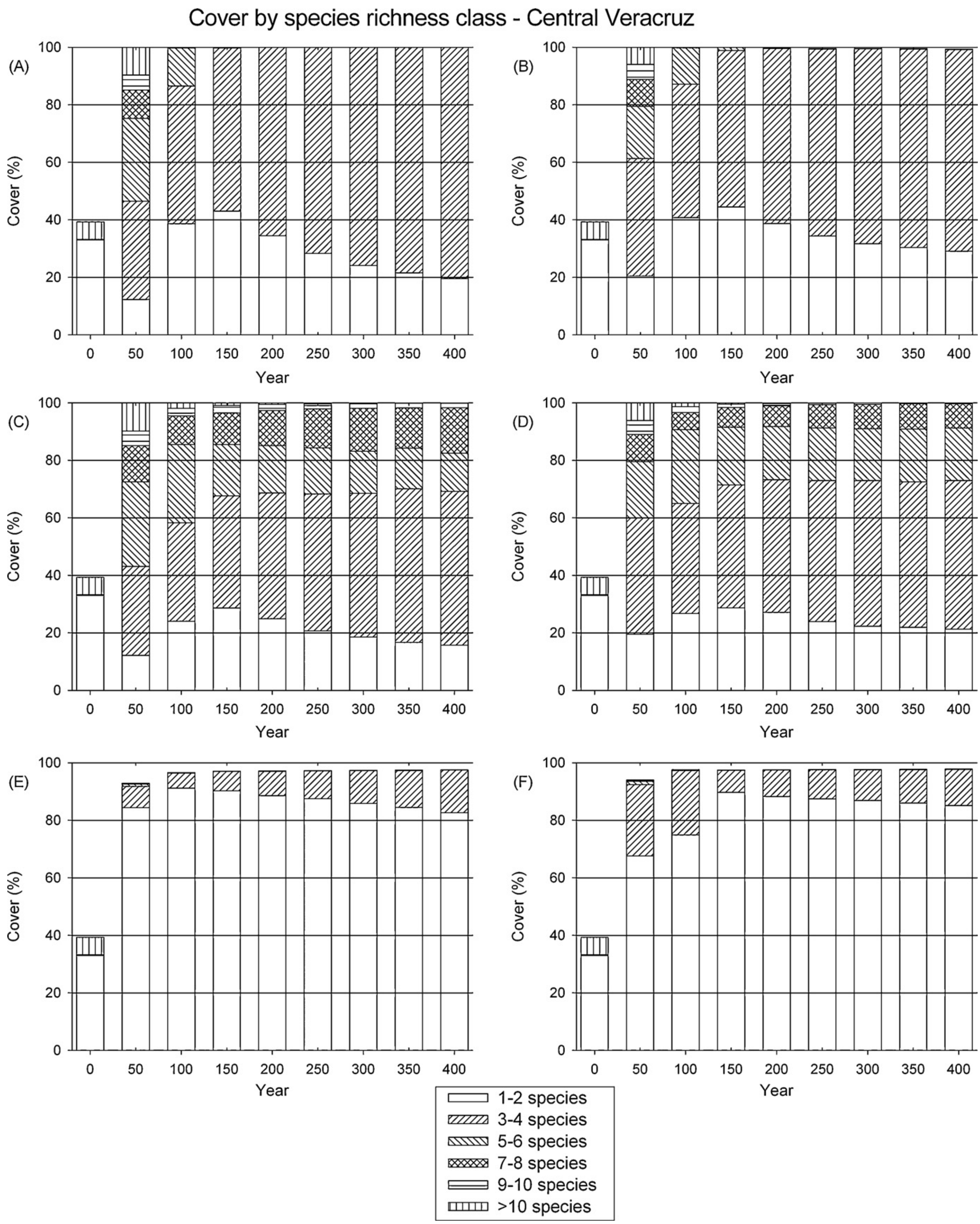

Fig. 7. Relative cover (%) of simulated landscape occupied by each species richness class under the six scenarios in Central Veracruz. Species richness classes refer to the 22 species that were modelled (out of 97 recorded species). (A) NO-DIST scenario, (B) GRAZ scenario, (C) SIF scenario, (D) SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

Table 4
Descriptive statistics for the percentage cover of all tree species >10 yr in Tablon and Central Veracruz under the six scenarios for the best-calibrated model runs over 400 years simulations.

	TAB				VER			
	Min	Max	Median[a]	S.D.	Min	Max	Median[a]	S.D.
NO-DIST	79.58	97.62	92.33a	6.59	99.63	99.97	99.97a	0.14
GRAZ	67.91	96.21	78.66b	10.2	98.61	99.73	99.13b	0.36
SIF	82.03	93.31	88.95abc	3.72	92.35	93.61	92.78c	0.40
SIF-GRAZ	74.39	90.13	79.56bd	5.31	91.72	92.97	92.34d	0.48
LFF	83.07	92.40	86.39abc	3.13	50.78	63.80	60.91e	4.19
LFF-GRAZ	67.98	86.33	74.86bd	6.04	9.621	24.25	23.39f	4.95

Min, minimum (%), Max, maximum (%), Median = median value (%), S.D. = standard deviation (%), based on outputs maps at intervals of 50 years (starting at year 50) in each study area. See Section 2.5 for scenarios abbreviations.

[a] Within each study area, median values not grouped by the same letter are significantly different (Mann–Whitney test, $P < 0.05$).

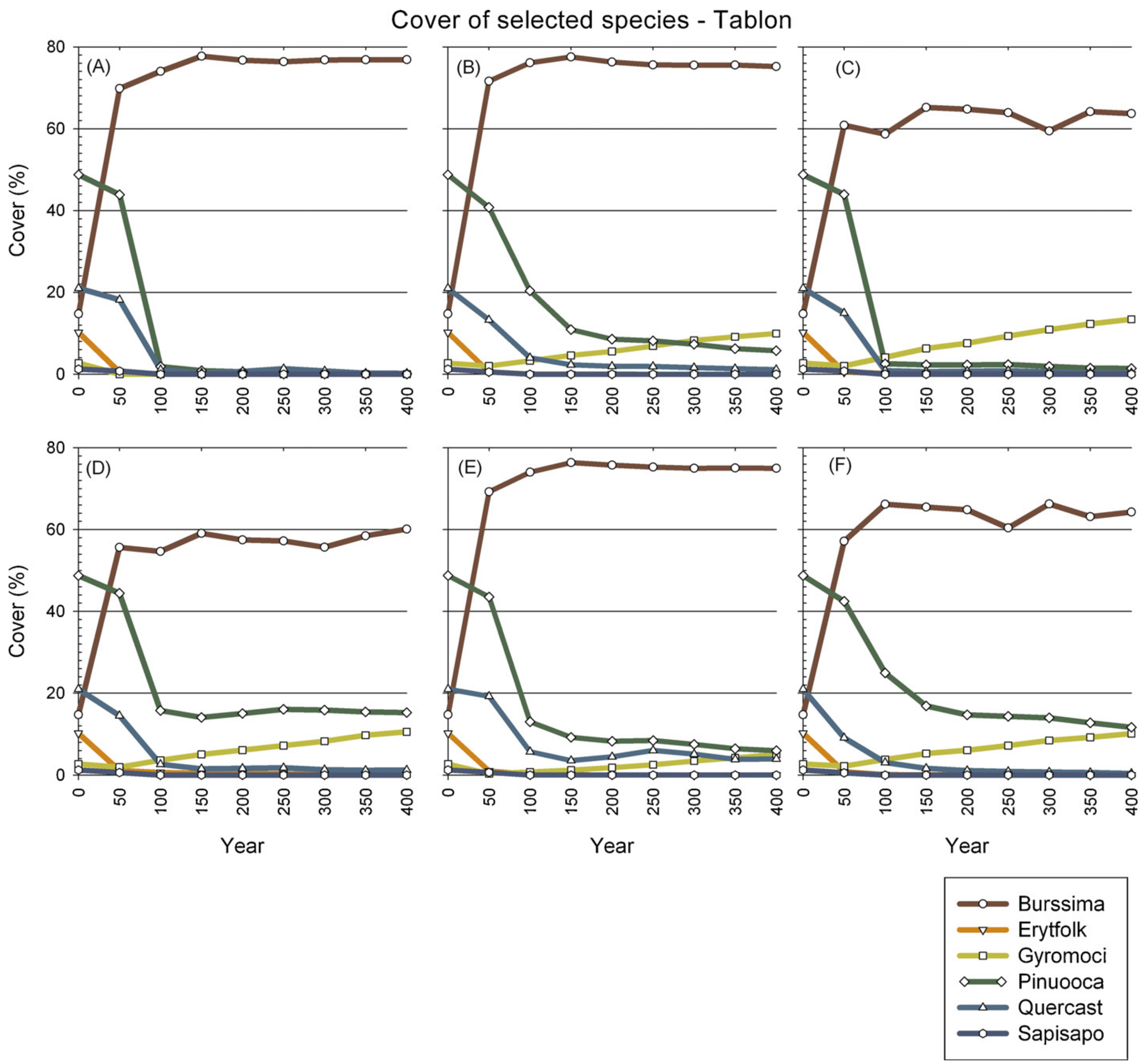

Fig. 8. Relative cover (%) of simulated landscape occupied by each selected species under the six scenarios in Tablon. Species differ in their post-fire regeneration method, shade and fire tolerance and represent different functional groups according to Noble and Gitay (1996) (see Section 3 for details). All age classes are represented. For species abbreviations see caption of Table 3. (A) NO-DIST scenario, (B) GRAZ scenario, (C), SIF scenario, (D) SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

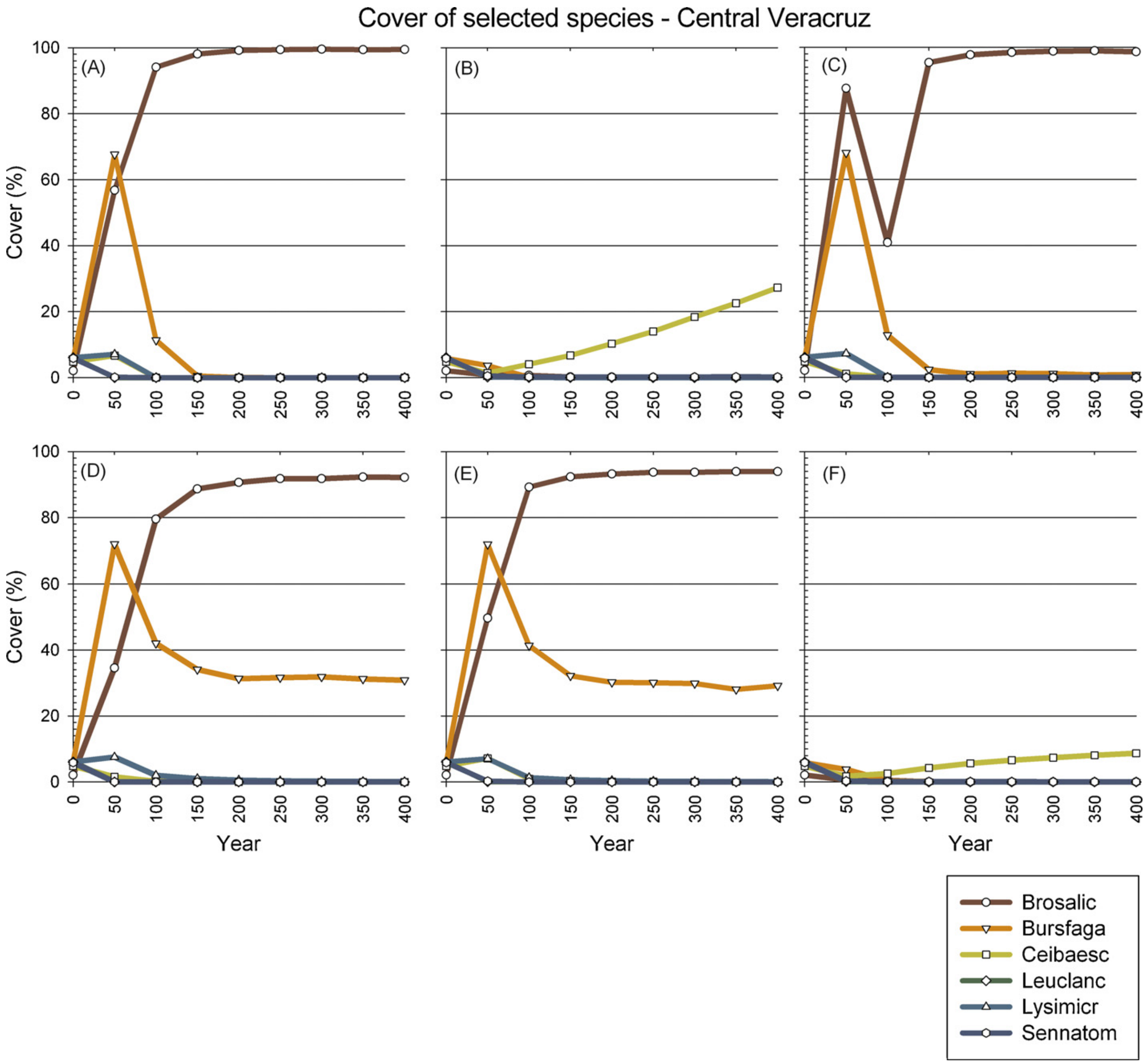

Fig. 9. Relative cover (%) of simulated landscape occupied by each selected species under the six scenarios in Central Veracruz. Species differ in their post-fire regeneration method, shade and fire tolerance and represent different functional groups according to Noble and Gitay (1996) (see Section 3 for details). All age classes are represented. For species abbreviations see caption of Table 2. (A) NO-DIST scenario, (B) GRAZ scenario, (C) SIF scenario, (D) SIF-GRAZ scenario, (E) LFF scenario, and (F) LFF-GRAZ scenario. For scenarios, abbreviations and description see Section 2.5.

Tablon, *Bursera simaruba* cover expanded over the 400 year simulation period under all of the scenarios, although its median cover was lower for GRAZ, LFF-GRAZ and SIF-GRAZ scenarios than under the NO-DIST, LFF, and SIF scenarios ($P < 0.001$; Mann–Whitney test). Other species, such as *Erythrina folkersii*, *Pinus oocarpa* and *Quercus castanea* declined under all of the scenarios, although displaying contrasting responses to different disturbance regimes. *Sapindus saponaria* declined to extinction under all of the scenarios after 100 years, probably owing to its low seed dispersal and low number of initial individuals (Fig. 8 and Table 5). Similarly in Central Veracruz, species displayed contrasting responses to disturbance. For example *Brosimum alicastrum* increased in cover under all of the scenarios except under LFF and LFF-GRAZ, whereas *Ceiba aesculifolia* expanded under LFF and LFF-GRAZ scenarios but declined rapidly under all of the other scenarios, going extinct under NO-DIST, GRAZ, and SIF-GRAZ after 50 years. Similarly *Senna atomaria* (SI) declined under all of the scenarios and was only maintained in the landscape under LFF and LFF-GRAZ (Fig. 9 and Table 5).

4. Discussion

4.1. Model limitations

As noted by Bugmann (2001), the value of forest models does not necessarily lie in their ability to make accurate predictions, but in their ability to help the understanding of processes and patterns by enabling exploration of the consequences of a set of explicitly stated assumptions. One of the main limitations common to all landscape disturbance and succession models, including LANDIS-II, is the difficulty of obtaining rigorous model validation, owing to

Table 5
Descriptive statistics for the percentage cover of selected species in Tablon and Central Veracruz under the six scenarios for the best-calibrated model runs over 400 years simulations.

Species	NO-DIST		LFF		SIF		GRAZ		LFF-GRAZ		SIF-GRAZ	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Tablon												
Burssim	68.9	6.81	68.7	6.76	67.8	6.67	57.3	5.37	58.0	5.50	52.6	4.76
Erytfolk	1.20	1.13	1.20	1.13	1.27	1.12	1.23	1.12	1.24	1.12	1.52	1.09
Gyromoc	0.30	0.30	5.81	0.97	2.44	0.53	7.61	1.39	6.11	0.96	6.11	1.02
Pinuooc	10.8	6.73	17.4	5.41	16.8	5.61	11.9	6.52	22.3	4.62	22.3	4.61
Quercast	4.86	2.79	5.37	2.33	8.09	2.29	4.46	2.60	4.27	2.28	5.19	2.44
Sapisap	0.22	0.15	0.20	0.14	0.21	0.14	0.22	0.15	0.19	0.14	0.20	0.14
Central Veracruz												
Brosalic	83.1	11.1	0.46	0.22	78.0	10.6	79.8	11.6	0.35	0.23	73.7	10.9
Bursfaga	9.47	7.39	1.08	0.71	33.2	5.76	10.4	7.32	1.13	0.71	34.5	5.70
Ceibaesc	1.27	0.86	12.2	3.00	1.49	0.87	0.64	0.53	5.50	0.80	0.72	0.53
Leuclanc	0.67	0.67	0.69	0.67	0.68	0.67	0.67	0.67	0.68	0.67	0.67	0.67
Lysimicr	1.46	0.97	0.69	0.67	1.77	0.91	1.47	0.98	0.69	0.67	1.97	0.94
Sennatom	0.66	0.64	0.86	0.62	0.68	0.64	0.65	0.65	0.73	0.64	0.65	0.65

$\bar{x}$ mean value (%), S.E. standard error (%), based on outputs maps at intervals of 50 years (starting at year 50). Species differ in their post-fire regeneration method, shade and fire tolerance, and represent different functional groups (see caption of Table 2 for details). See Table 3 for species abbreviations and Section 2.5 for scenarios abbreviations.

the lack of long-term data describing the ecological behaviour of forests, and to the stochastic nature of most of the models (Shifley et al., 2008). This problem becomes particularly severe in studies of tropical forests such as those explored here, where ecological information is particularly lacking (Cayuela et al., 2009). This lack of information also hinders model parameterisation. In our study, areas of particular uncertainty in model parameterisation included: (i) the initial forest age structure; (ii) the dispersal ability of the tree species; (iii) the establishment probability of the tree species across the landscape; and (iv) the impact of fire and grazing on the mortality of different age cohorts of trees. Application of the model identified these as knowledge gaps requiring further research.

We attempted to address these uncertainties by using a range of different approaches, including the use of high resolution remote sensing imagery, GARP and GAM models, reference to the scientific literature, and local experts' knowledge. While the results should clearly be viewed with caution, given the difficulties of accurate parameterisation, most of the model outputs were consistent with field observations. Other areas of uncertainty that might affect the dynamics of TDF in the future were not considered by our investigation, most notably the potential effects of climate change. Pennington et al. (2004), for example, suggested that TDF may disappear forever in the face of hotter and drier climates predicted under some climate change scenarios, owing to their difficulty to shift their ranges into available areas not already impacted by humans. It is important to consider such limitations when interpreting the results obtained.

4.2. Interaction between disturbances in Mexico's TDF

The impacts of anthropogenic disturbance on TDF, and the successional processes that govern responses to disturbance, have been the subject of some debate. In a recent review, Quesada et al. (2009) suggest that TDF may be particularly susceptible to human disturbance, as the growth rate and regeneration of plants is slow, reproduction is highly seasonal and most plants are outcrossed and dependent on animal pollination. However, our simulations suggest that forest cover can increase quite rapidly if protected from grazing and fire, a finding that is in accordance with previous field-based observations (e.g. Sampaio et al., 2007; Griscom et al., 2009). For example, Griscom et al. (2009) noted that in Panama, relatively diverse second-growth dry forests were developed within three years following pasture abandonment. Results obtained here also suggest that with time, an increasing proportion of the landscape becomes occupied by trees older than 60 years, in accordance with the observation made by Powers et al. (2009) indicating that in regenerating dry forests in Costa Rica, larger individuals increase asymptotically with stand age. These results highlight the potential scope for passive restoration of TDF, if forests can be adequately protected.

Our simulations indicate opposite trends with regards to species richness in the two study areas considered here, with the number of species tending to increase over time in Central Veracruz but to decline in Tablon, in the absence of disturbance. The trend in Central Veracruz is consistent with the findings of Marín-Spiotta et al. (2007), who indicated the recovery of secondary forests in Puerto Rico to species richness values close to those of a primary forest after 80 years following abandonment. One possible explanation for the opposite trend found in Tablon is that past fires may have had a great influence on the current composition of the forest, favouring the establishment of pioneer species. The majority of the species present initially were highly fire-tolerant but relatively shade-intolerant, and are therefore likely to disappear as a result of competitive processes as the canopy closes. Simulations also show that in both study areas in the absence of disturbance, the landscape is increasingly occupied by shade-tolerant and resprouting species with a relatively long seed dispersal distance; these species cover between 76 and 99% of the landscape after 200 years. These results are consistent with other studies that suggest shade-tolerant species tend to be dominant in secondary forests after 100–400 years since abandonment (e.g. Guariguata and Ostertag, 2001).

The scenario of no disturbance is unlikely ever to be observed in Mexico, however, as fire is a common occurrence in TDF, owing to both anthropogenic and natural causes (Rodriguez Trejo, 2008). Our simulations under both a scenario of small, surface, low intensity infrequent fires (SIF) and a scenario of large, crown, high-intensity frequent fires (LFF) suggest that forest cover can still recover quite quickly in terms of extent, owing to the high resprouting ability of the tree species. This finding also suggests that TDF is resilient to at least some anthropogenic disturbance regimes featuring fires. Similar findings have been reported in the field by Kennard et al. (2002), who demonstrated the high resprouting ability of TDF species after low intensity fire disturbance (similar to a SIF scenario in this study). Although the ability of many TDF species to resprout vegetatively after fire has long been recognised, its prevalence has been the subject of debate; some authors suggest that reproduction of tree species in TDF is primarily sexual rather than asexual (Quesada et al., 2009). In contrast, results of a recent systematic review of the literature indicate that following recent disturbance events in TDF, vegetative resprouts are the most prevalent individuals, although with time, individuals of seedling origin become more important in forest composition (McDonald et al., 2010). As noted by McDonald et al. (2010), vegetative reproduction could therefore play an important role in conferring resilience of TDF to anthropogenic disturbance and in determining the capacity for forest restoration, a finding supported by the current results.

Modelling results in both study areas suggest that the forest structure and composition differ markedly between SIF and LFF scenarios. Under SIF the landscape still supported high percentages of trees older than 60 years and a relatively high species number, whereas under LFF, these percentages were much lower. Consistent results have been reported by Otterstrom et al. (2006), who indicated that larger diameter trees in TDF of Nicaragua showed very low mortality under a fire treatment, suggesting that some TDF species are able to survive infrequent, low-intensity fires of small extent (equivalent to a SIF scenario in this study). In contrast with the SIF scenario, the LFF scenario explored here strongly modified the forest structure and composition in both Tablon and Central Veracruz, suggesting that large frequent fires are an issue of concern for TDF conservation in this region. This finding is consistent with other studies that have analysed the effects of increasing frequency of high intensity fires in Mexico and their potential destructive power as it was experienced in the 1997–1998 fire season (Cedeño, 2001; Roman-Cuesta et al., 2007; Manson et al., 2009).

Our simulations also suggest that over 400 years the landscape is increasingly occupied by relatively shade-tolerant species (such as *Bursera simaruba*, *Brosimum alicastrum* and *Bursera fagaroides*) under SIF, whereas only species with relatively high shade tolerance and high fire tolerance can expand under LFF conditions (such as *Bursera simaruba*, *Gyrocarpus mocinnoi* and *Ceiba aesculifolia*). Although species with low shade tolerance and high fire tolerance (such as *Pinus oocarpa* and *Senna atomaria*) can persist longer under LFF compared with SIF, species with low tolerance of both shade and fire disappear in both fire scenarios. These findings are consistent with the landscape dynamics described in Noble and Gitay (1996), who predicted that shade-tolerant species able to establish immediately after disturbance, with a sufficient dispersal ability or a long-lived seed pool (i.e. group DT and ST, species such as *Bursera simaruba* and *Gyrocarpus mocinnoi*), are unlikely to go extinct, whereas shade-tolerant species able to regenerate immediately after disturbance but vulnerable to disturbances with close temporal spacing (i.e. group GT, species such as *Brosimum alicastrum* and *Bursera fagaroides*) are likely to decline to local extinction under a frequent disturbance regime. In contrast, species able to regenerate only immediately after the disturbance by resprouting or via to a long-lived seed pool (i.e. group VI and SI, species such as *Ceiba aesculifolia*, *Senna atomaria* and *Pinus oocarpa*) are likely to go extinct under an infrequent disturbance regime.

The LANDIS-II projections reveal that when grazing is acting in combination with fire, the forest cover, structure and composition vary dramatically depending on the intensity, frequency and extent of the fires. For example, in both study areas, grazing was found to reduce forest cover to a greater extent when combined with a frequent, high intensity fire regime. In addition, our results suggested that a scenario of small, infrequent fires with grazing compared with small, infrequent fires acting alone significantly altered the forest structure in Central Veracruz but not in Tablon, a pattern that might be attributed to the different land use history of the two study areas. Foster et al. (2003) noted that past land use can influence the dynamics of forest succession, making it difficult to generate predictions and generalisations. However, our results highlight the importance of interactions between different forms of disturbance, an issue that has received relatively little research attention in the past. Paine et al. (1998) noted that disturbances can interact in ways that cannot be predicted by the study of a single disturbance, a finding that was further supported by simulations of a tropical moist forest stand in Puerto Rico (Uriarte et al., 2009). These results provide some explanation of the widely held belief that slash-and-burn practices followed by extensive pasture are one of the main causes of TDF destruction (Maass, 1995; Quesada and Stoner, 2004). For example, Miller and Kauffman (1998) noted that slashing, frequent burning, cultivation and grazing of a TDF in Mexico significantly reduced the number of woody individuals and the woody species diversity, and modified community structure by favouring a few tolerant species with high relative abundances. This is consistent with the results obtained here, where landscapes under combined fire and grazing were increasingly occupied by species that are relatively tolerant of these forms of disturbance. Few interactions between disturbances such as those explored here have been recorded previously in TDF at the landscape scale. Given the widespread occurrence of multiple human disturbances in dry forest (Miles et al., 2006), such interactions are likely to be widespread, and represent an urgent priority in terms of TDF restoration and conservation action.

4.3. Management implications

Evidence from ecological restoration initiatives elsewhere highlights the potential value of such approaches for increasing both biodiversity and the provision of ecosystem services (Rey Benayas et al., 2009). The results presented here suggest that passive restoration of TDF is achievable at the landscape scale in both study areas if grazing were excluded, and fire were to be carefully managed to achieve a regime of infrequent, low intensity fires. Of the four disturbance scenarios analysed, such a regime (SIF) was the only scenario that did not negatively affect forest cover, composition and structure of TDF. Achievement of ecological restoration of TDF in practice would depend not only on developing an effective approach to fire management (Roman-Cuesta et al., 2007), but also on providing appropriate incentives to landholders, as any restoration action will incur costs. Potential approaches include improved markets and payment schemes for ecosystem services (Jack et al., 2008) and the Clean Development Mechanism developed under the Kyoto protocol. Modelling approaches such as that presented here could help target such interventions effectively, by enabling the conditions under which restoration is most likely to be effective to be identified. However, analysis of both the costs and benefits of restoration actions are required to maximise return on investments in restoration (Rey Benayas et al., 2009).

This investigation also highlights the value of spatially explicit modelling tools (such as LANDIS-II) for exploring the potential impacts of anthropogenic disturbance on TDF, supporting suggestions that this approach can provide a useful element of a toolkit for sustainable forest management (Newton et al., 2009). Further elements of an emerging toolkit could potentially include models that enable the potential impacts of a full range of disturbances regimes to be explored. Further interactions between different frequencies and intensities of fire and grazing regimes could usefully be explored, together with interactions with other threats, such as tree cutting and climate change. Integrated analysis of different disturbance regimes, and the responses of TDF to different management interventions, would enable model outputs to directly inform the planning and implementation of dryland forest restoration.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.12.019.

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