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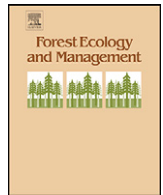
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Modeling landscape dynamics in an Atlantic Rainforest region: Implications for conservation

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ABSTRACT

The dynamics of the Atlantic Rainforest loss and recovery are still not fully understood despite its long history of human occupation. In this study, we investigated changes in an Atlantic Rainforest region due to major biophysical and human proximate causes. First, we modeled land-cover and land-use changes from 1962 to 2000, including deforestation and forest regrowth, and thereby simulated future landscape trajectories to assess their possible effects on the conservation of forest species of the Ibiúna Plateau, a region located in Southeastern Brazil within the Atlantic Rainforest biome. We modeled four scenarios (*status quo*, *random*, *law enforcement*, and *land-use intensification*) and simulated their resulting landscape trajectories for the year 2019 using DINAMICA. The landscape dynamics in the study region were particularly intense. During the first period of 1962–1981, the rate of forest regrowth ($3\% \text{ year}^{-1}$) was greater than the rate of deforestation ($2\% \text{ year}^{-1}$), whereas in the latter period of 1981–2000, increasing urbanization and the spreading of rural establishments resulted in more deforestation ($2.9\% \text{ year}^{-1}$) than regrowth ($1\% \text{ year}^{-1}$). These dynamics imprinted a heterogeneous landscape, leading to the predominance of progressively younger secondary forests with increasingly less capacity of hosting sensitive forest species. The influence of proximate causes on the dynamics of deforestation and forest regrowth showed consistent patterns, such as higher forest regrowth rates near rivers, on steep slopes and far from dirt roads, whereas losses in young secondary vegetation and forest were far from rivers, on gentle slopes and near urban areas. Of the modeled scenarios, only the *law enforcement* scenario may lead to the recovery of a network of interconnected forest patches, suggesting that simply the enforcement of current forest laws, which prohibit deforestation on unsuitable agricultural areas and along river margins and establish a minimum of 20% of forest remnant per rural property, may effectively favor forest species conservation in the short term (two decades) without the need of any forest restoration effort.

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1. Introduction

The Atlantic Rainforest is internationally recognized by its large number of species (1–8% of the world's species), of which a large amount is endemic (Myers et al., 2000; Galindo-Leal and Câmara, 2003). The last estimation from Mittermeier et al. (2005) identified 8000 endemic plant species (40% of endemism), 148 birds (16%), 71 mammals (27%), 94 reptiles (31%) and 286 amphibians (60%), to cite only the most studied taxonomic groups.

Nonetheless, the Atlantic Rainforest is probably one of the most threatened tropical biome. Originally, its extent reached out 1.48 million km², totalizing 17% of the Brazilian territory. However, by 2005, only 160,000 km² of its forests, equivalent to 11–12% of its

original forest cover, remained (Fundação SOS Mata Atlântica and INPE, 2008; Ribeiro et al., submitted for publication). Historically, deforestation of the Atlantic Rainforest was closely related to the major Brazilian economic cycles, beginning with the exploitation of Pau-Brasil, *Caesalpinia echinata* (16th century) and succeeded by the expansion of sugar cane (from 18th century) and the widespread conversion to pasturelands and coffee plantations (19th and 20th). More recently, deforestation has been related to urban sprawl and the expansion of *Eucalyptus* plantations (Dean, 1997; Drummond, 2004). Even today, despite legal restrictions on deforestation, the rate of forest loss is still high, ca. 0.25% per year (Fundação SOS Mata Atlântica and INPE, 2008).

As a consequence of five century of intense occupation, the Atlantic Rainforest is highly fragmented, holding forest fragments in average lesser than 100 ha (Jorge and Garcia, 1997; Viana et al., 1997; Ranta et al., 1998; Morellato and Haddad, 2000; Galindo-Leal and Câmara, 2003; Ribeiro et al., submitted for publication).

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Currently, more than 500 Atlantic Rainforest endemic species of different taxa are considered highly vulnerable to extinction (Conservation International do Brasil, 2000; Galindo-Leal and Câmara, 2003). Despite the high risk of species extinctions, the dynamics of Atlantic Rainforest loss and recovery have not yet been fully investigated, contrary to the large number of studies for the Brazilian Amazon (e.g. Skole and Tucker, 1993; Dale et al., 1996; Walker and Homma, 1996; Alves et al., 1999; Laurance et al., 2001; Achard et al., 2002; Metzger, 2002; Soares-Filho et al., 2002, 2004, 2006; Ferraz et al., 2005).

Landscape dynamics studies and models have been widely used to understand the proximate causes and underlying driving forces of tropical deforestation (see review in Geist and Lambin, 2002), to detect structural thresholds in deforestation patterns (Oliveira-Filho and Metzger, 2006), and also to forecast outcomes from different scenarios of land-use management, such as potential carbon emission and habitat loss (Soares-Filho et al., 2006), alterations in the hydrological cycle (Costanza et al., 2002), and climate change (Sampaio et al., 2007).

In this context, this study aimed: (i) to model the dynamics of deforestation and forest regrowth in a fragmented Atlantic Rainforest region in order to understand the major biophysical and human proximate causes controlling the dynamics from 1962 to 2000; (ii) thereby to simulate future changes in the landscape structure and composition to assess their potential effects on species conservation under a range of plausible land-use management scenarios.

2. Study site

The study site is located on the Ibiúna Plateau, 60 km west from the city of São Paulo (23°41'S–23°47'S; 47°02'W–47°07'W). This area belongs to the Serra do Mar ridge, a bio-geographical region (Silva and Casteleti, 2003) with the highest level of endemism for several taxonomic groups in the whole Atlantic Rainforest biome (Manne et al., 1999; Costa et al., 2000; Brown and Freitas, 2000). The study site encompassed an area of 7800 ha of which 31% is forested (Fig. 1). The Ibiúna Plateau is situated just above the Paranapiacaba Serra, in a transitional zone between the continuous (>80%) coastal rain forest in the south, and the highly deforested (<3%) and fragmented mesophyllous semi-deciduous forest of inland São Paulo State (Kronka et al., 2005). The forests of study site may be classified as “lower mountain rain forest” (Oliveira-Filho and Fontes, 2000), but also contain species from the *Araucaria* mixed forest, the semi-deciduous forest and Cerrado (woody savanna) regions (Catharino et al., 2006).

The region's substrate is predominantly composed of Pre-Cambrian crystalline rocks, essentially with high metamorphic grade, such as migmatites and granites (Almeida, 1964). Different relief systems can be observed, such as mountain plateau with steep slopes, mountain with moderate to gradual slopes, and alluvial plains ranging from 860 to 1060 m of elevation (Ross and

Moroz, 1997; Oliveira, 1999). According to the American Soil Taxonomy, the main soils in the region are alfisols, ultisols, oxisols and inceptisols (Ross and Moroz, 1997). The climate of Ibiúna is mild hot and humid Cfa type according to Köppen system (Köppen, 1948). Mean month temperatures range between 27 and 11 °C. The average annual precipitation is about 1300–1400 mm, with the driest months and the lowest average temperatures from April to August (30–60 mm/month) and the wettest (200–260 mm/month) and warmest months from November to March (SABESP, 1997).

On the Ibiúna Plateau, the dynamics of deforestation and forest regrowth have been strongly linked to the growth of the city of São Paulo, in terms of supply of charcoal for power generation, mainly during the Second World War, and lately for agricultural products (Seabra, 1971). More recently, better access to the region has led to an intense periurban expansion as well as to the proliferation of weekend country houses for middle-class families.

The boundaries of the study site were defined by a buffer zone surrounding 21 fragments that have been object of undergoing researches aiming to assess the effects of forest fragmentation on several taxonomic groups and ecological processes (e.g. Pardini et al., 2005; Uezu et al., 2005; Silva et al., 2007; Durigan et al., 2008; Martensen et al., 2008; among others).

3. Methods

3.1. Mapping landscape dynamics

We used aerial photographs from 1962 (1:25,000), 1981 (1:35,000) and 2000 (1:10,000) to map land-use and land-cover changes. As explained below, the same mapping procedure was applied to all imagery products to allow comparisons regarding classification accuracy and to reduce errors in the subsequent analyses.

The photos were scanned at 1 m resolution and georeferenced with an RMS error ranging from 5 to 12 m. Five land-use and land-cover classes were defined based on the level of detail available for the smallest scale imagery (1:35,000, Table 1). These classes included (1) buildings, (2) crops fields, (3) forest plantation, (4) forest and (5) young secondary vegetation (Fig. 2). Photo interpretation was performed by only two trained people in order to reduce errors related with different abilities of interpretation. All subsequent analyses and simulations were performed using raster layers at 15 m resolution.

We evaluated the mapping accuracy by visiting 65 vegetation points randomly distributed throughout the study area. As a result, we obtained an overall accuracy of 88% for the native vegetation classes and higher than 95% for the other land-use classes of the 2000 map (Silva et al., 2007). First, all five land-use and land-cover classes were used to quantify the changes in the landscape and to analyze the influence of proximate causes on them. Finally, in the scenario modeling process, the three land-use classes: (1) buildings, (2) crop fields, (3) forest plantation—were merged into

Table 1

Land-use and land-cover classes specified in the aerial photograph classification (Ibiúna Plateau, Brazil).

Land-use and land-cover classes	Description
Land-use	
Urban and rural buildings	Isolated buildings, hedges, grouped buildings, condominia, settlements
Crop fields	Mostly crop fields or fallow fields, but also with some areas used for cattle ranching or some abandoned/disturbed herbaceous vegetation, with or without shrubs
Forest plantation	Forest plantation with exotic species, e.g. <i>Pinus</i> spp. and <i>Eucalyptus</i> spp.
Land-cover	
Young secondary vegetation	Shrub to arboreal vegetation with up to 5–6 m height continuous canopy
Forest	Intermediate to old secondary forest with canopy height usually >10 m, with or without emergent trees up to 30–35 m

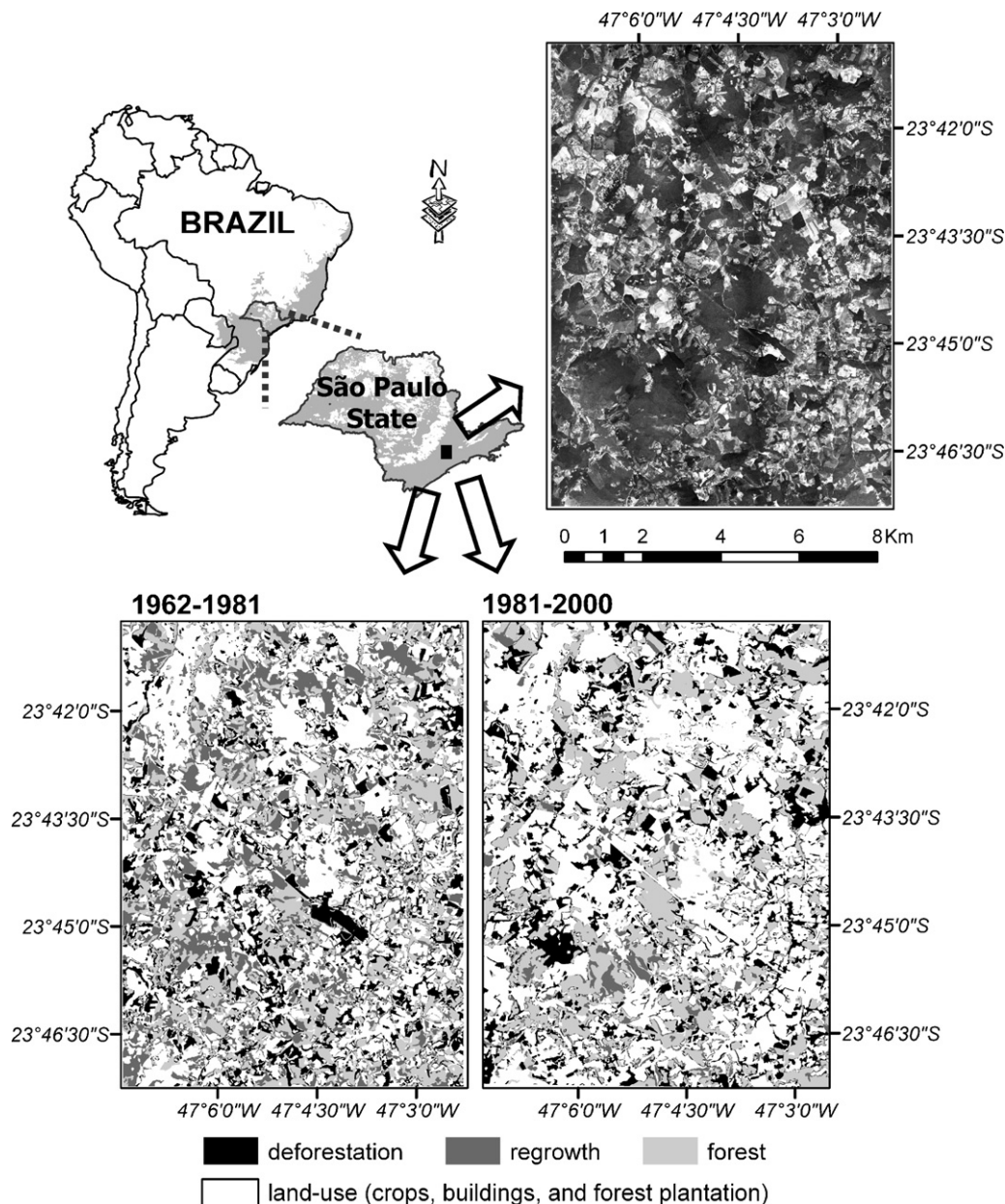


Fig. 1. The study region (box) in the State of São Paulo, Southeastern Brazil. The limits of the Atlantic Rainforest are depicted in gray in São Paulo (IF, 2005) and South America maps (CRIA, 2008). In detail, aerial photographs showing the landscape in April 2000 (forest cover in gray and black) and two maps showing the landscape dynamics for two time periods: 1962–1981 and 1981–2000.

a single class called “land-use”, resulting into four land-use/land-cover transitions comprising deforestation, forest regrowth, loss of young secondary vegetation, and regrowth of young secondary vegetation (Table 1).

3.2. Model calibration

We used the Weights of Evidence method (Soares-Filho et al., 2004) to select the variables most related to observed landscape changes as well as to quantify their influences on each of the modeled transitions. This method produces as a result transition probability maps that depict the integrated influence of proximate causes on the modeled transitions (Soares-Filho et al., 2004). The variables we examined comprised a set of biophysical and human factors that spatially determine the location of the changes thus referred as proximate causes. This set includes slope, elevation,

distances to rivers, major and secondary roads, urban centers, and distances to previously forested, regrowth and deforested areas (Tinker et al., 1998; Endress and China, 2001; Felicísimo et al., 2002; Nagendra et al., 2003; Soares-Filho et al., 2004; Hietel et al., 2004). All spatial variables were either derived from topographic map (1:10,000 scale, elevation level interval of 5 m) or from the series of derived landscape maps. Since Weights of Evidence coefficients are obtained for map categories of each spatial variable under analysis, all continuous gray-tone maps needed to be categorized. For elevation and slope, we used regular intervals, respectively, of 40 m (from 860 to >1020 m) and 5° (from 0° to >30°). For distance variables, such as distances to rivers and main roads, the distance classes followed geometric ranges (for example, 0–50, 50–100, 100–200, 200–400 m) in order to obtain narrower buffers closer to the geographical feature under consideration. A basic assumption for the Weights of Evidence method is that the

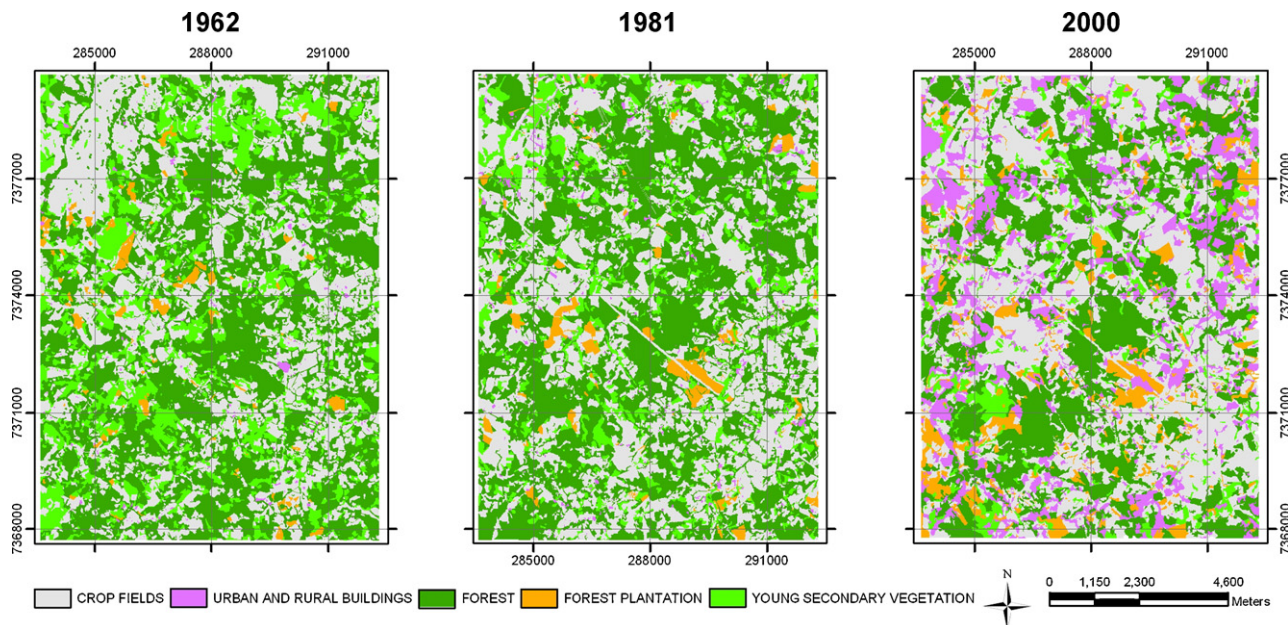


Fig. 2. Land-use and land-cover maps of the studied landscape for 1962, 1981 and 2000 (Plateau of Ibiúna, SE Brazil).

variables must be spatially independent. We tested the spatial independence of the aforementioned variables using the Crammer coefficient (V) and found that all variables, except the pair distance to secondary roads and distance to urban centers, have values lower than an empirical threshold ($V < 0.45$), and thus are spatially independent (Almeida et al., 2003).

3.3. Simulation set up and running

We used DINAMICA, a landscape dynamics cellular automata model (Soares-Filho et al., 2002, www.csr.ufmg.br/dinamica), to run the landscape change simulations. The model was calibrated for two time periods, i.e. 1962–1981 and 1981–2000, using the transition matrices and the Weights of Evidence coefficients obtained by cross-tabulating 1962 and 1981 maps and 1981 and 2000 maps. Finally, annual time-step simulation maps were produced from 1962 to 2000.

To approximate the simulated landscape structure of the actual one, we tested different models changing the parameters of the transition functions employed by DINAMICA: the Expander and the Patcher (Soares-Filho et al., 2002). These functions incorporate cellular automata local rules conceived to mimic the neighborhood influence on the transition of a cell state. The Expander is dedicated only to the expansion or contraction of previous patches of a certain land-use and land-cover class (Soares-Filho et al., 2002). In turn, the Patcher is designed to form new patches through a seedling mechanism (Soares-Filho et al., 2002). DINAMICA allows to split the quantity of simulated changes between these two functions as well as to vary the mean size, size variance and isometry of the simulated patches of change. Since DINAMICA transition functions employ a stochastic cell selection mechanism, 10 replicates were produced for each model tested.

The structure of the simulated landscapes was compared with the actual 2000 landscape using cluster and principal component analyses (Zar, 1999). We used FRAGSTATS[®] software (version 3.3; McGarigal and Marks, 1995) to measure a set landscape indices, which included the number of patches (NP), the largest patch index (LPI), the area-weighted mean patch area (AREA_AM) and the clumpiness index (CLUMPY). The simulated landscape with structure most similar to the 2000 landscape resulted from a

model with 80% of changes assigned to Expander and 20% to Patcher, and with deforestation simulated patches having 20 ha as mean patch size. Patch size variance was set to zero and isometry value was set to 2.0. The transition function parameters of the best fitted model, along with the Weights of Evidence derived for the 1981–2000 period, were employed to simulate the future landscape trajectories onto 2019 under each of the modeled scenarios.

3.4. Scenario modeling

Insights of the effects of land-use practices and management on a region's landscape dynamics can be evaluated by confronting scenarios consisting of alternative assumptions (Almeida et al., 2003; Soares-Filho et al., 2004, 2006). In this study, we modeled four scenarios to evaluate the implications of possible landscape trajectories on the conservation of the Ibiúna Plateau forests. These scenarios are *status quo*, *random*, *land-use intensification* (pessimistic scenario) and *law enforcement* (optimistic scenario). All scenarios, except the *random*, were established from plausible perspectives with respect to the land-use and land-cover observed trends as well as to the compliance of the current environmental laws. Resulting landscape changes within each modeled scenario were simulated from 2000 to 2019 using annual time-steps.

The *status quo* scenario, which was used as a baseline for comparison, assumed that historical trends observed during 1981–2000 time period will continue into the future. Thus, this scenario applies a Markovian approach, simply projecting the changes into the future using transition rates annualized from the 1981–2000 time-period transition matrix (for details see Soares-Filho et al., 2002). The *random* scenario involved the same approach of the *status quo* scenario; however, the influence of proximate causes on the landscape dynamics, as determined by the Weights of Evidence coefficients, was removed. In this manner, the *random* scenario aimed to assess the resulting landscape structure if the changes had no spatial influence. In the *land-use intensification* (pessimistic) scenario, we modified the 1981–2000 annualized transition matrix so that all changes from young secondary forest to forest were reallocated to the transition from young secondary vegetation to land-use, and then used this modified transition matrix to forecast

the future landscape trajectory. Hence, the *land-use intensification* scenario represents a reduction in fallow areas as a response to better access to the region provided by newly paved highways. In the *law enforcement* (optimistic) scenario, the annualized transition matrix of 1981–2000 had its deforestation rate set to zero to duly abide by the current environmental laws, which protect riparian forest and impede deforestation on steep slopes and on top of hills and ridges.

For each scenario, we performed 10 simulation replicates from 2000 to 2019 – similarly to Castro et al. (2005) – and analyzed the resulting landscapes with respect to their conservation potential for strictly forest species, which are most sensitive to forest fragmentation. In this step, we employed the landscape metrics: number of forest patches (NP), largest forest patch index (LPI), mean forest patch area (AREA_MN) and mean forest proximity index distribution (PROX_MN) calculated with a search radius of 800 m (McGarigal and Marks, 1995). These landscape metrics are significantly correlated; however, this is not a limitation for the proposed analysis.

The main objective of this analysis was to identify the best landscape configuration for forest species conservation, which is hypothetically a landscape with: (i) a high forest cover; (ii) a small number of forest fragments; (iii) a high largest forest patch index that can support stable populations and be source for small patches; (iv) a large mean forest patch area; and (v) a high mean forest proximity index. This analysis did not consider different perceptions of landscapes by individual species (Vos et al., 2001; Opdam et al., 2003; Fischer and Lindenmayer, 2007), nor the effect of the matrix on the function of the landscape (Antongiovanni and Metzger, 2005; Bélisle, 2005; Taylor et al., 2006; Umetsu and Pardini, 2007; Umetsu et al., 2008) and the quality of forest habitat (Harrison and Fahrig, 1995). However, this approach allowed for a preliminary comparison of the modeled scenarios with respect to their potential for biodiversity conservation, especially when there is no other biological information available. To test if there was significant difference between the modeled scenarios, we employed the test of variance (ANOVA) on each landscape metric (NP, LPI, AREA_MN, PROX_MN), using each of the 10 simulation runs per scenario as an independent value. When difference was found using ANOVA, Tukey's HSD post hoc test was used ($\alpha = 0.05$) (Zar, 1999).

4. Results

4.1. Landscape dynamics

The dominant land-use and land-cover for all three mapped years were forest (43.8% of the whole landscape in 1962, 48.3% in

1981, and 33.3% in 2000) and crop fields (36.2%, 37.7%, 35.8% for 1962, 1981, and 2000, respectively; Fig. 2). In 1962 and 1981, urban and rural buildings (0.6%, 1.5%) and forest plantation (2.2%, 3%) had little expression, however, in 2000, the areal percent of those land-use classes increased significantly (16.6% and 6.8%, respectively). Young secondary vegetation showed a constant reduction over time, decreasing from 17.2% in 1962 to 9.6% in 1981 and 7.6% in 2000, pointing out a tendency of land-use intensification. Both time periods were highly dynamic modifying approximately half of the landscape (50.7% between 1962 and 1981; 45.8% between 1981 and 2000).

Landscape dynamics between 1962 and 1981 were characterized by greater forest regrowth than deforestation (Fig. 3). While forest and young secondary vegetation were converted to crops (852.8 ha deforested and 393.7 ha young secondary vegetation loss), forest regrowth from abandoned crops fields (734.2 ha) and young secondary vegetation (735.8 ha) was also high. Regrowth of young secondary vegetation mostly occurred from crop fields (56.8% of the whole young secondary vegetation recovered between 1962 and 1981). The transition from forest to young secondary vegetation, which probably represented deforestation followed by regrowth, also contributed to the young secondary vegetation class in 1981 (238.8 ha). The total area of deforestation was 1232.5 ha (64.9 ha/year) and the total area of forest regeneration was 1566 ha (82.4 ha/year). Young secondary vegetation increased 593.6 ha and lost 1162.9 ha. Thus, this trend resulted in a reduction of young secondary vegetation (–569.3 ha) and in an expansion of forest (333.4 ha).

The second time period (1981–2000) was characterized by an expansion of urban and rural buildings (1020% or 1125.2 ha) and a reduction in the native vegetation extent (Fig. 4). The increase of urban and rural buildings took place at the expense of crop fields (48.8% of the whole urban and rural buildings in 2000) and forest land (32%). In 2000, 17.7% of the whole forest and 11% of young secondary vegetation in 1981 were replaced by urban and rural buildings and crop fields. Most young secondary vegetation in 2000 was forest in 1981 (359.1 ha, corresponding to 63.2% of young secondary vegetation in 2000), suggesting that land was abandonment soon after deforestation. In this time period, total deforestation was 1543.7 ha (81.2 ha/year), while forest regrowth was 424.6 ha (22.3 ha/year). Young secondary vegetation increased 479.8 ha and at the same time lost 623.1 ha. As a result, losses in forest cover and in young secondary vegetation amounted, respectively, to 1117.1 and 143.3 ha.

The Weights of Evidence analysis allowed us to identify the influence of spatial determinants on the analyzed transitions. Some patterns were consistent, particularly, higher forest regrowth near

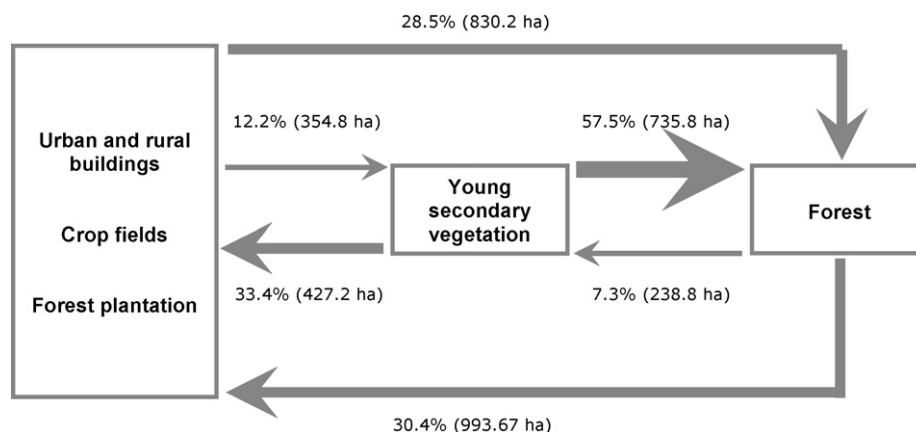


Fig. 3. Net (%) and gross (ha) rates of deforestation and regrowth for 1962–1981 time period.

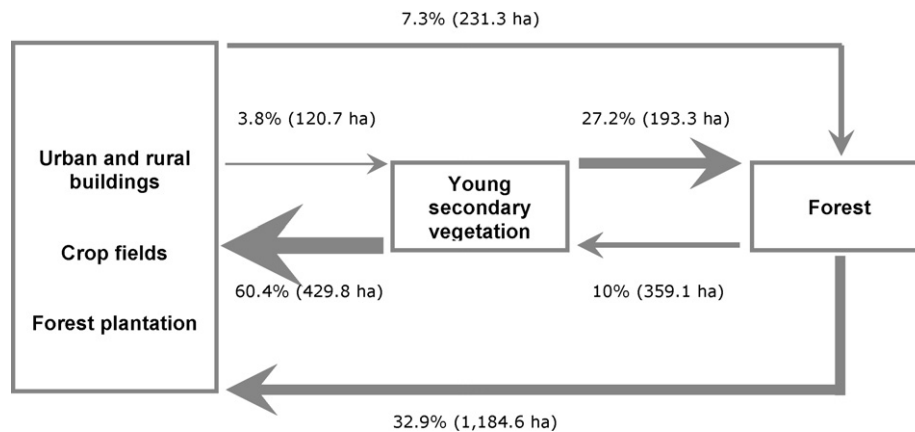


Fig. 4. Net (%) and gross (ha) rates of deforestation and regrowth for 1981–2000 time period.

rivers, on steep slopes and far from dirt roads (Fig. 5). On the contrary, losses in young secondary vegetation and forest were higher far from rivers, on gentle slopes and near urban cores (Fig. 5). Other significant relationships were found for specific transitions, such as higher forest regrowth at higher elevations and far from main roads. In general, the influences of spatial determinants, representing proximate causes, were consistent between the two time periods under analysis.

4.2. Forecasted trends

The four modeled scenarios resulted in landscapes with different forest cover (Fig. 6), except the *status quo* and *random* scenarios (23.5%), which used the same 1981–2000 transition matrix. The *land-use intensification* scenario produced an increase of converted land-use area (2000: 59.2%; 2019: 77.4%) and a decrease of forest cover (2000: 33%; 2019: 16.7%). The *law enforcement* scenario was the only one to show an increase of forest cover (2019: 37.8%).

With respect to the spatial configuration of the forest, the worst-case scenarios, characterized by high deforestation rates and forest fragmentation, were represented by *land-use intensification* and *random* (Table 2). The *law enforcement* scenario represented the best-case in terms of its potential for conserving forest species. In turn, the *status quo* scenario showed an intermediate situation (Fig. 6). If current landscape change trends continue over the next 19 years, the number of forest fragments shall increase by 15%, the size of the largest forest patch by 23%, and the mean size of forest fragments shall decrease by 34% and the proximity between them decrease by 29%. The *land-use intensification* and *random* scenarios showed the least favorable landscapes for forest species conservation. Those scenarios will increase the number of forest patches by 38% in the pessimistic scenario and 45% in the *random* scenario and decrease the size of the largest forest patch (respectively, by 62%, 35%), the mean size of forest

fragments (by 63%, 47%) and the proximity between them (by 84%, 56%). The optimistic *law enforcement* scenario is the only one that could reverse these negative trends, producing a decrease of 13% in the number of forest patches and an increase of 78% in the size of the largest forest patch, 32% in the mean size of forest fragments and 56% in the proximity between them in comparison with 2000.

5. Discussion

5.1. Landscape dynamics and proximate causes

The landscape dynamics in the study region were particularly intense. From 1962 to 1981, the deforestation rate was equal to 2% year⁻¹, increasing to 2.9% year⁻¹ between 1981 and 2000. These rates were greater than the deforestation rates observed from 1995 to 2000 for the Atlantic Rainforest in the state of São Paulo (0.3% year⁻¹), as well as for the whole Atlantic Rainforest (0.5% year⁻¹, SOS Mata Atlântica, 2001). The deforestation rates we observed in this portion of the Atlantic Rainforest were also higher than the rates for Latin America (0.38% year⁻¹) and for the tropical forests of the world as a whole (0.5% year⁻¹, Achard et al., 2002), and were similar to the deforestation rates observed along the Amazon deforestation arc (2.2% year⁻¹, Ferraz et al., 2005).

Forest regrowth rates in our study area were also high (1962–1981: 3% year⁻¹; 1981–2000: 1% year⁻¹) when compared with the observed ones for tropical regions—from 0.19% year⁻¹ in Southeast Asia to 0.04% year⁻¹ in Latin America (Achard et al., 2002). As a consequence of this particularly high turnover of deforestation and regrowth, there is very little primary forest remaining in our study area. Notice that only 1357 ha (18.2% of the whole landscape) of the forest cover from 1962 was left unchanged in 2000.

These dramatic landscape dynamics emphasize how threatened is the Atlantic Rainforest, which is still under a great pressure despite the Brazilian environmental laws and other measures issued to curb deforestation. Although some studies suggest that

Table 2

Main results obtained with ANOVA and Tukey's HSD post hoc tests when comparing the four forecasted scenarios for 2019. SD: Standard deviation.

	Status quo		Random		Land-use intensification (pessimistic)		Law enforcement (optimistic)		ANOVA		Tukey HSD
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	F	p	
Number of patches (NP)	309.8	9.7	378.5	34.7	369.2	14.7	231.2	4.6	199.16	<0.001	All differences significant ($p < 0.001$)
Largest patch index (ha) (LPI)	8.2	2.1	4.3	1.1	2.4	0.3	11.5	2.2	54.71	<0.001	All differences significant ($p < 0.001$)
Mean patch area (ha) (AREA_MN)	6.2	0.2	5.1	0.5	3.4	0.1	12.3	0.2	2586.34	<0.001	All differences significant ($p < 0.001$)
Proximity index (PROX_MN)	331.7	106.6	191.2	39.4	69.6	12.9	840.8	176.9	89.90	<0.001	Status quo = random; other differences significant ($p < 0.001$)

the forest cover has stabilized and could even be increasing (Kronka et al., 2005), our results and those from other sites in the Atlantic Rainforest (Baptista and Rudel, 2006) and from other tropical regions (Neeff et al., 2006) suggest that stable or increasing

forest cover is a result of the replacement of older forests by younger forests. Moreover, from 2000 to 2005 more than 170,000 ha of Atlantic Rainforest were lost (Fundação SOS Mata Atlântica and INPE, 2008).

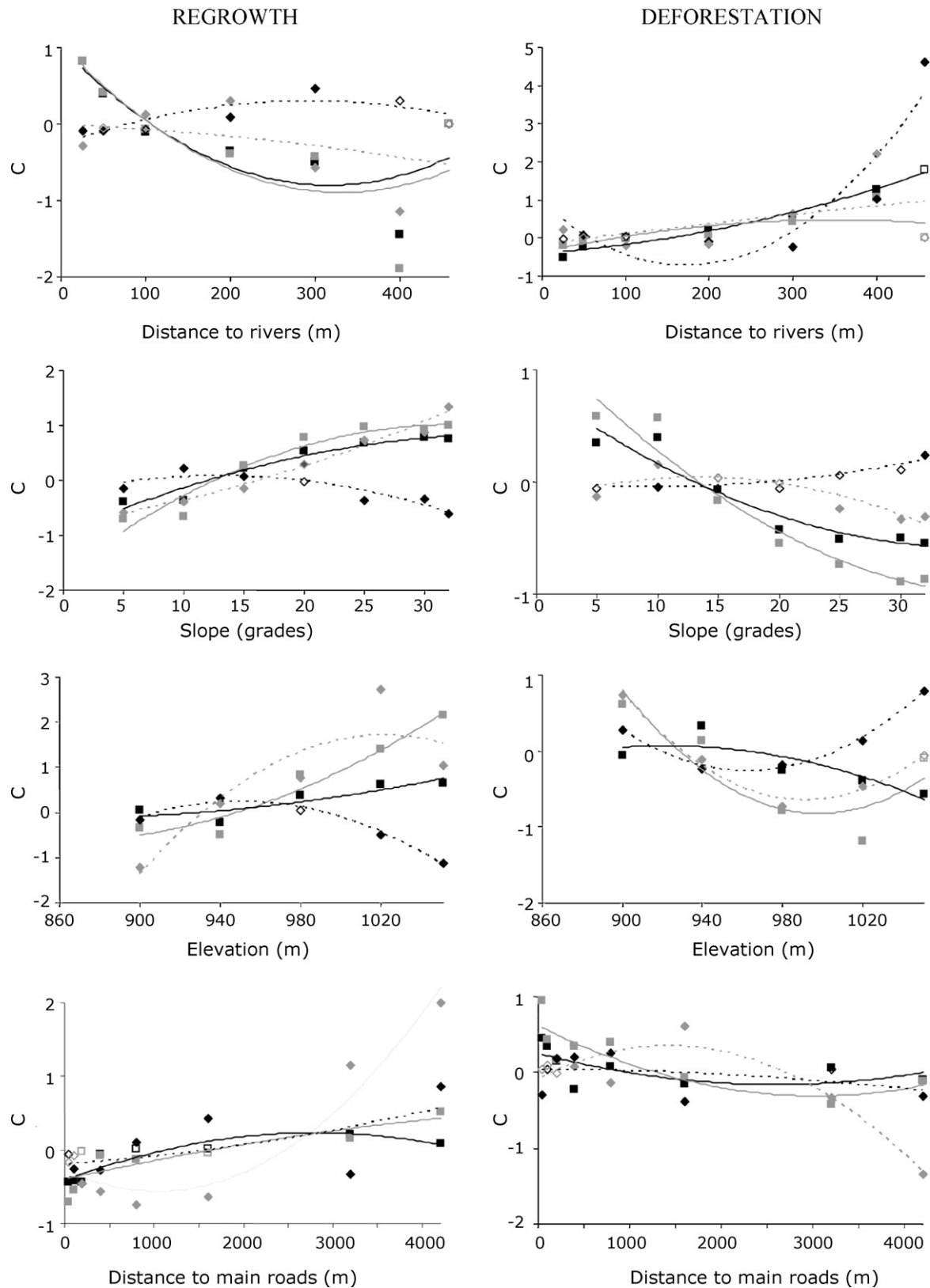


Fig. 5. Contrast values (C) obtained from the Weights of Evidence analyses for regrowth and deforestation showing the influence of some of the spatial determinants (proximity to rivers, slope, elevation, distance to main roads, and distance to urban areas). Positive values encourage a transition whereas negative values disfavor.

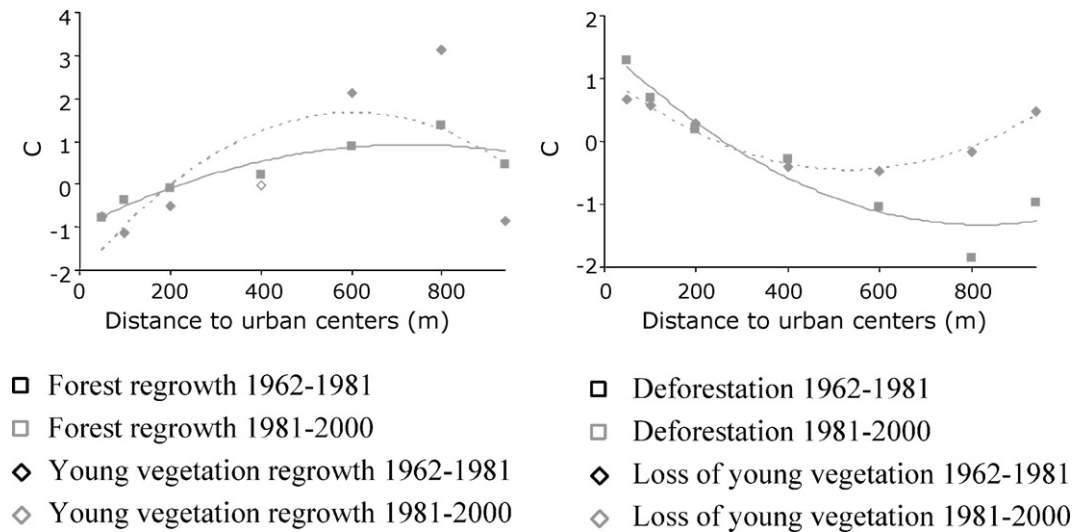


Fig. 5. (Continued).

The transformation of mature forest to secondary forests is a common process in the tropics (Brown and Lugo, 1990; Gehring et al., 2005; Mayaux et al., 2005; Wright, 2005), and has profound ecological effects, particularly related to CO₂ balance (Steininger, 2004) and species conservation (Chazdon, 2003; Wright and Muller-Landau, 2006; Gardner et al., 2007a). The secondary forest of Atlantic Rainforest can sustain a high diversity of birds (Dunn, 2004; Becker and Agreda, 2005; Uezu et al., 2005), small mammals (Wu et al., 1996; Pardini et al., 2005), frogs, reptiles (Dixo, 2005; Gardner et al., 2007b; Ficetola et al., 2008) and plants (Martin et al., 2004; Bernacci et al., 2006), thus those forests play an important role in species conservation. However, some of the most endangered and sensitive species have close relation with the structure and composition of primary forest, and thus need primary forests to survive. This seems to be particularly the case of 37 bird species in the study region (Develey and Metzger, 2006), native montane birds of Malaysia (Soha et al., 2006), and large mammals in the Brazilian Amazon (Parry et al., 2007). The conversion of forests in cultural landscape where young secondary forest fragments dominate hinders the survival of many species, hence reducing biodiversity (Gardner et al., 2007a).

The time interval adopted in this study is reasonable long (19 years) to embrace different short-term trends in the socio-economic drivers of deforestation and regrowth. Thereof, the observed landscape dynamics should be understood as a net result of these different short-term trends over the two time-periods under consideration. But, despite this broad temporal scale, it is possible to assert that the shift in the balance between deforestation and regrowth rates from 1962–1981 to 1981–2000 is a common tendency over the whole Atlantic Rainforest of São Paulo State (Dean, 1997). In the early 20th century, there was an increase in charcoal production in that region, mainly during the Second World War because of the oil supply crisis (Dean, 1997). Demand for charcoal decreased henceforth, thus contributing to a forest recovery as observed during the 1962–1981 time-period. Another plausible explanation for the intense forest regrowth can be attributed to the issue of forestry laws in 1965, constraining natural resources exploitation. This earlier time-period could suggest the beginning of a forest transition, i.e. the transition from deforestation to forestation (Rudel et al., 2005), however, the later time period (1981–2000) was characterized by the comeback of deforestation and decline of regrowth rates. Those changes are associated with the improvements of roads, which allowed better

access to the region, and to the expansion of large-scale agriculture that does not make use of fallow periods. This situation is common for most part of the Serra do Mar region, suggesting that forest regrowth is not a general process in Southern Brazil (Baptista and Rudel, 2006). For the study region, the rate of deforestation was even higher than the regional rates due to the close proximity to the city of São Paulo, thus reflecting a land speculation process triggered by the establishment of country houses and condominiums.

As observed in tropics, deforestation was higher near roads (Apan and Peterson, 1998; Tinker et al., 1998; Nagendra et al., 2003; Soares-Filho et al., 2004; Cabral et al., 2007) and in lower and less steep terrain where transport and mechanical agriculture are easier (Apan and Peterson, 1998). Deforestation was likely far from rivers, probably because those rivers are non-navigable and riparian vegetation is protected by environmental law. Native forest regrowth showed an opposite pattern for the same reasons, occurring far from roads, steep terrain and near rivers. Forest regrowth was also higher near young secondary vegetation. Guariguata and Ostertag (2001) and DeWalt et al. (2003) found a similar pattern suggesting that native vegetation patches work as a source of propagules for regrowth. Thus, loss of forest and the transformation of primary to secondary forests did not occur homogeneously or randomly; they were more likely to have occurred in sites more suitable for agriculture (Flamenco-Sandoval et al., 2007; Killeen et al., 2007; Fearnside, 2008). This common pattern of landscape dynamics (Pressey et al., 1996; Scott et al., 2001) points out the importance of valuing biodiversity in impacted sites when selecting areas for conservation (Margules and Pressey, 2000; Metzger and Casatti, 2006).

5.2. Implications of the modeled scenarios for conservation

Small changes in the transition matrix led to very distinct landscapes. Only the optimistic scenario (no deforestation allowed) increased forest cover and decreased the number of forest patches in the landscape. The increase of forest cover in the optimistic scenario was mostly due to forest regrowth, instead of agriculture abandonment. Those results suggest that forest preservation efforts should be accompanied by actions that could stimulate forest regrowth, especially where forest regrowth is more likely and land is less suitable for crop production. This scenario also showed that the application of the environmental

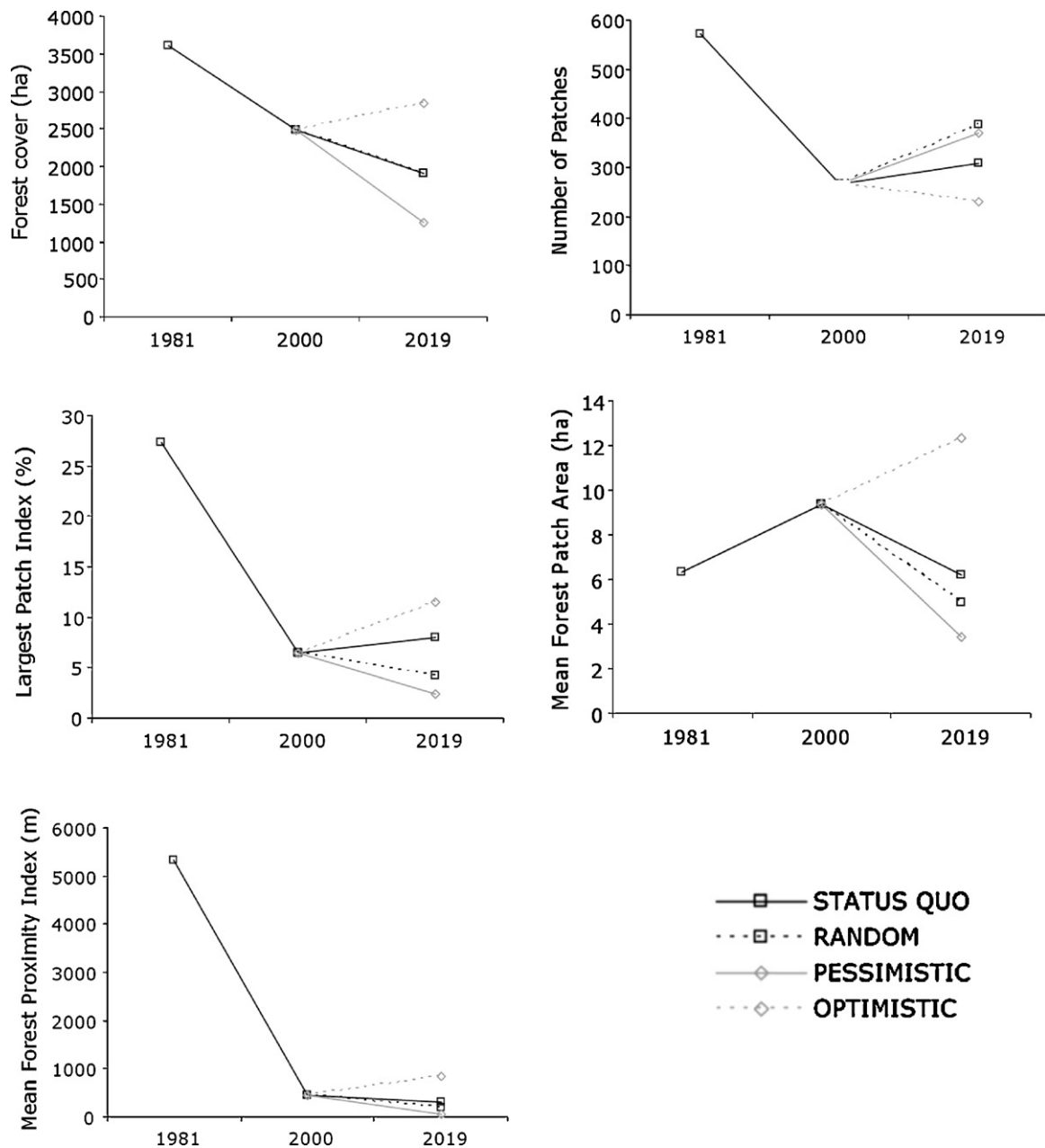


Fig. 6. Main changes in the forest cover and in the forest spatial configuration from 1981 to 2019 for the four modeled scenarios. NP: Number of forest patches; LPI: largest forest patch index; AREA_MN: mean forest patch area; PROX_MN: mean forest proximity index distribution.

laws could result in more forest cover in the short run without the need of expensive forest restoration investments.

The implications of landscape dynamics in conservation of forest biodiversity are paramount because many Atlantic Rain-forest species depend on large patches (Chiarello, 1999; Silva and Tabarelli, 2000; Maldonado-Coelho and Marini, 2004; Pardini et al., 2005; Uezu et al., 2005; Faria et al., 2007; Giraudo et al., 2008; Püttker et al., 2008), are edge intolerant (Stevens and Husband, 1998; Alvarenga and Pôrto, 2007; Hansbauer et al., 2008; Püttker et al., 2008; Santos et al., 2008) and thus respond positively to connectivity (Dário and Almeida, 2000; Silva and Tabarelli, 2000; Pardini et al., 2005; Uezu et al., 2005; Francisco et al., 2007; Nunes and Galetti, 2007). The optimistic scenario encompassed the best spatial configuration needed by forest species, allowing an increase of forest cover to 37.8% in 2019. That forest cover lies above the supposed fragmentation threshold of 30% of forest cover (Andrén,

1994), below which the effects of fragmentation tend to increase dramatically. Thus, the spatial configuration of the optimistic scenario would improve conservation of species that require larger forest areas (Pardini et al., 2005; Uezu et al., 2005; Faria et al., 2007; Uehara-Prado et al., 2007; Giraudo et al., 2008; Hansbauer et al., 2008). Conversely, the pessimistic scenario represents a real threat to the region's biodiversity because of its low forest cover (16.7%) and high isolation of forest fragments. In the pessimistic scenario, only species not sensitive to fragmentation are likely to occur. Those species would occur in a such unfavorable condition, given that they cannot cross the matrix or use its resources to extend their home range (Anjos, 2006; Bianconi et al., 2006; Faria, 2006; Lira et al., 2007; Umetsu and Pardini, 2007; Uezu et al., 2008; Umetsu et al., 2008). The *status quo* and *random* scenarios showed a different spatial distribution of the transitions between land-uses and land-covers, even though both were generated using the same

transition matrix. The *status quo* scenario resulted in a landscape more favorable for biodiversity conservation than the *random* scenario, indicating that when economic activities tend to form clusters, larger fragments of native vegetation remain, which favor directly biodiversity conservation (Franklin and Forman, 1987; Li et al., 1993; Forman and Mellinger, 1999; Metzger, 2001).

One of the main drivers of biodiversity impoverishment in tropical forests is land-use and land-cover changes (Sala et al., 2000). The inferences made in this study should be considered with caution because they were based solely on analysis of landscape spatial configuration. However, our approach can be useful when extensive biodiversity inventories or ecological data are not available or are difficult to obtain, as landscape metrics are strongly related to biodiversity indicators (Margules et al., 2002; Metzger, 2006). Within this context, historical studies describing land-use and land-cover dynamics and simulations of future landscapes represent a powerful tool to foresee the consequences of landscape dynamics on biodiversity conservation.

6. Conclusion

The Brazilian Atlantic Rainforest has experienced extensive changes in its land-use and land-cover during the last 100 years, with high rates of both deforestation and regrowth, resulting in a fragmented landscape dominated by progressively younger secondary forests. These changes have reduced the amount of habitat for forest species. Modeled scenarios indicated that simply the enforcement of current environmental laws could be very effective in increasing the forest cover and for improving the chance of forest species conservation. Conversely, if current deforestation and regrowth trends across the Atlantic Rainforest continue, native forest cover may reduce drastically, further threatening species that require large and undisturbed patches of native forest.

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