

# Natural forest regrowth under different land use intensities and landscape configurations in the Brazilian Atlantic Forest

Daniella Schweizer<sup>a,c,\*</sup>, Gunnar Petter<sup>d</sup>, Ricardo Gomes César<sup>b</sup>, Silvio Ferraz<sup>b</sup>,  
Vanessa de Souza Moreno<sup>b</sup>, Pedro H.S. Brancalion<sup>b</sup>, Harald Bugmann<sup>d</sup>

<sup>a</sup> ETH Zürich, Department of Environmental Systems Science, Ecosystem Management, CH-8092 Zurich, Switzerland

<sup>b</sup> Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Pádua Dias Av. 11, Piracicaba, SP 13400-970, Brazil

<sup>c</sup> Restor.eco, Fraumünsterstrasse 16, CH-8092 Zürich, Switzerland

<sup>d</sup> ETH Zürich, Department of Environmental Systems Science, Forest Ecology, CH-8092 Zurich, Switzerland

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## ABSTRACT

Natural forest regrowth is considered the most cost-effective strategy to promote large-scale forest restoration, but regrowth trajectories and their consequences for nature and people can be highly variable. This uncertainty may obstruct devoting land, time and resources in promoting this restoration approach. Process-based models allow to simulate forest regrowth under different scenarios and may thus support decision making to manage areas in ways that maximize forest restoration based on natural forest regrowth. In the present study, we used the process-based model LandClim to assess the following questions: 1) How does land use intensity affect forest growth, aboveground biomass (AGB) and tree species diversity in agricultural landscapes in the long term? 2) How do different land use configurations affect the structure and expansion of second-growth forests? We based our study on six 4 × 4 km agricultural landscapes, dominated by pastures and sugarcane, in the Brazilian Atlantic Forest region. We parameterized and validated LandClim for the study region by comparing model outputs with published estimates and information from field data collected across the six landscapes. We then simulated natural forest regrowth under different land use intensities in the six landscapes and analyzed how land use intensity and landscape configuration affect AGB, tree species diversity and the spatial dynamics of second-growth forests. Our results showed negative effects of increased land use intensity on landscape biomass accumulation due to limited forest cover expansion. Landscapes dominated by sugarcane had lower forest regrowth potential than pasture-dominated landscapes due to lower likelihood of abandonment, and limited rates of seed availability and seedling growth. Land use intensity and landscape configuration were also important factors for tree diversity changes. However, temporal patterns differed, and while AGB reached a plateau after 100–150 years, tree diversity peaked between 30 and 70 years. Thus, the effects of land use intensity and landscape configuration on forest AGB and tree diversity take decades to be fully expressed, highlighting the importance of a long-term commitment in restoration projects.

## 1. Introduction

Natural forest regrowth has generally been promoted as one of the main paths to achieve large-scale restoration (Chazdon and Guariguata, 2016; Crouzeilles et al., 2017), as it is more cost-effective and scalable than active restoration approaches (Strassburg et al., 2016; Molin et al., 2018). Tropical second-growth forests are particularly efficient in recovering carbon stocks (Poorter et al., 2016, 2021) and tree diversity (Rozendaal et al., 2019) while improving livelihoods (de Souza et al.,

2016).

Although forests are regenerating naturally across the Neotropics (Nanni et al., 2018), it is difficult to predict where and how regrowth will occur, as it can be driven by a myriad of biophysical and socio-economic factors at different spatial scales (Arroyo-Rodríguez et al., 2017; Borda-Niño et al., 2020). For example, at large spatial scales tree diversity is driven primarily by climate, topography and disturbance regimes (Arroyo-Rodríguez et al., 2017); yet, at the landscape scale factors such as connectivity, forest cover, and the size and shape of forest

\* Corresponding author.

E-mail address: [daniellaschweizer@gmail.com](mailto:daniellaschweizer@gmail.com) (D. Schweizer).

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remnants become relevant (Arroyo-Rodríguez et al., 2017; Crouzeilles et al., 2019a). In addition, specific land use practices can have crucial effects on landscape-wide forest regrowth dynamics (Molin et al., 2017; César et al., 2021).

After centuries of intense deforestation and the stabilization of native forest cover in the past two decades, the Atlantic Forest has featured a net increase of forest cover since 2005 (De Rezende et al., 2015; Rosa et al., 2021), due to large-scale natural regrowth and coordinated restoration efforts (Crouzeilles et al., 2019b). However, forest regrowth remains patchy (Ribeiro et al., 2009). Moreover, the regeneration potential on abandoned pastures and marginal agricultural lands has not yet been realized and management decisions to intensify land use threaten regrowth (Latawiec et al., 2015; Alves-Pinto et al., 2017). It is thus important to understand and predict the effect that current and potential land use management decisions and resulting landscape configurations have on Atlantic Forest regrowth in the long term. This understanding can inform management decisions that exploit the full potential of forest regrowth of landscapes and maximize restoration diversity and ecosystem service outcomes.

Empirically, one can analyze forest cover dynamics under different land use scenarios by space-for-time substitution, i.e. sampling across landscapes with different land use configurations (Walker et al., 2010), remote sensing of time series, or forest inventories. These types of studies, in the Atlantic Forest, have shown that the extent of remnant forests and the type of land use significantly affect attributes of secondary forests, such as biomass and species diversity (Molin et al., 2017; César et al., 2021).

Forest landscape models can complement empirical research by exploring temporal and spatial scales that are not accessible by traditional on-the-ground methods (Bugmann et al., 2014). Such models have widely been used to simulate the effects of biophysical factors (e.g., climate, disturbances; Petter et al., 2020; Elkin et al., 2013) and of human activities (e.g., forest management Thom et al., 2018; Rammer and Seidl, 2015) on long-term forest dynamics. These spatially-explicit models are generally suitable for simulations of complex landscapes in which forests and other land use types interact dynamically. Hence they could be valuable to explore the effects of land use management decisions on the structure, biomass accumulation, diversity and expansion of secondary forests. However, to date they have mainly been applied in boreal, temperate or Mediterranean regions (Petter et al., 2020).

Here, we present the first application of the forest landscape model LandClim in tropical forests. We validate the model and simulate the effects of different land use intensity scenarios and landscape configurations on the recovery trajectories of aboveground biomass (AGB) and tree diversity in second-growth forests within the Brazilian Atlantic Forest to assess the following questions: 1) How does land use intensity affect forest growth, aboveground biomass (AGB) and tree species diversity in agricultural landscapes in the long term? 2) How do different land use configurations affect the structure and expansion of second-growth forests? Answering these questions can support management decisions within ambitious restoration programs underway in this region, such as the Atlantic Forest Restoration Pact (Richards et al., 2015; Crouzeilles et al., 2019b), as well as other restoration programs across the tropics.

## 2. Materials and methods

### 2.1. Study area

The study area is located in the Corumbataí watershed in the interior of São Paulo State, southeastern Brazil. The basin encompasses an area of 1,700 km<sup>2</sup>. The region's climate is Cwa (dry-winter humid subtropical) according to the Köppen-Geiger classification system. The basin receives ~1,350 mm annual precipitation concentrated in the summer months between November and March (Atlas Ambiental, 2002). A mean annual temperature of ~20 °C is recorded, with a monthly minimum

around 15 °C and a maximum around 29 °C (Alvares et al., 2014). The landscapes of the study area are located at the ecotone between the Atlantic Forest and Cerrado (42% and 58% of the basin, respectively), with a range of vegetation types from open grasslands to dense woodlands (Durigan and Ratter, 2006). Elevation ranges from 470 to 1,060 m above sea level. We focused our study on Seasonal Semideciduous Forests, which occur both in the Atlantic Forest and the Cerrado. The main land use types in the basin are sugarcane (43.7%), extensive pastures (29.4%), native forest remnants (12.4%), and eucalypt plantations (7.3%) (Ferraz et al., 2014). Forest patches are scattered throughout the landscape, as native forest areas occur mainly along riparian buffers and on agriculturally marginal land.

For the simulations, we used six 4 × 4 km landscapes (Fig. 1, Table S1), which were selected based on a diversity-variability analysis (Ferraz et al. 2014). This analysis was conducted by dividing the basin into square grids of different sizes ranging from 1 to 5 km<sup>2</sup> and applying the Shannon landscape diversity index to each grid size. The final grid size was 4 × 4 km because it best captured the diversity of landscape configurations in the basin. The final selection of the landscapes was limited to areas that contained > 10% remnant forest to guarantee the presence of forest patches in the analysis. For a detailed description of landscape selection see Ferraz et al., 2014.

### 2.2. Forest landscape model

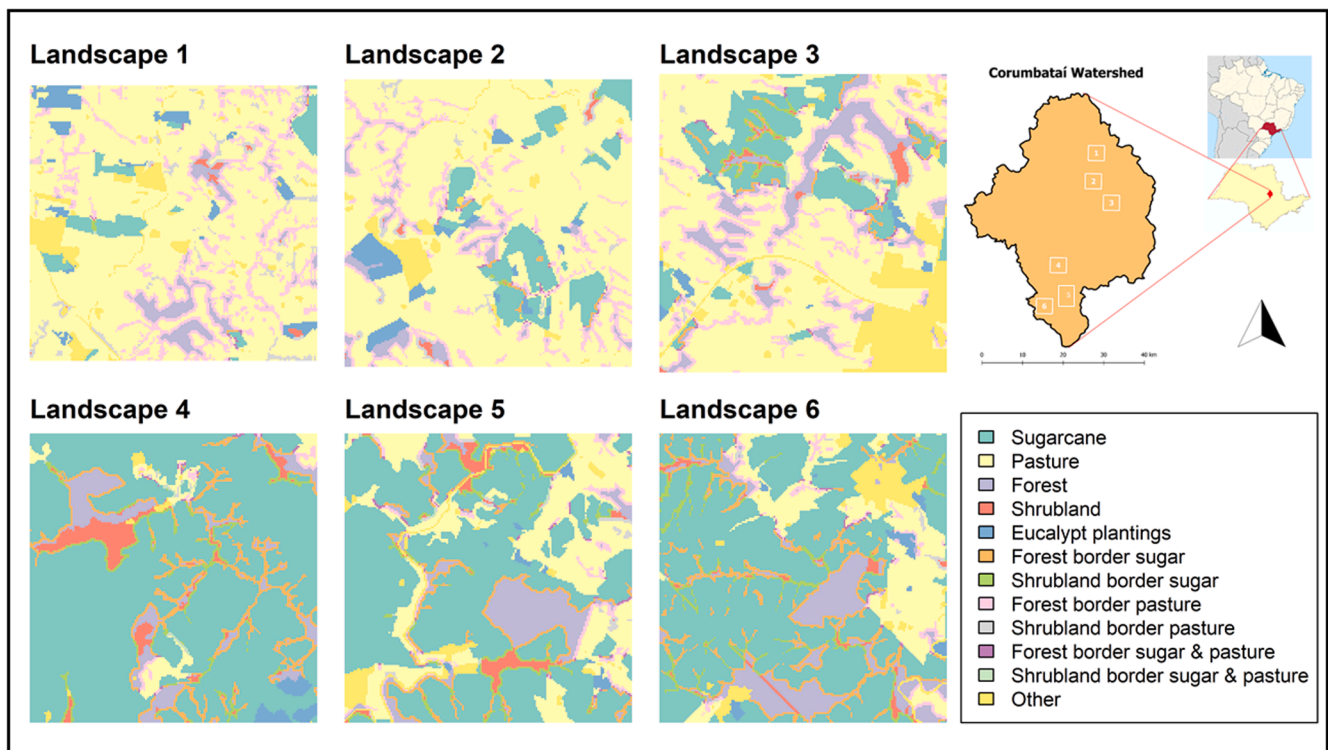
We employed the spatially explicit forest landscape model LandClim, which is commonly used to simulate temperate forest dynamics at the landscape level (~100–100,000 ha) over decades to centuries (Schumacher and Bugmann, 2006). In this model, the landscape is divided into grid cells (here 25 × 25 m) representing local environmental conditions (climate, terrain, and soil). Driven by the abiotic conditions in each grid cell, the establishment, growth and mortality of tree cohorts are modelled considering biotic interactions, mainly competition for light. In addition, spatial interactions between grid cells can be simulated, such as seed dispersal or the spread of fire or pathogens (Temperli et al., 2013). Each tree species represented in the model is characterized by a range of parameters specifying the species-specific life history traits and environmental tolerances.

### 2.3. Abiotic input data for the simulations

LandClim requires as input data a set of environmental attributes characterizing each grid cell across the landscape. The minimal set consists of elevation (m a.s.l.), slope (°), aspect (°), soil water holding capacity (WHC; cm), monthly mean temperatures (°C), and monthly precipitation sums (mm). Maps of land use types can also be used as input, and for each land use category specific model rules can be applied (e.g., different management rules). We used the land use classification maps (Fig. 1) developed by Ferraz et al. (2014).

Temperature and precipitation data from 1990 to 2010 were obtained from one weather station close to each study landscape ([https://www.cnpq.embrapa.br/projetos/bdclima/balanco/index/index\\_sp.html](https://www.cnpq.embrapa.br/projetos/bdclima/balanco/index/index_sp.html)). We selected a random sample of climate data from this period and used it as model input. This means that all simulations were conducted under the current climate and that climate change was not considered, as we were mainly interested in modelling the effect of landscape configuration and land use intensities without the interference of climatic effects, which remain difficult to predict.

The WHC describes the maximum amount of plant-available water that can be stored in the (upper) soil, it influences local soil moisture dynamics and thus sets the boundaries for the effects of drought stress on trees (Phillips et al., 2010). The WHC can hence be an important factor for growth and survival of trees (Ganatsios et al., 2021; Meza et al., 2018; Phillips et al., 2010). However, the importance of WHC for forest dynamics varies depending on the climate, edaphic conditions, and the local forest community. For instance, it has been observed that soil



**Fig. 1.** Land use configurations in the six  $4 \times 4$  km study landscapes. Landscapes 1 to 3 feature strong dominance by pastures, whereas in landscapes 4 to 6 sugarcane dominates. We added a separate coding for pixels surrounding forest that border pasture or sugarcane to model border effects of sugarcane or pasturelands on forests. See Ferraz et al. (2014) for original land use maps.

water uptake from greater soil depths is an important mechanism to sustain gross primary productivity during periods of low rain (Nepstad et al., 1994; Elliott et al., 2006). In forests where trees get most of their water from deep soil layers, WHC – which describes the capacity in the upper soil layers – may thus be less important (Broedel et al., 2017). Since we had no field data for WHC in the six landscapes, we tested the effect of this factor on simulated forest dynamics through a sensitivity analysis in which we used different WHC values (10, 20, 30 cm) and compared simulated forest dynamics. Under the prevailing climatic conditions, the effect of changes in this parameter in the model was minor, i.e., changes in WHC values did not have a significant effect on simulation results. On this basis, we decided to use a constant WHC of 20 cm across and within all landscapes.

In LandClim, terrain data (elevation, slope, aspect) are generally used to spatially extrapolate point data of temperature and precipitation based on lapse rates. Here, differences across landscapes are based exclusively on differences in the land use configuration and do not include differences in terrain properties, as we were interested in testing the effect solely of the management scenarios after model validation

#### 2.4. Model parameterization and validation

LandClim has been parameterized and validated for temperate forests in Europe and North America (Schumacher et al., 2004; Temperli et al., 2013). Therefore, in a first step, we parameterized and validated the model for the environmental conditions and species in the tropical, semideciduous Atlantic Forest as a prerequisite for simulating land use intensity scenarios. The main step in this regard was the determination of parameter values of a species pool that reflects Atlantic Forest woody species and with which the structure and dynamics of such forests can be adequately simulated.

LandClim requires the following species parameters to simulate forest dynamics: maximum age, age at maturity, maximum biomass growth rate ( $R_{max}$ ), maximum height, effective and maximum dispersal

distance, leaf habit, foliage type, minimum degree-days, minimum temperature, vegetative reproduction, tolerance to shade, drought, fire, browsing and nitrogen, and the presence of serotinous cones (see Table S2 for a description of each parameter).

Most of these parameters are not known for Atlantic Forest tree species. Therefore, we set initial parameter ranges that represent the empirical ranges across the native species based on literature values and discussions with experts. For those parameters that are not independent of each other, we also estimated correlations and their strengths (relative deviation from estimated trends). Maximum age and maximum biomass were negatively related to maximum growth rate, i.e., the faster a tree grows, the shorter its life span and the lower its wood density (Chen et al., 2017). Similarly, age at maturity, age of vegetative reproduction, and maximum height were positively correlated with maximum age. Shade and drought tolerance were positively correlated with maximum biomass, representing the later successional species. Uncorrelated parameters were allowed to randomly vary within pre-defined ranges, or they had fixed values (cf. Table S2).

After establishing the value ranges, we generated specific parameter values for single species by randomly sampling from the value ranges for all independent parameters. The values of the dependent parameters were estimated based on their correlations and correlation strength to the independent parameters within the ranges given. On this basis, we generated a species pool of 250 species, drawing the same number of species from each of the five shade tolerance classes (i.e., 50 species each). We used 250 species as this number represents the average richness in secondary forests of the study area (based on César et al., 2018) and initialized the model with the same number of species from each shade tolerance class

To validate the model, i.e., to test whether Atlantic forests can be reproduced adequately using the species pool generated, we used a homogeneous, flat landscape of one  $km^2$  that consisted of forest as the single land use type. We did not use the real landscapes where several land use types coexist (Fig. 1). We carried out simulation runs over 500

years, and evaluated the results based on the following criteria: (1) Total aboveground biomass (AGB) in the equilibrium state should be in the range of 200–350 Mg/ha. This range corresponds to values derived from studies in old-growth, semi-deciduous Atlantic Forests (Barbosa et al., 2014; Becknell et al., 2018), and particularly, based on a field sampling effort of over 3000 trees conducted in the landscapes we simulated (César et al., 2018); (2) the equilibrium state should be reached after around 300–400 years (Pugh et al., 2019); (3) the frequency distributions of age and diameter at breast height (DBH) should be realistically right-skewed as observed in the field (César et al., 2018); (4) the relative proportion of species should shift with time in favor of shade-tolerant species; and (5) species richness at the end of the simulation should be within the values observed in old-growth Atlantic Forests.

We ran simulations changing the ranges of one parameter at a time, while keeping all others within their initial value ranges (Table S2). We repeated the process for each species parameter, except those with fixed values. We identified four parameters that strongly affected model outputs: maximum age, maximum growth rate, maximum AGB and maximum height. Using a full-factorial design, we generated species pools under several combinations of the ranges of these parameters and carried out simulation runs. The parameter range combination that showed the best fit with the validation criteria was selected as the best set, and it formed the basis for the subsequent scenario simulations.

The process of generating the species pool contains a random element, and the model itself employs stochasticity to simulate many of the demographic processes. To assess the influence of these factors on the simulation results, we generated ten species pools using the best parameter combination (shown in Table S2) and carried out ten simulation runs per species pool. Relative to the validation criteria (cf. above), the results differed only marginally. Hence, we randomly selected one species pool with which all scenario simulations were carried out.

## 2.5. Scenario simulations

We defined three scenarios representing low, medium and high land use intensity. For each scenario, we adapted model parameters (e.g., seedling establishment probability, browsing intensity and fire disturbance parameters) in the different land use types (forest, pasture, silviculture, shrubland, sugarcane) to mimic different land use intensities (more details in Table S3).

The low-intensity scenario reflects the abandonment all productive land uses in the landscapes, i.e., sugarcane, pasturelands and eucalypt plantations. Seedlings were hence allowed to establish in these land use types. We used different establishment probabilities per land use to reflect hurdles for seedling establishment due to the former productive land use type, such as higher soil compaction on former sugarcane fields and presence of Eucalyptus stumps in former plantations (Holl, 1999; Table S3).

In the mid-intensity land use scenario, we simulated selective harvesting of eucalypt so that some adult eucalypt trees remained and natural recruitment of other tree species occurred beneath the plantation, as reported for this area (César et al., 2018). In addition, we simulated extensive cattle ranching, thus allowing natural tree recruitment to occur on the pastures in spite of grazing. We simulated grazing by increasing the browsing intensity parameter of LandClim. We also simulated fire occurrence as this is a common practice on extensive cattle ranching land, affecting tree recruitment on the pastures and the edges of forests and shrublands. We did not allow natural recruitment on sugarcane areas, which remained under cultivation with regular management-ignited fires extending into the forest-shrubland-border. This reflects the common past practice of burning the straw and allowing manual harvesting (Table S3).

The high-intensity land use scenario captures mechanized agricultural practices. Thus, we simulated the complete clear-cut of eucalypt and clearing of all understory vegetation so that no natural recruits

remained on the plantation areas. The only recruitment allowed in this scenario was that of eucalypt to simulate regular replanting. In addition, we mimicked intense cattle grazing on the pastures and on trees in the border areas of the remnant forests and shrublands by increasing the browsing intensity parameter. Tree seedlings were not allowed to recruit neither the pastures due to intense grazing and burning, nor on sugarcane areas. Sugarcane fields and pasture lands burned regularly (once a year) and affected the borders and the core areas of forests and shrublands (Table S3).

We excluded other productive land use types such as citrus plantations from the simulations as they covered small areas (classified as “Other” in Fig. 1).

In the study landscapes, the maximum age of forest remnants, estimated from remotely sensed data, was 53 years (Ferraz et al., 2014). However, several fragments had been present before the first remote sensing images were taken. Thus, we considered an average age of 80 years for older remnant forest patches in the landscape and carried out spin-up runs over 80 years to generate the remnant forest areas present across the landscapes. These landscapes served as the starting point to our scenario simulations, with the simulations running for 200 years into the future in each landscape under the three scenarios.

## 2.6. Analysis of simulation results

We evaluated the variations in woody AGB and tree species diversity across time for each of the six landscapes in each of the three land use intensity scenarios. We mapped variations in AGB changes per cell and mapped changes in the Shannon species diversity index, based on the AGB of the different species in each cell across the landscapes. We used linear regression to assess the effects of (1) the ratio of forest to sugarcane and pasture areas, (2) the ratio of forest border to core areas (estimated as the number of cells classified as forest core versus forest border), (3) the intensity scenarios (low, medium, high), and (4) time on (a) biomass change in time across the landscape (per hectare), (b) tree species diversity (Shannon index based on average biomass per species in the landscape), (c) average species number per landscape and (d) ratio of shade-tolerant to shade-intolerant species aggregated into classes of shade tolerance (1 to 5). We evaluated all possible explanatory variable combinations, tested the significance of the relationships using ANOVA, and compared the models based on the AIC.

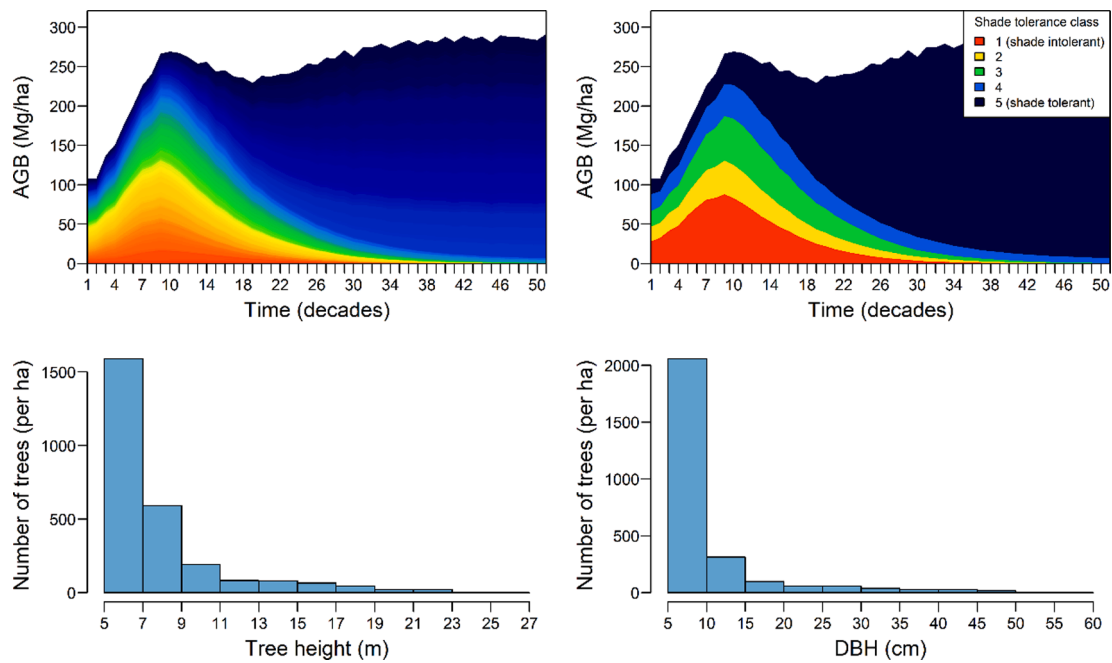
## 3. Results

### 3.1. Model validation

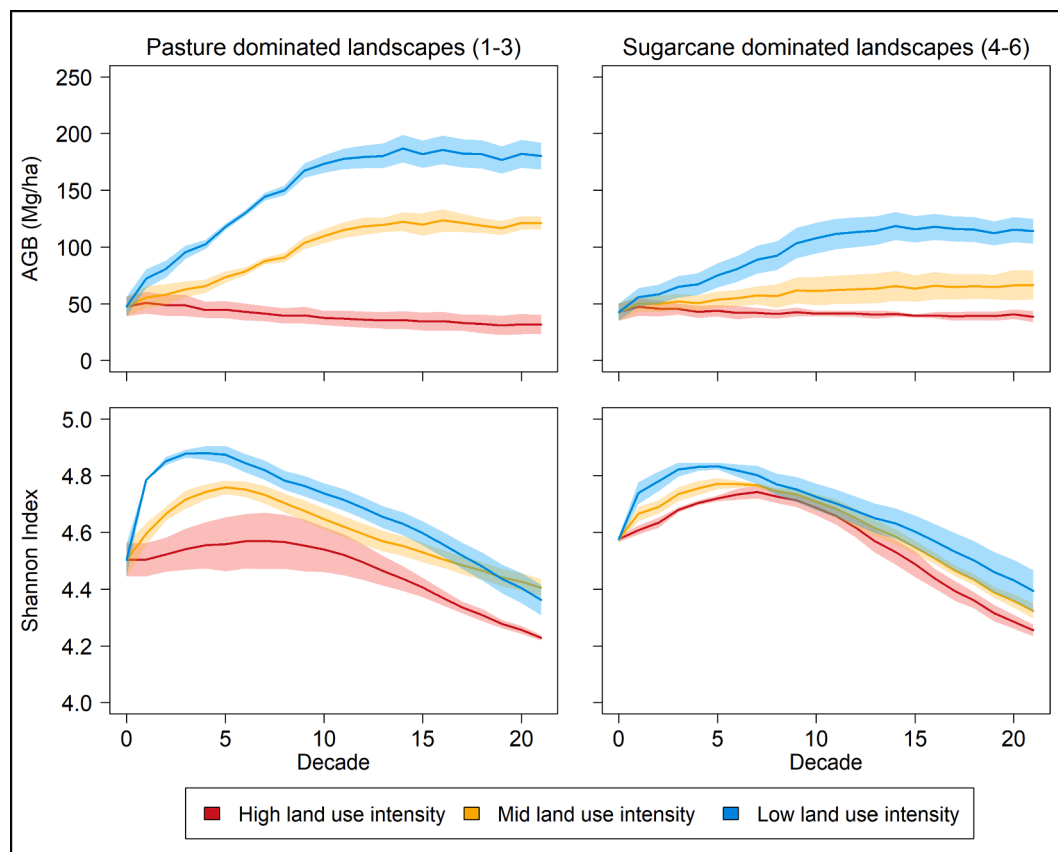
LandClim yielded aboveground biomass (AGB) values of c. 250–280 Mg/ha in the equilibrium state after decade 30 (Fig. 2A). After an initial increase, shade-intolerant pioneer species decreased in number during forest succession (Fig. 2B). The DBH and height distribution of the trees at the end of the simulation were right-skewed, with most tree individuals between 5 and 7 m in height and 5 and 10 cm in DBH. Trees obtained a maximum height of 25 m and a maximum DBH of 60 cm (Fig. 2C & 2D). The simulated forest at equilibrium retained over 120 species.

### 3.2. Effects of land use intensity on biomass and tree diversity dynamics

We found a significant effect of land use intensity on AGB and diversity changes. In the case of biomass, the effects of increasing land use intensity became stronger with time (Fig. 3, Table 1). In the low intensity scenario, average AGB across the landscape consistently increased to reach a peak at around 12 decades, while in the medium and high intensity scenarios, AGB accumulated progressively less with time. In the high intensity scenario, AGB remained almost constant or decreased even slightly through time across all landscapes, regardless of land use configuration (Fig. 3). In addition, in sugarcane-dominated



**Fig. 2.** Model validation results. A) Aboveground biomass (AGB) trajectory across time, with each shaded line representing a species within a shade tolerance class, B) Species aggregated by shade tolerance groups (red: shade intolerant, dark blue: shade tolerant), C) Height distribution in equilibrium state, D) Diameter at breast height (DBH) distribution in equilibrium state (reached after 30 decades). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Average aboveground biomass (AGB) and tree diversity changes across the landscapes through time. We combined landscapes as being dominated by pasturelands (left panels) vs. sugarcane plantations (right panels).

**Table 1**

ANOVA of best model relating landscape scale AGB and diversity changes across time for the six landscapes.

Change of AGB per hectare ( $R^2 = 0.86$ )					
Source	Df	MS	F	p	Effect size
Time	1	82,177	520.89	<0.0001	0.193
Core to edge ratio of forest	1	23,024	145.94	<0.0001	0.054
Time $\times$ Land use intensity	2	131,239	831.87	<0.0001	0.615
Residuals	373	158			
Shannon index ( $R^2 = 0.62$ )					
Time	1	3.527	415.48	<0.0001	0.416
Land use intensity	2	0.775	91.34	<0.0001	0.183
Core to edge ratio of forest	1	0.061	7.23	<0.0001	0.022
Forest to sugarcane ratio	1	0.188	22.13	0.007	0.006
Residuals	372	0.008			

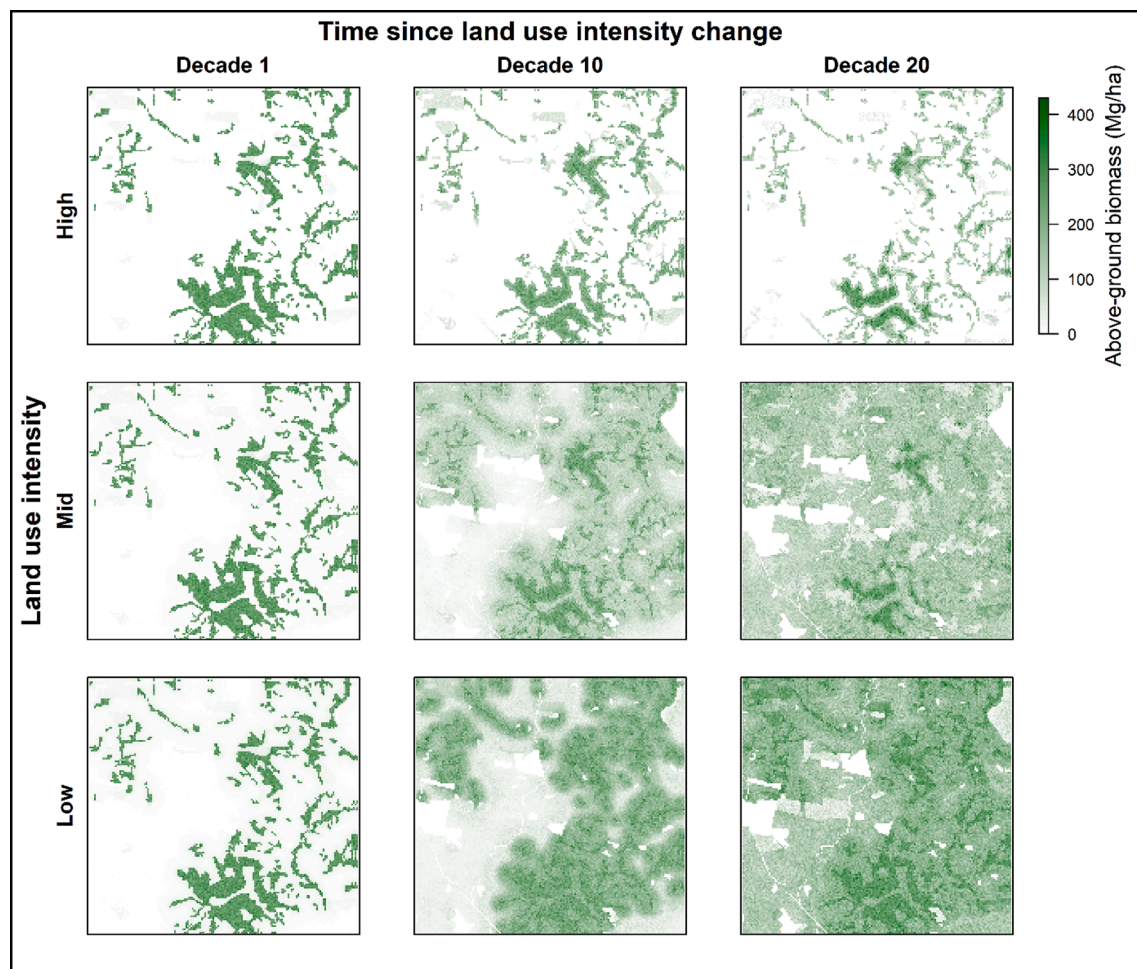
landscapes, AGB values remained lower through time and AGB accumulated at a lower rate than in landscapes dominated by pasturelands, regardless of land use intensity. Tree species diversity, expressed as the landscape-wide Shannon index based on AGB per species, initially increased regardless of land use intensity, peaked at around three to eight decades, and decreased thereafter (Fig. 3). Land use intensity and the dominant land use type across the landscape affected only slightly the rate of diversity changes and the maximum tree diversity that were reached per landscape. However, after 15 decades, the differences between the low and medium land use intensity scenario disappeared in most landscapes.

In the high intensity land use scenario, AGB values  $> 250$  Mg/ha were limited to forest and shrubland remnants that had already been present in the landscape at the beginning of the simulation, as there was no natural forest regrowth on pasturelands (Fig. 4). In addition, in the high intensity scenario fire and grazing in the pasturelands and sugarcane fields reduced AGB along the edge of the forest and shrubland patches (Fig. 4). In the mid land use intensity scenario, trees established in pastures, but the extensive cattle grazing management regime limited AGB values to a maximum of 200 Mg/ha in most areas. In the low intensity scenario, which includes the abandonment of all productive land use types (sugarcane, silviculture, and pastures), trees established across the landscape and biomass reached values  $> 200$  Mg/ha in most of the area (Fig. 4, Figs. S1–S5).

We found that early in the succession ( $<5$  decades), tree diversity increased outside core forest areas in the mid and low intensity scenarios, but then showed a decreasing tendency with time. In the high intensity scenario, tree diversity within forest remnants diminished through time due to fire and grazing (Fig. 5). Comparing the six landscapes, tree diversity was reduced when the dominant land use type was sugarcane compared to pasture, nearly independent of land use intensity (Figs. S6 to S10).

### 3.3. Effects of landscape configuration on biomass and tree diversity dynamics

Landscape configuration affected AGB and tree diversity. The ratio of forest core to forest edge was significant in the best models explaining



**Fig. 4.** Aboveground biomass (AGB) accumulation through natural forest regrowth in landscape 1, for the three land use intensity scenarios and three specific periods. Maps for the other five landscapes can be found in the Supplementary Material (Figs. S1–S5).

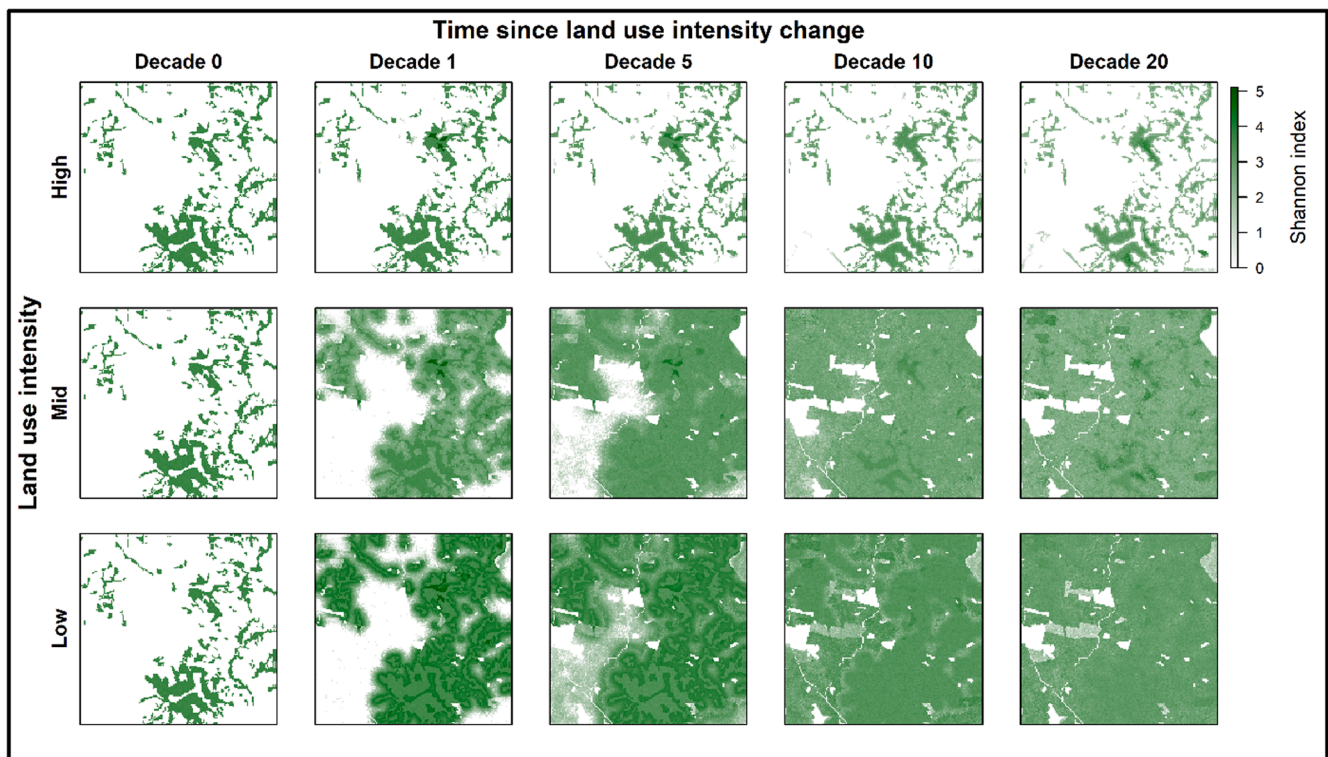


Fig. 5. Tree diversity across landscape 1 at different time steps under different land use intensity scenarios. Results for the other five landscapes can be found in the Supplementary Material (Figs. S6 to S10).

the changes of AGB and tree diversity: the larger the core forest area, the less likely it was that management actions such as fire or grazing affected AGB or diversity accumulation through time (Table 1). Species numbers and the ratio of shade-tolerant to shade-intolerant species were significantly related to the ratio of forest to sugarcane and the land use intensity scenario (Table S4). Land use intensity and time were also highly significant in the models, i.e., the overall effects of land use configuration on AGB accumulation and tree diversity became clearly evident after multiple decades only.

## 4. Discussion

### 4.1. Model validation

Our work presents the first application of LandClim in tropical forests. LandClim was originally parameterized for temperate tree species and has been tested in several studies across Europe and in the United States (Briner et al., 2012; Temperli et al., 2012; Schwörer et al., 2016; Thrippleton et al., 2018; Schuler et al., 2019; Petter et al., 2020). We demonstrated that LandClim can also be applied to simulate the dynamics of AGB and tree diversity in tropical forest landscapes, such as the highly threatened and fragmented Brazilian Atlantic Forest.

We obtained AGB values of around 250 Mg/ha after ~10 decades of succession, reaching an equilibrium state after approximately 30 decades, is within the range of values for biomass observed in old-growth Atlantic Forest sites and in other Neotropical forest ecosystems (Aide et al., 2000; Martin et al., 2013; Poorter et al., 2016; Poorter et al., 2021). In addition, the simulated AGB values agree with second-growth remnant forest patches found within the study area (César et al., 2018).

As tropical old-growth forests harbor a higher diversity of species than temperate forests, another important validation aspect was whether our simulated forests retained a realistic number of species in the old-growth stage. Indeed, simulated forests at equilibrium retained over 120 species after 50 decades, a value within the range of many estimates from tropical old-growth forests (e.g., Guariguata et al., 1997;

Goosem et al., 2016; Rozendaal et al., 2019). Yet, this value is lower than the number of species found in the study areas by César et al., (2018), possibly due to a simulation time of 200 years, compared to an average age of 50 years for the forest remnants in the study landscapes and thus the longer effect of community interactions, such as competition, on species richness.

The reverse J-shaped distribution of DBH, with the highest number of stems in the smaller diameter classes, i.e., at around 5 to 10 cm (Fig. 2D), resembles the shape of the distribution observed in old-growth tropical and subtropical forests (i.e., do Nascimento et al., 2014; Gonçalves et al., 2017; Gebeyehu et al., 2019). The simulated stem density in the equilibrium state of ~620 trees per ha for all trees > 10 cm DBH is in the range for Neotropical forests, which is typically 500–700 stems per hectare (Banin et al., 2012; Chao et al., 2008). Likewise, the simulated stem density of ~230 trees per ha for all trees > 20 cm DBH agrees with the values reported by César et al. (2018) for reference forests in the Corumbataí basin. However, the number of simulated trees in the diameter class 5–20 cm (~2500) is larger than observed by César et al. (2018). This could be due to the structure of LandClim, in which trees are introduced into the community not as seedlings but as saplings and are counted for the first time when they are already slightly above 5 cm in DBH. This approach results in a disproportionately large fraction of small trees in the 5–7 cm DBH class. This approach could be improved to better represent the small size classes in the simulations. However, these classes represent only a very small fraction of total biomass, and therefore this inaccuracy does not significantly affect the simulation results of total AGB and diversity.

Initializing the simulation with the same proportion of shade-tolerant and intolerant species (50 species each), we observed the expected shift in biomass of species in different shade tolerance classes with succession. After an initial increase in the biomass of the shade intolerant species, the shade tolerant species started to gain dominance after c. 10 decades, which agrees well e.g. with the Neotropical secondary forest succession depicted by Guariguata and Ostertag (2001). Some shade intolerant species were able to persist over time. This

pattern relates to natural gap dynamics (Tabarelli and Mantovani, 2000), which are characteristic of both the model and reality (Chazdon, 2008; Lohbeck et al., 2014; Marcilio-Silva et al., 2016).

#### 4.2. Effects of land use intensity on biomass and tree diversity dynamics

We observed strong effects of land use intensity on biomass and tree diversity dynamics in our simulations, both when averaged over the entire landscape (Fig. 3) and also in terms of the spatial patterns in the landscape (Figs. 4 and 5).

In the low and mid intensity scenarios, the average AGB values reached a plateau after 12 decades of simulation. The fastest accumulation and highest AGB values were observed on the abandoned pastures in the low intensity scenarios, while extensive cattle grazing in the mid intensity scenarios only allowed forests with low stocking density to establish. The low seedling establishment probabilities on abandoned sugar cane fields in the low intensity scenario as a consequence of soil compaction, which led to low forest biomass on this land use type, even when land use intensity decreased. The decrease of the average AGB in the high land use intensity scenarios was a result of the limited area available for forest regrowth in combination with frequent disturbances at the forest borders due to cattle grazing (pastures) and fires (sugarcane), which typically occur in this area when intensively managed (César et al., 2021; Rosa et al., 2021). At the start of the simulations, the forest remnants were undisturbed, and the subsequent forest loss due to disturbances was higher than forest regrowth, i.e., the overall net AGB balance was negative.

Differences between the land use intensity scenarios were also evident with respect to tree diversity. The general increase in tree diversity in the first decades was a result of forest expansion and the colonization of early-successional tree species in the new forest areas, which were rare in the forest remnants at the beginning of the simulation. Even in the high intensity areas, diversity initially increased as succession proceeded in the shrubland patches. Increases in diversity during early succession are typical and have been documented for sites across the Atlantic Forest (Liebsch et al., 2008). In the low intensity pasture areas, where forest growth was less restricted, a rich tree community with species from all shade tolerance classes established in the first decades, similarly to what was observed in the validation runs (Fig. 2). In contrast, in the mid intensity pastures and sugarcane fields, tree diversity was lower since the restrictions to the establishment that had been imposed in the simulation allowed fewer species to colonize these areas. After the initial increase, tree diversity decreased in all scenarios, which can be related to forests reaching an equilibrium, which in turn resulted in increased competition for light among species and competitive exclusion of light demanding species. This declining trend of diversity in the late successional stages agrees with theoretical expectations (Guariguata and Ostertag, 2001) and was observed in other studies under both high land use intensity and land abandonment (Niedrist et al., 2009).

#### 4.3. Effects of landscape configuration on biomass and tree diversity dynamics

The effect of land use intensity on AGB and diversity changed depending on the configuration of the land use types. Differences in the ratio of forest versus sugarcane, as well as the ratio of forest core area and forest edge were significant factors explaining variations in AGB and tree diversity in the simulations. In areas with a low forest to pasture ratio, land use intensity did not affect AGB as much as in areas with a low forest to sugarcane ratio. Interestingly, this effect was not linear for tree diversity. Tree diversity stayed between values of 4.4 and 4.8 (Shannon index) across all six landscapes, regardless of the dominant land use type. Empirical work in the study areas found that the effect of neighboring land use type, mainly sugarcane, on tree diversity and AGB of secondary forests was greater than that of other factors such as patch age

(Molin et al., 2017; César et al., 2021). Our model allowed to elucidate that these effects become much better visible and significant after several years, thus emphasizing the importance of a long-term perspective for planning sustainable management strategies.

Lastly, our simulation showed that, under appropriate land use conditions, forests can regrow quickly and accumulate biomass, which corroborates previous research on the role of natural forest regrowth for achieving large-scale forest restoration and mitigating climate change (Chazdon et al., 2016; Poorter et al., 2021). However, the spatial pattern of land use, such as higher or lower prevalence of degraded pasturelands and the proximity of forest remnants, will strongly co-determine the temporal development and quality (in terms of AGB and species richness) of second-growth forests (César et al., 2021).

#### 4.4. Methodological considerations

Using LandClim, we were able to simulate long-term second-growth forest expansion based on the characteristics of land use types that currently occur in the Atlantic Forest region, and our simulations yielded plausible results. However, due to the lack of comparable long-term experiments for model validation, they should clearly be considered as scenarios rather than real-world predictions. We had to make several strong assumptions regarding the factors affecting forest dynamics in the different land use types, such as establishment probabilities or probabilities of fire disturbances, which influence spatial landscape dynamics. These assumptions are mainly based on expert knowledge rather than on empirical data. Accordingly, our simulations can demonstrate forest dynamics and the effects of land use parameters under the conditions assumed, but further experiments and more detailed analyses of existing data are needed to increase the specificity of the predictions.

LandClim allows for simulating forest landscape dynamics across large spatial and temporal extents, yet our use of LandClim to simulate Atlantic Forest regrowth relied on several assumptions and simplifications that may lead to biases. The main challenge was to obtain species parameters for the Atlantic Forest flora. We generated species pools based on life history parameter ranges found in the literature and through discussion with experts. This approach was sufficient to reproduce the main characteristics of Atlantic Forest remnants, yet it is obviously not sufficient to estimate the dynamics of specific real-world species. Consequently, the LandClim application presented here is not appropriate to provide information for managing specific species, which is a commonly monitored indicator of restoration success (e.g., Aide et al., 2000).

In addition, grouping species into five shade tolerance classes simplifies trees life history strategies, as shade tolerance should ideally be treated as a continuous variable (Lienard et al., 2015). We recommend further research on species life history traits for the improvement of model-based predictions of forest regrowth.

We also had to simplify the study landscapes in terms of their physical properties related to soil, climate and topography. If more accurate measurement data had been available, this could have led to a more differentiated view on forest regrowth predictions across the landscapes. We, however, were mainly interested in the effects of land use intensity and land use type configurations as drivers of change of the extent and quality of forest regrowth, and therefore we decided to treat the physical parameters of the landscapes as homogenous.

We used a constant WHC value of 20 cm based on a sensitivity analysis, in which the WHC had only minor effects on the model results. In reality, changes in WHC may have a larger effect than in the model. However, we are not aware of studies from that area analyzing and quantifying this effect. In our case, we are confident that the choice of a constant WHC is appropriate, because we were not simulating effects of climate change, i.e., all simulations were carried out under the prevailing climate conditions, and for these conditions, the model was validated. If the effects of climate change were to be simulated, the WHC would be of critical importance and more attention would need to be

paid to this factor. Lastly, for our scenarios, we assumed that the landscape configuration is constant over 200 years, while in reality it is most likely to be quite dynamic. For example, if biofuel demands continue to increase, as occurred in the past decades (Durigan and Ratter, 2006), sugarcane is most likely to replace pastures and thus reduce the regrowth potential for forests in the Atlantic Forest landscapes.

Overall, we were able to demonstrate that LandClim can be successfully employed in tropical forest ecosystems in a restoration context, yet its application can certainly be improved by expanding research on tropical trees' life history traits, biophysical conditions and management approaches in human-modified tropical landscapes.

## 5. Conclusions

The Atlantic Forest is a global hotspot for tropical rainforest restoration (Brancalion et al., 2019), yet human-induced disturbances arising from land use decisions continue to threaten remnant forest areas and limit forest regrowth (De Lima et al., 2020; Rosa et al., 2021), with negative impacts for biodiversity and carbon stocks (De Lima et al., 2020). Our study shows that forest landscape restoration planning must consider the critical role of human-induced disturbances in shaping regrowth trajectories and the achievement of environmental benefits.

A model such as LandClim can serve land use planners, restoration practitioners and managers in general to foresee how different land use decisions and policies can affect, positively or negatively, natural forest regrowth. Several recent papers aimed to identify priority areas for ecosystem restoration (e.g. Brancalion et al., 2019; Strassburg et al., 2020), but none of them considered land use intensities as disturbance regimes that can determine restoration success, which highlights the potential contribution of our study for future prioritization.

Land abandonment and tree expansion have been documented across the globe, for example in Europe (Lasanta et al., 2017; Janus and Bozek, 2019) and Latin America (Aide et al., 2013; Nanni et al., 2018). Under current economic and social trends, land abandonment may continue in marginal agricultural areas in the Atlantic Forest of Brazil, such as those studied here (Baptista and Rudel, 2006; Walker, 2012; De Rezende et al., 2015; Bicudo da Silva et al., 2017). This indicates that natural forest regrowth on abandoned pasturelands is a likely scenario for upscaling restoration in the Atlantic Forest in the near future. In addition, incentives for landowners to allow marginal, less productive pasture areas to regenerate back to forest can be an important strategy employed to upscale restoration (Latawiec et al., 2015).

The ability to improve predictions regarding where and how natural forest regrowth is more likely to occur, and to simulate scenarios under various land use intensity strategies, is key to prioritize areas for forest restoration aimed at achieving current global restoration targets, such as the Bonn Challenge, and other restoration commitments to be made between 2021 and 2030, during the United Nations Decade on Ecosystem Restoration.

## CRediT authorship contribution statement

**Daniella Schweizer:** Conceptualization, Methodology, Formal analysis, Validation, Writing – original draft. **Gunnar Petter:** Methodology, Formal analysis, Validation, Writing – original draft, Visualization. **Ricardo Gomes César:** . **Silvio Ferraz:** . **Vanessa de Souza Moreno:** . **Pedro H.S. Brancalion:** Conceptualization, Supervision. **Harald Bugmann:** Supervision.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120012>.

## References

- Aide, T.M., Clark, M.L., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M.J., Muñoz, M., 2013. Deforestation and Reforestation of latin America and the Caribbean (2001–2010). *Biotropica* 45 (2), 262–271.
- Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. *Restor. Ecol.* 8 (4), 328–338.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2014. Köppen's climate classification map for Brazil. *Meteorologist Zeitschrift* 22 (6), 711–728.
- Alves-Pinto, H.N., Latawiec, A.E., Strassburg, B.B.N., Barros, F.S.M., Sansevero, J.B.B., Iribarem, A., Crouzeilles, R., Lemgruber, L., C. Rangel, M., Silva, A.C.P., 2017. Reconciling rural development and ecological restoration: Strategies and policy recommendations for the Brazilian Atlantic Forest. *Land Use Policy* 60, 419–426.
- Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biol. Rev.* 92 (1), 326–340.
- Atlas Ambiental, 2002. ATLAS AMBIENTAL da bacia do rio Corumbataí. Available in: <<http://www.rc.unesp.br/igce/ceapla/atlas>> (15 May 2002).
- Banin, L., Feldpausch, T., Phillips, O., Baker, T., Lloyd, J., Affum-Baffoe, K., Arets, E., Berry, N., Bradford, M., Brien, R., Davies, S., Drescher, M., Higuchi, N., Hilbert, D., Hladik, A., Iida, Y., Kamariah, A.S., Kassim, A.R., King, D.A., Lewis, S., 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecol. Biogeogr.* n/a–n/a.
- Baptista, S.R., Rudel, T.K., 2006. A re-emerging Atlantic forest? Urbanization, industrialization and the forest transition in Santa Catarina, southern Brazil. *Environ. Conserv.* 33, 195–202.
- Barbosa, J.M., Melendez-Pastor, I., Navarro-Pedreño, J., Bitencourt, M.D., 2014. Remotely sensed biomass over steep slopes: An evaluation among successional stands of the Atlantic Forest, Brazil. *ISPRS J. Photogramm. Remote Sens.* 88, 91–100.
- Becknell, J.M., Keller, M., Piotto, D., Longo, M., Nara dos-Santos, M., Scaranello, M.A., Bruno de Oliveira Cavalcante, R., Porder, S., 2018. Landscape-scale lidar analysis of aboveground biomass distribution in secondary Brazilian Atlantic Forest. *Biotropica* 50 (3), 520–530.
- Bicudo da Silva, R.F., Batistella, M., Moran, E.F., Lu, D., 2017. Land Changes Fostering Atlantic Forest Transition in Brazil: Evidence from the Paraíba Valley. *The Professional Geographer* 69 (1), 80–93.
- Borda-Niño, M., Meli, P., Brancalion, P.H.S., 2020. Drivers of tropical forest cover increase: A systematic review. *Land Degrad. Dev.* 31 (11), 1366–1379.
- Brancalion, P.H.S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F.S.M., Almeida Zambrano, A.M., Baccini, A., Aronson, J., Goetz, S., Reid, J.L., Strassburg, B.B.N., Wilson, S., Chazdon, R.L., 2019. Global restoration opportunities in tropical rainforest landscapes. *Science. Advances* 5, eaav3223.
- Briner, S., Elkin, C., Huber, R., Grêt-Regamey, A., 2012. Assessing the impacts of economic and climate changes on land-use in mountain regions: A spatial dynamic modeling approach. *Agric. Ecosyst. Environ.* 149, 50–63.
- Broedel, E., Tomasella, J., Cândido, L.A., von Randow, C., 2017. Deep soil water dynamics in an undisturbed primary forest in central Amazonia: Differences between normal years and the 2005 drought. *Hydrol. Process.* 31 (9), 1749–1759.
- Bugmann, H., Coomes, D.A., Burslem, D.F.R.P., Simonson, W.D., 2014. Forests in a greenhouse atmosphere: predicting the unpredictable? In: Coomes, D.A., Burslem, D. F.R.P., Simonson, W.D. (Eds.), *Forests and Global Change*. Cambridge University Press, Cambridge, pp. 359–380. <https://doi.org/10.1017/CBO9781107323506.017>.
- César, R.G., Moreno, V.S., Coletta, G.D., Chazdon, R.L., Ferraz, S.F.B., de Almeida, D.R. A., Brancalion, P.H.S., 2018. Early ecological outcomes of natural regeneration and tree plantations for restoring agricultural landscapes. *Ecol. Appl.* 28 (2), 373–384.
- César, R.G., Moreno, V.d.S., Coletta, G.D., Schweizer, D., Chazdon, R.L., Barlow, J., Ferraz, S.F.B., Crouzeilles, R., Brancalion, P.H.S., 2021. It is not just about time: Agricultural practices and surrounding forest cover affect secondary forest recovery in agricultural landscapes. *Biotropica* 53 (2), 496–508.

- Chao, K.-J., Phillips, O.L., Gloor, E., Monteagudo, A., Torres-Lezama, A., Martínez, R.V., 2008. Growth and wood density predict tree mortality in Amazon forests. *J. Ecol.* 96 (2), 281–292.
- Chazdon, R.L., 2008. Chance and determinism in tropical forest succession. In: Carson, W.P., Schnitzer, S.A. (Eds.), *Tropical forest community ecology*. Blackwell Scientific, Oxford, UK, pp. 384–408.
- Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Almeyda Zambrano, A.M., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Duran, S.M., Espirito-Santo, M.M., Fandino, M.C., Cesar, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., Orihuela-Belmonte, E., Peña-Claros, M., Perez-Garcia, E.A., Piotto, D., Powers, J.S., Rodriguez-Velazquez, J., Romero-Perez, I.E., Ruiz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Poorter, L., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* 2, 10.
- Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica* 48 (6), 716–730.
- Chen, L., Xiang, W., Wu, H., Lei, P., Zhang, S., Ouyang, S., Deng, X., Fang, X., 2017. Tree growth traits and social status affect the wood density of pioneer species in secondary subtropical forest. *Ecol. Evol.* 7 (14), 5366–5377.
- Crouzeilles, R., Barros, F.S.M., Molin, P.G., Ferreira, M.S., Junqueira, A.B., Chazdon, R.L., Lindenmayer, D.B., Tymus, J.R.C., Strassburg, B.B.N., Brancalion, P.H.S., Fajardo, A., 2019a. A new approach to map landscape variation in forest restoration success in tropical and temperate forest biomes. *J. Appl. Ecol.* 56 (12), 2675–2686.
- Crouzeilles, R., Ferreira, M.S., Chazdon, R.L., Lindenmayer, D.B., Sansevero, J.B.B., Monteiro, L., Iribarrem, A., Latawiec, A.E., Strassburg, B.B.N., 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Sci. Adv.* 3, 1–7.
- Crouzeilles, R., Santiami, E., Rosa, M., Pugliese, L., Brancalion, P.H.S., Rodrigues, R.R., Metzger, J.P., Calmon, M., Scaramuzza, C.A.D.M., Matsumoto, M.H., Padovezi, A., Benini, R.d.M., Chaves, R.B., Metzger, T., Fernandes, R.B., Scarano, F.R., Schmitt, J., Lui, G., Christ, P., Vieira, R.M., Senta, M.M.D., Malaguti, G.A., Strassburg, B.B.N., Pinto, S., 2019b. There is hope for achieving ambitious Atlantic Forest restoration commitments. *Perspect. Ecol. Conserv.* 17 (2), 80–83.
- De Lima, R.A.F., Oliveira, A.A., Pitta, G.R., de Gaspar, A.L., Vibrans, A.C., Chave, J., ter Steege, H., Prado, P.I., 2020. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. *Nat. Commun.* 11, 6347.
- de Rezende, C.L., Uezu, A., Scarano, F.R., Araújo, D.S.D., 2015. Atlantic Forest spontaneous regeneration at landscape scale. *Biodivers. Conserv.* 24 (9), 2255–2272.
- Durigan, G., Ratter, J.A., 2006. Successional changes in cerrado and cerrado/forest ecotonal vegetation in western São Paulo state, Brazil, 1962–2000. *Edinburgh J. Botany* 63 (1), 119–130.
- Elkin, C., Gutiérrez, A.G., Leuzinger, S., Manusch, C., Temperli, C., Rasche, L., Bugmann, H., 2013. A 2 °C warmer world is not safe for ecosystem services in the European Alps. *Global Change Biol.* 19.
- Elliott, S., Baker, P.J., Borchert, R., 2006. Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Glob. Ecol. Biogeogr.* 15 (3), 248–257.
- Ferraz, S.F.B., Ferraz, K.M.P.M.B., Cassiano, C.C., Brancalion, P.H.S., da Luz, D.T.A., Azevedo, T.N., Tambosi, L.R., Metzger, J.P., 2014. How good are tropical forest patches for ecosystem services provisioning? *Landscape Ecol.* 29 (2), 187–200.
- Ganatsios, H.P., Papaioanou, A.G., Mantranas, K., Psilovikots, T., Mpekiri, S., Marotta, F., Ouzounidis, N., 2021. The environmental impact of the water holding capacity of soil in a Mediterranean oak ecosystem. *Carpathian J. Earth Environ. Sci.* 16 (2), 493–506.
- Gebeyehu, G., Soromessa, T., Bekele, T., Teketay, D., 2019. Species composition, stand structure, and regeneration status of tree species in dry Afromontane forests of Awi Zone, northwestern Ethiopia. *Ecosyst. Health Sustain.* 5 (1), 199–215.
- Gonçalves, F.M.P., Revermann, R., Gomes, A.L., Aidar, M.P.M., Finckh, M., Juergens, N., 2017. Tree Species Diversity and Composition of Miombo Woodlands in South-Central Angola: A Chronosequence of Forest Recovery after Shifting Cultivation. *Int. J. Forestry Res.* 2017, 1–13.
- Goosem, M., Paz, C., Fenham, R., Preece, N., Goosem, S., Laurance, S.G.W., Zobel, M., 2016. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. *J. Veg. Sci.* 27 (3), 504–514.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M., Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecol.* 132, 107–120.
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *For. Ecol. Manage.* 148 (1–3), 185–206.
- Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: Seed rain, seed germination, microclimate, and soil. *Biotropica* 31, 229–242.
- Janus, J., Bozek, P., 2019. Land abandonment in Poland after the collapse of socialism: Over a quarter of a century of increasing tree cover on agricultural land. *Ecol. Eng.* 138, 106–117.
- Lasanta, T., Arnáez, J., Pascual, N., Ruiz-Flaño, P., Errea, M.P., Lana-Renault, N., 2017. Space-time process and drivers of land abandonment in Europe. *Catena* 149, 810–823.
- Latawiec, A.E., Strassburg, B.B.N., Brancalion, P.H.S., Rodrigues, R.R., Gardner, T., 2015. Creating space for large-scale restoration in tropical agricultural landscapes. *Front. Ecol. Environ.* 13 (4), 211–218.
- Liebsch, D., Marques, M.C.M., Goldenberg, R., 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biol. Conserv.* 141 (6), 1717–1725.
- Lienard, J., Florescu, I., Strigul, N., 2015. An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS ONE* 10.
- Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., van Breugel, M., Bongers, F., Dalling, J., 2014. Changing drivers of species dominance during tropical forest succession. *Funct. Ecol.* 28 (4), 1052–1058.
- Marcilio-Silva, V., Pillar, V.D., Marques, M.C.M., 2016. Functional turnover and community assemblage during tropical forest succession. *Commun. Ecol.* 17 (1), 88–97.
- Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. *Proc. R. Soc. B* 280 (1773), 20132236. <https://doi.org/10.1098/rspb.2013.2236>.
- Meza, F.J., Montes, C., Bravo-Martínez, F., Serrano-Ortiz, P., Kowalski, A.S., 2018. Soil water content effects on net ecosystem CO<sub>2</sub> exchange and actual evapotranspiration in a Mediterranean semiarid savanna of Central Chile. *Sci. Rep.* 8, 8570.
- Molin, P.G., Chazdon, R., Frosini de Barros Ferraz, S., Brancalion, P.H.S., Butt, N., 2018. A landscape approach for cost-effective large-scale forest restoration. *J. Appl. Ecol.* 55 (6), 2767–2778.
- Molin, P.G., Gergel, S.E., Soares-Filho, B.S., Ferraz, S.F.B., 2017. Spatial determinants of Atlantic Forest loss and recovery in Brazil. *Landscape Ecol.* 32 (4), 857–870.
- Nanni, A.S., Sloan, S., Aide, T.M., Graesser, J., Edwards, D., Grau, H.R., 2018. The neotropical reforestation hotspots: A biophysical and socioeconomic typology of contemporary forest expansion. *Global Environ. Change* 54, 148–159.
- do Nascimento, L.M., de Sá Barretto Sampaio, E.V., Rodal, M.J.N., Lins-e-Silva, A.C.B., 2014. Secondary succession in a fragmented Atlantic Forest landscape: evidence of structural and diversity convergence along a chronosequence. *J. Forest Res.* 19 (6), 501–513.
- Nepstad, D.C., de Carvalho, C.R., Davidson, E.A., Jipp, P.H., Lefebvre, P.A., Negreiros, G.H., da Silva, E.D., Stone, T.A., Trumbore, S.E., Vieira, S., 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372 (6507), 666–669.
- Niedrist, G., Tasser, E., Lüth, C., Dalla Via, J., Tappeiner, U., 2009. Plant diversity declines with recent land use changes in European Alps. *Plant Ecol.* 202 (2), 195–210.
- Petter, G., Mairota, P., Albrich, K., Bebi, P., Bruna, J., Bugmann, H., Haffenden, A., Scheller, R.M., Schmatz, D., Seidl, R., Speich, M., Vacchiano, G., Lischke, H., 2020. How robust are future projections of forest landscape dynamics? Insights from asymptotic comparison of four forest landscape models. *Environ. Model. Software* 134, 104844.
- Phillips, O.L., van der Heijden, G., Lewis, S.L., Lopez-Gonzalez, G., Aragao, L., Lloyd, J., Malhi, Y., Monteagudo, A., Almeida, S., Davila, E.A., Amaral, I., Andelman, S., Andrade, A., Arroyo, L., Aymard, G., Baker, T.R., Blanc, L., Bonal, D., de Oliveira, A.C.A., Chao, K.J., Cardozo, N.D., da Costa, L., Feldpausch, T.R., Fisher, J.B., Fyllas, N.M., Freitas, M.A., Galbraith, D., Gloor, E., Higuchi, N., Honorio, E., Jimenez, E., Keeling, H., Killeen, T.J., Lovett, J.C., Meir, P., Mendoza, C., Morel, A., Vargas, P.N., Patino, S., Peh, K.S.H., Cruz, A.P., Prieto, A., Quesada, C.A., Ramirez, F., Ramirez, H., Ruelas, A., Salamao, R., Schwarz, M., Silva, J., Silveira, M., Slik, J.W.F., Sonke, B., Thomas, A.S., Stropp, J., Taplin, J.R.D., Vasquez, R., Vilanova, E., 2010. Drought-mortality relationships for tropical forests. *New Phytol.* 187, 631–646.
- Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espirito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruiz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. *Nature* 530 (7589), 211–214.
- Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Almeyda Zambrano, A.M., Amani, B., Andrade, J.L., Brancalion, P.H.S., Broadbent, E.N., de Foresta, H., Dent, D.H., Derroire, G., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Fantini, A.C., Finegan, B., Hernández-Jaramillo, A., Hernández-Stefanoni, J.L., Hietz, P., Junqueira, A.B., N'dja, J.K., Letcher, S.G., Lohbeck, M., López-Camacho, R., Martínez-Ramos, M., Melo, F.P.L., Mora, F., Müller, S.C., N'Guessan, A.E., Oberleitner, F., Ortiz-Malavassi, E., Pérez-García, E.A., Pinho, B.X., Piotto, D., Powers, J.S., Rodríguez-Buritica, S., Rozendaal, D.M.A., Ruiz, J., Tabarelli, M., Teixeira, H.M., Valadares de Sá Barretto Sampaio, E., van der Wal, H., Villa, P.M., Fernandes, G.W., Santos, B.A., Aguilar-Cano, J., de Almeida-Cortez, J.S., Alvarez-Davila, E., Arreola-Villa, F., Balvanera, P., Becknell, J.M., Cabral, G.A.L., Castellanos-Castro, C., de Jong, B.H.J., Nieto, J.E., Espirito-Santo, M.M., Fandino, M.C., García, H., García-Villalobos, D., Hall, J.S., Idárraga, A., Jiménez-Montoya, J., Kennard, D., Marín-Spiotta, E., Mesquita, R., Nunes, Y.R.F., Ochoa-Gaona, S., Peña-Claros, M., Pérez-Cárdenas, N., Rodríguez-Velázquez, J., Villanueva, L.S., Schwartz, N.B., Steininger, M.K., Veloso, M.D.M., Vester, H.F.M., Vieira, I.C.G., Williamson, G.B., Zanini, K., Hérault, B., 2021. Multidimensional tropical forest recovery. *Science* 374 (6573), 1370–1376.

- Pugh, T.A.M., Arneth, A., Kautz, M., Poulter, B., Smith, B., 2019. Important role of forest disturbances in the global biomass turnover and carbon sinks. *Nat. Geosci.* 12 (9), 730–735.
- Rammer, W., Seidl, R., 2015. Coupling human and natural systems: Simulating adaptive management agents in dynamically changing forest landscapes. *Global Environ. Change* 35, 475–485.
- Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv.* 142 (6), 1141–1153.
- Richards, R.C., Rerolle, J., Aronson, J., Pereira, P.H., Gonçalves, H., Brancalion, P.H.S., 2015. Governing a pioneer program on payment for watershed services: Stakeholder involvement, legal frameworks and early lessons from the Atlantic forest of Brazil. *Ecosyst. Serv.* 16, 23–32.
- Rosa, M.R., Brancalion, P.H.S., Crouzeilles, R., Tambosi, L.R., Piffer, P.R., Lenti, F.E.B., Hirota, M., Santiami, E., Metzger, J.P., 2021. Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. *Sci. Adv.* 7 (4) <https://doi.org/10.1126/sciadv.abc4547>.
- Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., 2019. Biodiversity recovery of Neotropical secondary forests. *Sci. Adv.* 5.
- Schuler, L.J., Bugmann, H., Petter, G., Snell, R.S., 2019. How multiple and interacting disturbances shape tree diversity in European mountain landscapes. *Landscape Ecol.* 34 (6), 1279–1294.
- Schumacher, SABINE, Bugmann, HARALD, 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. *Global Change Biol.* 12 (8), 1435–1450.
- Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecol. Model.* 180 (1), 175–194.
- Schwörer, C., Fisher, D.M., Gavin, D.G., Temperli, C., Bartlein, P.J., 2016. Modeling postglacial vegetation dynamics of temperate forests on the Olympic Peninsula (WA, USA) with special regard to snowpack. *Clim. Change* 137 (3–4), 379–394.
- de Souza, S.E.X.F., Vidal, E., Chagas, G.d.F., Elgar, A.T., Brancalion, P.H.S., 2016. Ecological outcomes and livelihood benefits of community-managed agroforests and second growth forests in Southeast Brazil. *Biotropica* 48 (6), 868–881.
- Strassburg, B.B.N., Barros, F.S.M., Crouzeilles, R., Iribarrem, A., Santos, J.S.D., Silva, D., Sansevero, J.B.B., Alves-Pinto, H.N., Feltran-Barbieri, R., Latawiec, A.E., 2016. The role of natural regeneration to ecosystem services provision and habitat availability: a case study in the Brazilian Atlantic Forest. *Biotropica* 48 (6), 890–899.
- Strassburg, B.B.N., Iribarrem, A., Beyer, H.L., Cordeiro, C.L., Crouzeilles, R., Jakovac, C. C., Braga Junqueira, A., Lacerda, E., Latawiec, A.E., Balmford, A., Brooks, T.M., Butchart, S.H.M., Chazdon, R.L., Erb, K.-H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P.F., Kapos, V., Leclère, D., Miles, L., Obersteiner, M., Plutzer, C., de M. Scaramuzza, C.A., Scarano, F.R., Visconti, P., 2020. Global priority areas for ecosystem restoration. *Nature* 586 (7831), 724–729.
- Tabarelli, M., Mantovani, W., 2000. Gap-phase regeneration in a tropical montane forest: the effects of gap structure and bamboo species. *Plant Ecol.* 148, 149–155.
- Temperli, C., Bugmann, H., Elkin, C., 2012. Adaptive management for competing forest goods and services under climate change. *Ecol. Appl.* 22 (8), 2065–2077.
- Temperli, C., Bugmann, H., Elkin, C., 2013. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. *Ecol. Monogr.* 83 (3), 383–402.
- Thom, D., Rammer, W., Garstenauer, R., Seidl, R., 2018. Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. *Biogeosciences* 15 (18), 5699–5713.
- Thrippleton, T., Bugmann, H., Folini, M., Snell, R.S., 2018. Overstorey-Understorey Interactions Intensify After Drought-Induced Forest Die-Off: Long-Term Effects for Forest Structure and Composition. *Ecosystems* 21 (4), 723–739.
- Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. *J. Ecol.* 98, 725–736.
- Walker, R., 2012. The scale of forest transition: Amazonia and the Atlantic forests of Brazil. *Appl. Geogr.* 32 (1), 12–20.