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Multi-purpose forest management in the tropics: Incorporating values of carbon, biodiversity and timber in managing *Tectona grandis* (teak) plantations in Costa Rica

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ABSTRACT

Plantation forestry is the ultimate alternative in reforesting degraded tropical ecosystems and in provisioning multiple ecosystem services beyond timber production. Therefore, we studied the management of *Tectona grandis* L.f. (teak) plantations in Costa Rica and simulated alternative management strategies incorporating simultaneously the values of carbon storage, biodiversity and timber production. Alternative management strategies included (1) extension of rotations, (2) reduced thinning and (3) conversion of even-aged to uneven-aged systems. Evaluation criteria were carbon storage in biomass, stand structural diversity as a proxy of biodiversity, and economic return from timber harvests. For growth predictions under future climatic conditions, we calibrated the hybrid forest growth model 3PG. We found that carbon storage could be increased by increasing rotation periods (e.g. +29.7% of carbon for a 50% increase in rotation length) and a no thinning management (+9.5% of carbon). For rotation extension associated economic losses were high (e.g. at 5% discount rate, the Land Expectation Value (LEV) decreased by 25.1% for a 50% extension of rotations). For thinning LEV increased with a low-thinning regime, but decreased with a no-thinning management (+9.5% and −23.6%, respectively). Payments for ecosystem services (PES) increased economic return by about 3–4%. Structural diversity increased by conversion to uneven-aged forest stands (Gini coefficients for basal area increased from 0.21 to 0.52). Economic returns from timber harvests were almost equal for even-aged and uneven-aged systems at 1% discount rate (max. −2% of LEV). At 5% discount rate, we observed economic losses of 11.1–20.1% compared to the even-aged scenario. At 10% discount rate, economic losses ranged between 43.6 and 104%. We concluded that extension of rotations and reduction of thinning intensity can be used as management strategies to increase the carbon storage of teak plantations. However, to compensate the associated economic losses through a PES scheme, payments for carbon sequestration need to be increased and special incentives for longer rotation periods and low thinning management need to be developed. The transformation into uneven-aged forest stands requires active investment at discount rates higher than 1%. Whether this investment can be offset by benefits from biodiversity and increased forest resilience is unknown and requires further investigations. Other measures of biodiversity conservation, such as the use of native and mixed tree species and the retention of old trees and deadwood are moreover necessary.

1. Introduction

With a loss of approximately 7 million hectares of forest per year, deforestation remains a substantial problem in the tropics (FAO, 2016). Deforestation involves the loss of a wide range of ecosystem services, including climate regulation, carbon storage and habitat provision for wildlife species that act as pollinators, seed dispersers or contribute to pest control (Lawton et al., 2001; Nasi et al., 2002). The loss of natural forest is partially compensated by an increase in planted forest area. By 2010, planted forests constituted 6.6% of the global forest area, and this percentage was expected to rise to 7.5% by 2020. Timber provision and economic returns from timber harvests are commonly the main goals of forest plantations (FAO, 2010). However, since it became apparent that climate change and the rate of biodiversity loss have already exceeded planetary limits, the need for managing forests for climate change mitigation and biodiversity conservation has risen (FAO, 2010; Rockström et al., 2009).

The world's forests play a major role in the carbon balance and have

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great potential to mitigate climate change by sequestering carbon in forest biomass. Forests sequester 4.05 ± 0.67 Pg $year^{-1}$ of carbon, which is about half as much as global CO_2 emissions from fossil fuel combustion (Le Quéré et al., 2009; Pan, 2011). Seventy per cent of this (2.83 ± 0.93 Pg $year^{-1}$ of carbon) is sequestered by tropical forests, but at the same time tropical deforestation causes the release of 2.94 ± 0.47 Pg $year^{-1}$ of carbon. Thus, the global net sequestration of forests is only 1.11 ± 0.82 Pg $year^{-1}$ of carbon (Pan, 2011). Consequently, the global carbon balance could be improved significantly, if tropical deforestation could be stopped and partly reversed by reforestation. Chazdon et al. (2016) suggest that tropical secondary forests in Latin America have the potential to sequester a total of 8.48 Pg of carbon during the next 40 years. Currently planted forests constitute 3% (584 000 ha) of the total forest area in Central America with a growing trend of 3.14% annually (FAO, 2010). Management strategies for increasing carbon storage of tropical forest plantations include extending the rotation length and reducing thinning intensity (Kaul et al., 2010; Schroeder, 1992).

The current rate of species extinction is estimated to be about 100–1000 times higher than the average rate in earth’s history (Millennium Ecosystem Assessment, 2005; Rockström et al., 2009). Most biodiversity losses occur in tropical forests, where species diversity and the number of endemic species are also highest (Dirzo and Raven, 2003; Millennium Ecosystem Assessment, 2005; Myers et al., 2000). Although primary forests have much higher value for biodiversity conservation, the complementary function of planted forests has been increasingly recognized (Barlow et al., 2007; Brockerhoff et al., 2008; Hartley, 2002; Mang and Brodie, 2015; Pawson et al., 2008). Teak, being an exotic species in Costa Rica, has shown to have limited capability for recruiting woody regeneration of native species (Healey and Gara, 2003). Yet, when comparing establishment of teak plantations to other land use alternatives typically considered in Costa Rica, then teak plantations appear quite promising with regard to biodiversity conservation as they provide forest cover and offer reliable economic returns at the same time (de Camino Velozo et al. 2016; Griess and Knoke, 2011; Hallet et al., 2011; Pérez, 2005).

Especially large-scale clear-cut harvesting has been criticized by environmental non-governmental organizations and the public for negatively impacting forest biodiversity (Pawson et al., 2006). In the scientific community however, the debate is more differentiated, since impacts of clear-cutting depend largely on species, region and scope of the study (Pawson et al., 2006). Mostly open-habitat species and early-successional specialists profit from clear-cut harvests, whereas late-successional and closed-forest species are negatively affected (Niemelä et al., 2007; Pawson et al., 2006, 2011). Ecological theories further suggest that biodiversity can be better maintained when forest management imitates natural structures and processes. The increase in stand heterogeneity and the small-scale disturbances that go along with uneven-aged forest management are thus regarded as having a positive impact on the conservation of forest biodiversity (Kuuluvainen et al., 2012). Uneven-aged forest management has further proven to be an attractive alternative to clear-cut management, mainly for the following reasons: (a) the creation of spatial heterogeneity at stand level leading to increased ecosystem resilience (Guldin, 2011), (b) the ability to compete economically with even-aged management systems (Hanewinkel, 2002; Kuuluvainen et al., 2012) and (c) higher social acceptance (O’Hara, 2001; Pawson et al., 2006). Although intensively studied and applied in temperate and boreal forests, the literature is almost void of studies focusing on uneven-aged plantation forests in the tropics. This study therefore aims at exploring economic and ecological consequences of this management option for teak plantation forestry in Costa Rica.

The demand for wood products is increasing along with growing human populations, increasing income and consumption, and the increasing need for replacing non-renewables with renewable resources (FAO, 2016). Currently, the demand for timber is largely met by plantation-grown timber. In the tropics, planted forests accounted for 65% of roundwood timber production in 2012 (Payn et al., 2015). In order to avoid further deforestation it is thus important that timber provision by plantations remains at the present level or increases. To achieve this, it is important that forest plantations are economically attractive to landowners.

Accounting for 12% of the global annual tropical timber trade, *Tectona grandis* (teak) is economically one of the world's most important tropical tree species (FAO, 2015). The increasing demand for general utility teak has created a market for fast-grown, small diameter logs from Latin American plantations (Kollert and Cherubini, 2012). In 2015 Costa Rica thus exported 207,239 m^3 of teak roundwood, corresponding to 21.7% of the country’s total timber harvest (OFN, 2015). Due to its economic importance globally and locally, research on teak has been manifold and the existing knowledge is considerable. This makes teak a good model species.

The objective of the study was to simulate alternative forest management strategies for teak plantations in Costa Rica and to evaluate and compare these strategies with regard to climate change mitigation, biodiversity conservation and economic return from timber harvests. Our reference management was an even-aged stand, which was clear-felled after 20 years and regularly thinned from below. Alternative management strategies for climate change mitigation included extended rotation periods and reduced thinning intensities. We evaluated these strategies with regard to carbon storage in biomass, net present value (NPV) and land expectation value (LEV). We further evaluated to what extent economic losses could be compensated by payments for ecosystem services (PES). For biodiversity conservation, we simulated transformation into a continuously covered, uneven-aged forest system. We evaluated the transformation with regard to structural diversity (of basal area) and economic return. In order to have growth predictions under future climatic conditions, we first calibrated the hybrid forest growth model 3PG for teak in Costa Rica and then prepared growth predictions for four different climate change scenarios.

2. Material and methods

2.1. Model parametrization and validation

2.1.1. Model description

The basic, generic 3PG model was developed by Landsberg and Waring (1997). 3PG has proven to make good predictions for a large number of species and regions (Landsberg et al., 2003). It requires relatively little input data: monthly average temperature, precipitation, solar radiation, site fertility, soil texture and forest stocking. The model was developed for even-aged plantations and the output is monthly increment at stand level. The core of the model is a photosynthesis sub-model for net primary production (NPP). NPP is allocated to three biomass components (stem, foliage, roots) and the allocation process is influenced by DBH (diameter at breast height). The foliage biomass forms a feedback loop with the photosynthesis sub-model. The model further includes sub-models for water balance, litter production, mortality and thinning.

2.1.2. Stand data

Time series of growth observations were obtained from even-aged forest stands at three different production sites in Costa Rica: San Rafael (10.73 N, 84.50 W; 52 m altitude), Upala (10.96 N, 85.05 W; 41 m altitude) and Javillos (10.38 N, 84.54 W; 136 m altitude). There were several forest stands at each production site, each of them between 0.71 ha and 20.6 ha large. DBH and height were recorded for all stands using permanent plots that represent 2% of the plantation area. Measurements were made approximately every year, but actual days of measurement are known and age is expressed in years with two decimals. Stem biomass and stand volume were calculated using allometric equations from (Pérez and Kanninen, 2003a, 2003b). In San Rafael two forest stands, established in different years, were monitored. One stand, established in 2007, was monitored from age 2.92 to 8.00 years and the

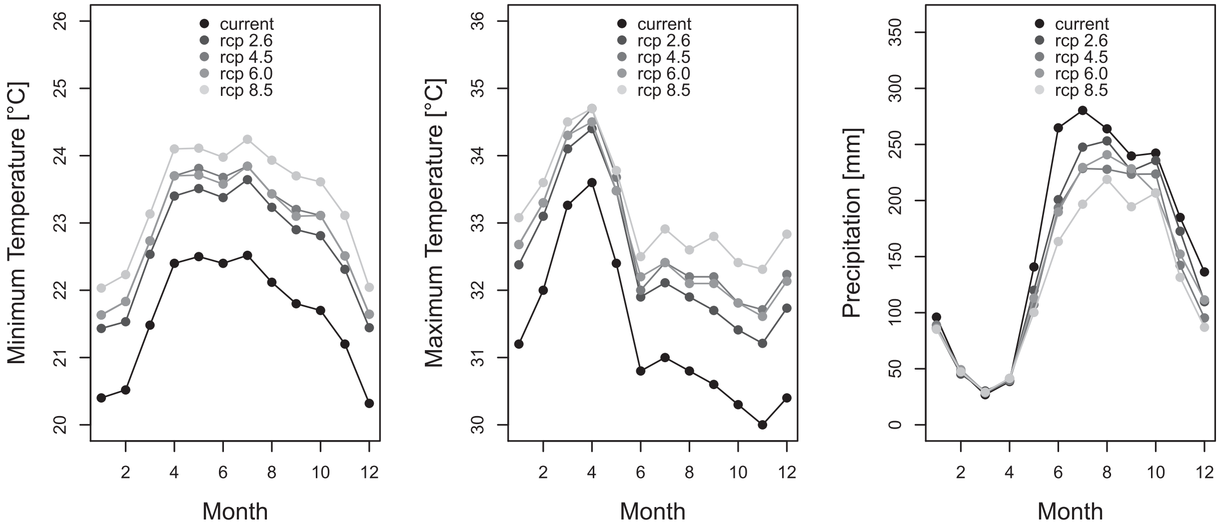

Fig. 1. Climate data (minimum temperature, maximum temperature and precipitation) for current and future climate conditions for the Upala stand. Four GHG concentration trajectories (rcp 2.6, rcp 4.5, rcp 6.0, rcp 8.5) are included.

other one, established in 2008, from age 2.64 to 6.75. Initial stocking was 625 trees ha^{-1} and thinning was scheduled at ages 5.58/4.33, 10.00 and 15.00 with 419, 314 and 236 remaining stems ha^{-1}, respectively. The soil texture was classified as clay. In Upala monitoring covered stand ages from 1.08 to 4.17 years. In this case the initial stocking was 833 trees ha^{-1}. Thinning at Upala was scheduled at ages 5.00, 10.00 and 15.00 with 625, 469 and 300 remaining stems ha^{-1}, respectively. The soil texture was classified as clay-loam. Measurements in Javillos took place at ages from 10 to 18 years. Initial stocking was 625 trees ha^{-1} and thinning was scheduled at ages 10.50 and 13.00 with 469 and 375 remaining stems ha^{-1}, respectively. The soil texture class was also clay-loam. As data availability was quite low, especially for older stands, simulation results from empirical modelling were used as an additional reference to support the calibration of the model (Pérez and Kanninen, 2005). Among the scenarios examined by these authors, we applied the scenario for highly fertile sites and the management goal of DBH maximization. Corresponding thinning ages were: 4, 8, 12, 18 and 24 years with remaining stems of 556, 333, 200, 150 and 120 trees ha^{-1} and initial stocking of 1111 trees ha^{-1}.

2.1.3. Model input data

For initializing the simulation, some model specific input data had to be assumed. Initial stem and foliage biomass was 10 g tree^{-1} each. Initial root biomass was 5 g tree^{-1}. Initial age was zero. Estimation of site fertility rating (FR) was based on the site classification chart for teak in The Caribbean (Keogh, 1979), and site fertility was estimated as 0.7 for San Rafael and 1 for Upala and Javillos. Thinning was carried out from below and thus the biomass of trees removed in thinning was estimated as 80% of average tree biomass.

In addition to site-specific input data, climate data were needed. Monthly average temperature and precipitation data were downloaded from the *WorldClim* database version 1.4. For the model calibration, current climate data from 1960 to 1990 with a spatial resolution of 30 arc-seconds were used. Radiation data were downloaded from the US-National Solar Radiation Data Base (US-NSRDB). The applied atmospheric CO_2 concentration was 385 ppm (NOAA).

2.1.4. Calibration and validation

Behling (2009) and Pontes (2011) calibrated 3PG for teak in Brazil, but predictions computed using their parameter values did not fit the observed teak data from Costa Rica. Therefore 3PG was calibrated for teak in Costa Rica using the data from San Rafael, Upala and Javillos. Based on literature review, an initial value or a range of values was defined for each 3PG parameter. These values were either results of physiological experiments, parameter values from the Brazilian calibrations or default values estimated for 3PG by Sands (2010). Manual adjustments of the values of twenty parameters were made until a visually good agreement was achieved between the model output and the observed stand data. The reference data from Pérez and Kanninen (2005) were compared to a simulation where the model input was the same as for the Upala stand (assuming the same FR), but the thinning regime was replaced with the one used by Pérez and Kanninen (2005). For all stands at all times of thinning, we compared the following output variables: WS = stem biomass (t ha^{-1}), mean DBH (cm), mean height (m) and mean yield = stand volume (m^3 ha^{-1}). Calibration and implementation were made in the R environment and results may differ if the parameters are implemented in a different environment. The R code can be supplied on request.

Data from the second stand monitored in San Rafael was set aside for validation. The normalized root mean squared error (NRSME) was used as a measure of deviation (in %) between observed and simulated values.

2.1.5. Predictions under future climate conditions

Climate data for prediction of future growth were also downloaded from the *WorldClim* database version 1.4 (see Fig. 1). We used monthly means of predictions for the period 2041–2060, which were prepared using the CCSM4 model. This model was supposed to produce the best predictions for Costa Rica (Hidalgo and Alfaro, 2015). We tested four different greenhouse gas (GHG) concentration trajectories: representative concentration pathways (rcp) 2.6, 4.5, 6.0 and 8.5. Further we made a sensitivity analysis on how changes in precipitation and temperature affect teak growth.

2.2. Management strategies

Alternative forest management strategies tested were (1) extension of rotation, (2) reduced thinning and (3) transformation into uneven-aged forests.

The business-as-usual scenario (BAU) was even-aged management with clear-cut at age 20. Thinning was carried out from below at ages 4, 8, 12 and 16 with intensities of 25%, 33%, 33% and 25%, respectively (Fig. 2). The initial tree density was 625 trees ha^{-1}. Stand characteristics were adopted from Upala and thus for highly fertile stand conditions (see sections 2.1.2 and 2.1.3). The future climate scenario for Upala with rcp 4.5 was used.

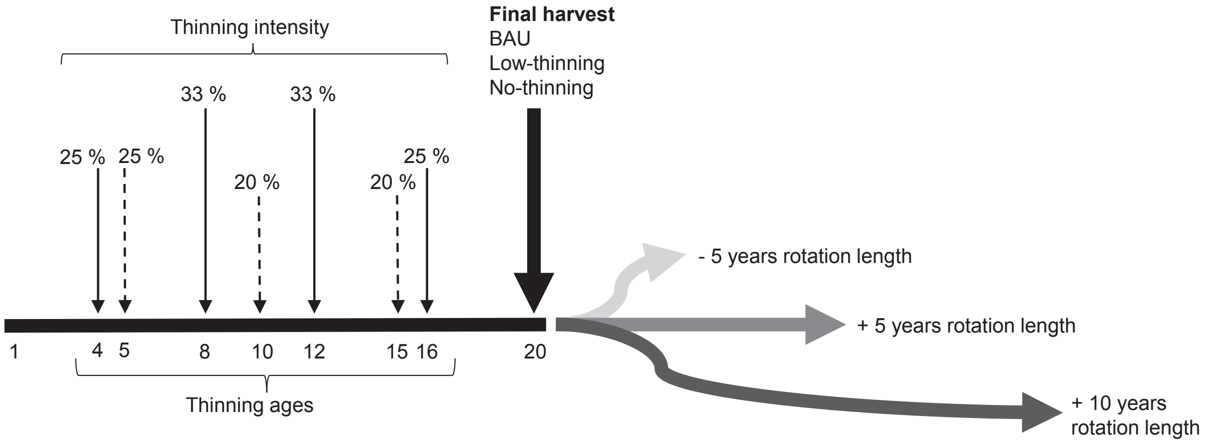

Fig. 2. Schematic overview of business-as-usual management (BAU) and alternative management strategies for climate change mitigation. The alternative management included three thinning alternatives and four different rotation lengths. BAU thinning is indicated by unbroken lines, low-thinning by dashed lines. Extension of rotation was simulated for extensions of −5, + 5 and +10 years, which means total rotation lengths of 15, 20 (BAU), 25 and 30 years.

Alternative management strategies for climate change mitigation aimed to increase carbon storage in biomass. To this end we simulated various rotation periods (15, 20, 25, and 30 years) and reduced thinning intensities (Fig. 2). The latter comprised a low-thinning regime with thinning intensities of 25%, 20% and 20% at ages 5, 10 and 15, respectively, and a no-thinning regime.

Carbon storage was calculated for each time step by multiplying total, accumulated biomass (stem, foliage, roots) predicted at that time step with an average carbon concentration of 0.495 (Kraenzel et al., 2003). Since most of the carbon in biomass is released shortly after harvest, we calculated mean carbon stored during one rotation (Schroeder, 1992).

For biodiversity conservation we simulated transformation from even-aged management to an uneven-aged, continuous-cover forest system. To enable simulating uneven-aged systems with a stand-level forest growth model, we applied a group harvesting system. In this system each harvest unit was treated as a miniature stand (Fig. 3). It can be thought of as a minimum patch size age class forest system. The patch size was chosen such that it ensured sufficient light incidence for regeneration of a light-demanding species like teak. According to Nyland (2003) this corresponds to a patch width about twice the height of surrounding trees. We therefore used a patch size of 0.25 ha, corresponding to a patch width of 50 m. Harvest age was 20 years. We simulated stands containing the following numbers of differently aged tree groups: 1 age group (A1) = even-aged, 2 age groups (A2), 4 age groups (A4), 5 age groups (A5), 10 age groups (A10) and 20 age groups (A20). The time interval between patch harvests was determined by dividing the harvest age with the number of different age groups. Consequently, in A1, A2, A4, A5, A10 and A20 harvests took place every 20, 10, 5, 4, 2 and 1 years, respectively. Since each of the 0.25 ha

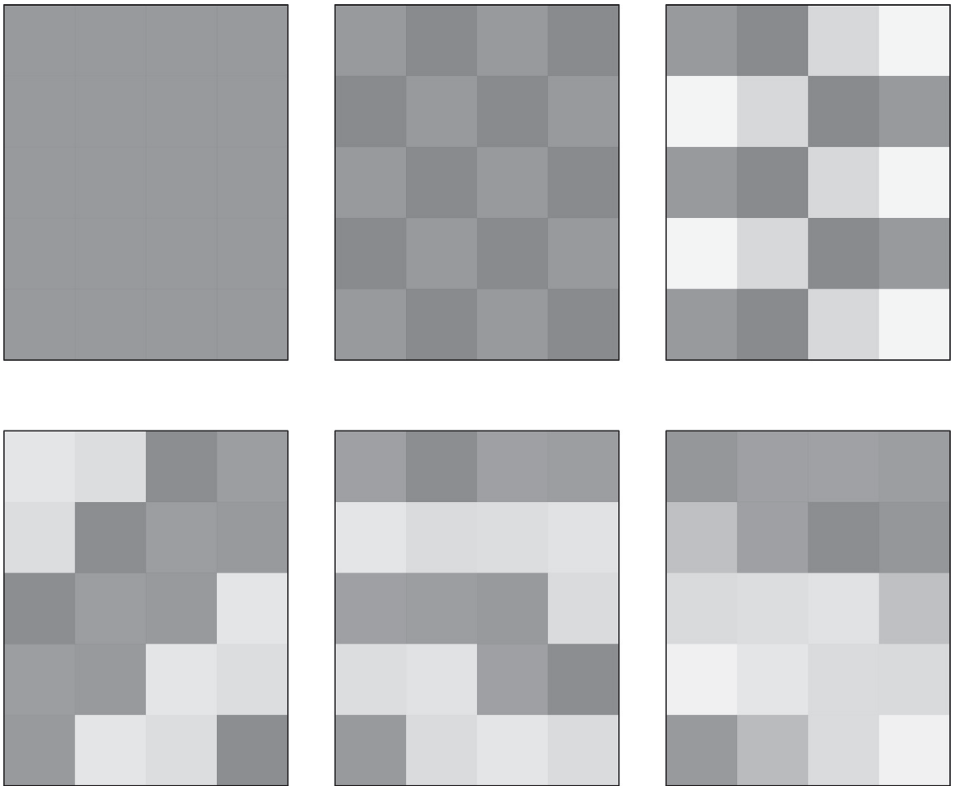

Fig. 3. Schematic overview of the uneven-aged forest system (group harvesting). Large rectangles represent a stands. A square inside a rectangle represents a group of trees, which belongs to one management unit (miniature-stand, 0.25 ha). Shades of grey represent the age of tree groups. Rectangles explained from left to right: Top row: even-aged/BAU, 2 age groups, 4 age groups; Bottom row: 5 age groups, 10 age groups and 20 age groups. The best way to arrange patches of differently aged tree groups (squares) is at random (not shown here).

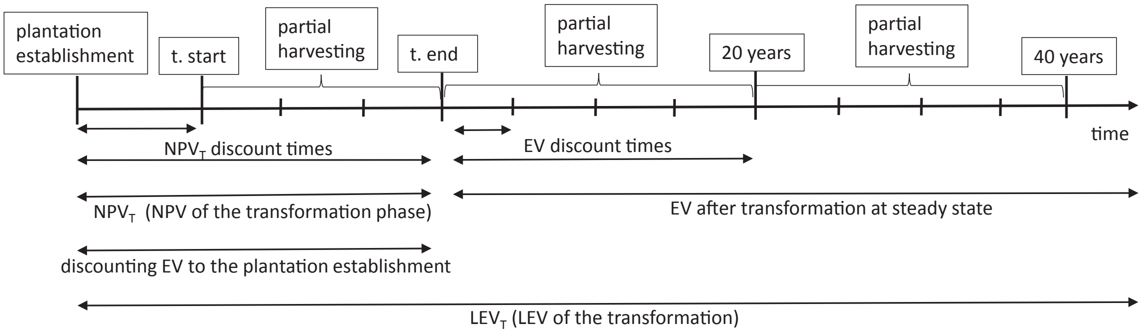

Fig. 4. Schematic overview of time frames and discounting times used in the economic evaluation of the transformation into uneven-aged forest management; t. start = transformation start, t. end = transformation end, NPV = net present value, EV = expectation value, LEV = land expectation value.

patches constituted a very small even-aged stands, thinning was applied in all scenarios.

The Gini Coefficient (GC) was used as an index for quantifying structural diversity at stand level. It was calculated using basal areas. The GC is assumed to best represent characteristics of uneven-aged forests, since it has been shown to respond not only to changes in the total range of diameters, but also to changes in diameter distributions (Lexerød and Eid, 2006). The Gini Coefficient ranges between 0 and 1, where 0 represents perfect equality and 1 perfect inequality. Compared to BAU we thus expect an increase in the Gini coefficient for uneven-aged forest stands, caused by higher structural heterogeneity.

2.3. Economic return from timber harvests

To evaluate economic return from timber harvests of even-aged plantations we calculated the net present value (NPV) of a single rotation and the land expectation value (LEV) of an infinite number of identical rotations. For the economic analysis of carbon storage we also calculated revenues from payments for ecosystem services (PES). In Costa Rica forest owners can receive up to 756,258 CRC ha^{-1} (=1336 US$ ha^{-1}) from the governmental institution *Fonafifo* for reforestation with teak (Ministerio de Ambiente y Energia, 2015). Payments are made during the first 5 years as follows: 50% in the first year, 20% in the second year, 15% in the third year, 10% in the fourth year and 5% in the fifth year. The contract lasts for 16 years.

For economic evaluation of the uneven-aged forest systems, we calculated the net present value of the transformation phase (NPV$_T$), the expectation value (EV) of the uneven-aged system resulting after transformation at steady state and the transformation LEV (LEV$_T$) (see Fig. 4). LEV$_T$ was defined as the sum of NPV$_T$ and EV discounted to the time of plantation establishment. Stand ages at transformation start were chosen such that LEV$_T$ was maximized. For all economic calculations we considered revenues and costs from the final harvest and from thinning, establishment costs, maintenance costs and administration costs. Annual discount rates of 1%, 5% and 10% were considered. Price data was obtained from the Costa Rican national forestry office (OFN, 2013). They reported a linear increase in prices with tree diameter. Costs were estimated based on data from the afforestation company Puro Verde Paraíso Forestal S.A., part of the *FuturoVerde Group*. Economic formulations of NPV, LEV, and EV as well as price and cost data, can be found in Appendix B.

3. Results

3.1. Growth modelling

The final 3PG parameter values, method of estimation and references are shown in Appendix A. Relative deviations (NRMSE) between observed and modelled data ranged between 3.0% and 40.0%, but were on average about 11% (Table 1). An exception was observed for height predictions for the Javillos stand, which showed a deviation of as much as 78.9%. This strong deviation was due to inconsistencies in the observed height data, which indicated that after age 11 trees were becoming shorter with increasing age. We thus assumed that these observed height data were faulty and therefore expected high deviations. It should be noted that yield calculations were based on height and DBH and thus deviations in these variables also affected yield estimations. Observed stem biomass and yield data was moreover calculated using allometric equations (see section 2.1.2).

On average, climate change simulations predicted a temperature increase of 1–2 °C and a reduction of precipitation of about 400 mm year^{-1} (see Fig. 1). The precipitation loss mainly occurred during the rainy season. Climate change scenarios were very similar for all calibration sites. According to simulations with 3PG, climate change negatively affected teak growth at all calibration sites. Compared to current climate conditions, losses in yield ranged between 4 and 8% for San Rafael, between 2 and 4% for Javillos and between 6 and 12% for Upala (losses were smallest for rcp 2.6 and highest for rcp 8.5). A sensitivity analysis showed that the simulated growth reduction under future climate scenarios could be attributed to an increase in temperature. A 10% increase in temperature led to approximately 19% decrease in teak yield and a 10% decrease in temperature caused an increase of about 9% in teak yield for the climate at San Rafael. For Upala it was −24.3% and +13.0% respectively. Predicted changes in precipitation showed negligible effects on teak growth predictions: 0.01% increase in yield for a 10% increase in precipitation and 0.1% decrease in yield for a 10% decrease in precipitation for San Rafael and +0.05% and −0.1% for Upala, respectively. Average temperatures (current and future) were about 0.6 °C higher for Upala than for San Rafael. Current annual precipitation was 2967 mm for San Rafael and 1962 mm for Upala. Under rcp 8.5 annual precipitation was 2518 mm and 1646 mm, respectively.

3.2. Climate change mitigation and economic implications

For the BAU scenario, accumulated mean carbon storage in standing biomass (stem, foliage, roots) was 76.9 Mg ha^{-1} of C for a 20 year

Table 1
Deviations between modelled and observed data given in percent as normalized root mean squared error (NSRME). Values are stated for calibration and validation data (SR 2008) and various stand-level variables (means). (SR = San Rafael, P. & K. 2005 = Pérez and Kanninen, 2005, WS = stem biomass).

Output variable	NRMSE [%] for calibration and validation data				
	SR 2007	Javillos	Upala	P. & K. (2005)	SR 2008
WS [t ha^{-1}]	6.0	40.0	20.4	7.2	11.1
DBH [cm]	4.9	20.6	30.1	3.0	10.3
Height [m]	11.2	78.9	17.8	3.5	3.5
Yield [m^3 ha^{-1}]	6.3	81.3	17.3	9.7	10.2

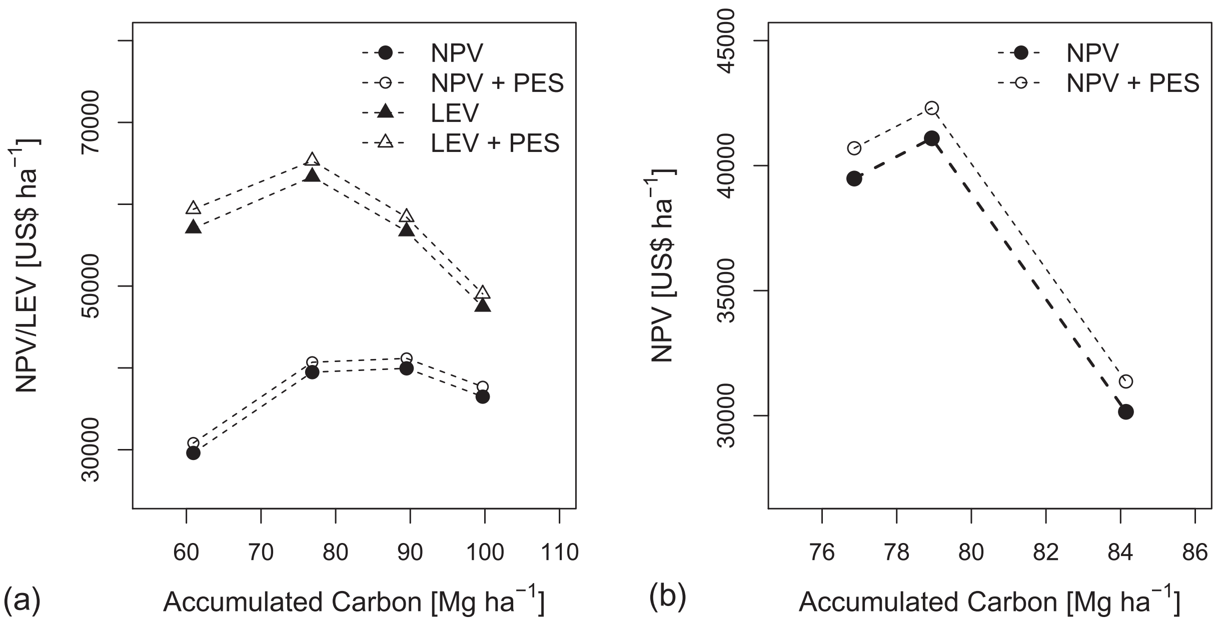

Fig. 5. (a): Relationships between accumulated carbon storage in biomass and economic return (net present value (NPV) and land expectation value (LEV)). The symbols represent different rotation lengths: 15, 20, 25 and 30 years – from left to right. Open symbols represent economic return including revenues from payments for ecosystem services (PES). (b) Symbols represent different thinning intensities: BAU, low thinning, no thinning – from left to right.

rotation period. When extending rotations it increased to 89.5 Mg ha^{-1} of C (+16.4%) for a 25 year rotation and to 99.7 Mg ha^{-1} of C (+29.7%) for a 30 year rotation (Fig. 5a). Consequently, mean carbon storage was lower for a rotation period of 15 years (60.9 Mg ha^{-1} of C or −20.7% of BAU carbon storage). At 5% discount rate, the economically optimal rotation length for one rotation period was 23 years, and thus NPV was slightly higher (+1.2%) for the 25 year rotation than for the BAU scenario (39,948 US$ ha^{-1} and 39,482 US$ ha^{-1}, respectively). For lower or even higher rotation periods (15 and 30 years), NPV was considerably lower than for the BAU scenario (−25.0% and −7.6% respectively). For an infinite number of equal rotations, the economically optimal rotation length was 18 years. LEV of the business as usual scenario was thus the highest (among those investigated) with 63,363 US$ ha^{-1}. LEV was 10.0% lower for a 15 year rotation period, 10.5% lower for a 25 year rotation period and 25.1% lower for a 30 year rotation period. Revenues from the Costa Rican payment for ecosystem services increased NPV and LEV by 3.0–4.1%.

Variation in thinning intensity showed a different pattern (Fig. 5b). A lower thinning intensity slightly increased mean carbon storage to 78.9 Mg ha^{-1} of C (+2.7%) and NPV to 41,092 US$ ha^{-1} (+4.1%). For the no-thinning regime carbon storage increased to 84.1 Mg ha^{-1} of C (+9.5%), but NPV decreased to 30,153 US$ ha^{-1} (−23.6%).

3.3. Biodiversity conservation and economic implications

The stand structural diversity expressed as the Gini Coefficient increased digressively with increasing age diversity (Fig. 6a). At steady state the Gini Coefficient ranged between 0.21 for even-aged stands and 0.52 for uneven-aged stands with 20 different age groups (Table 2). Structural diversity in the even-aged scenario resulted from natural within-stand variation in tree growth.

Economic return was almost equal for the even-aged and the uneven-aged systems at 1% discount rate (−0.8 to −2.4% of LEV_T) (Fig. 6b and Table 2). At 5% discount rate, we observed economic losses between 11.1% and 20.1% compared to the even-aged scenario. At 10% discount rate, economic losses ranged between 43.6% and 104%. These losses resulted from two aspects of the transformation process: First, NPV_T was reduced between 33.4% and 40.2% of the even-aged scenario at 5% discount rate and between 69.1% and 140% at 10% discount rate (Fig. 6c and Table 2). The income reduction from transformation harvests was due to early harvesting of some tree groups (see transformation start ages in Table 2). Second, harvests of future generations were delayed (see transformation end ages in Table 2). At steady state after transformation, the EV of the uneven-aged systems was between 42.7% and 73.1% higher than for the even-aged scenario at 5% discount rate and between 144% and 260% higher at 10% discount rate (Fig. 6d). However, discounting EV to the year of plantation establishment strongly reduced its value (Table 2).

Since we chose to maximize LEV_T, transformation start ages became earlier with increasing discount rates. With early transformation ages, EV discounted to the plantation establishment remained higher, but revenues during the transformation phase (NPV_T) decreased. By choosing later transformation ages, losses from the transformation harvests would be replaced by losses caused by a delay in the harvest of future tree generations. Irregularities in the shapes of the curves were mainly a result of the timing of thinning.

4. Discussion

4.1. Growth modelling

3PG growth predictions were in line with empirical simulation results (Bermejo et al., 2004; Pérez, 2008; Pérez and Kanninen, 2005), partly because Pérez and Kanninen (2005) was used for reference in the calibration. NRMSE varied considerably, but was on average about 11%, which is similar to deviations observed in 3PG calibration for other species (Amichev et al., 2016; Augustynczik et al., 2017; Jégo et al., 2017). Since teak is well studied, many parameter values could be obtained from physiological experiments previously published (see Appendix A). Nevertheless, the data availability for calibration with Costa Rican teak was rather low (especially for mature stands), and although 3PG is a very robust model, which has shown to produce reasonable predictions even when calibrated using very limited data (Landsberg et al., 2003), we recommend further validation of our model parameters. Further we see increased uncertainties for the thinning sub-model, since data from un-thinned stands were not available for calibration. Instead we used results from a thinning trial from Kanninen et al. (2004) for calibrating the thinning sub-model. He found that basal

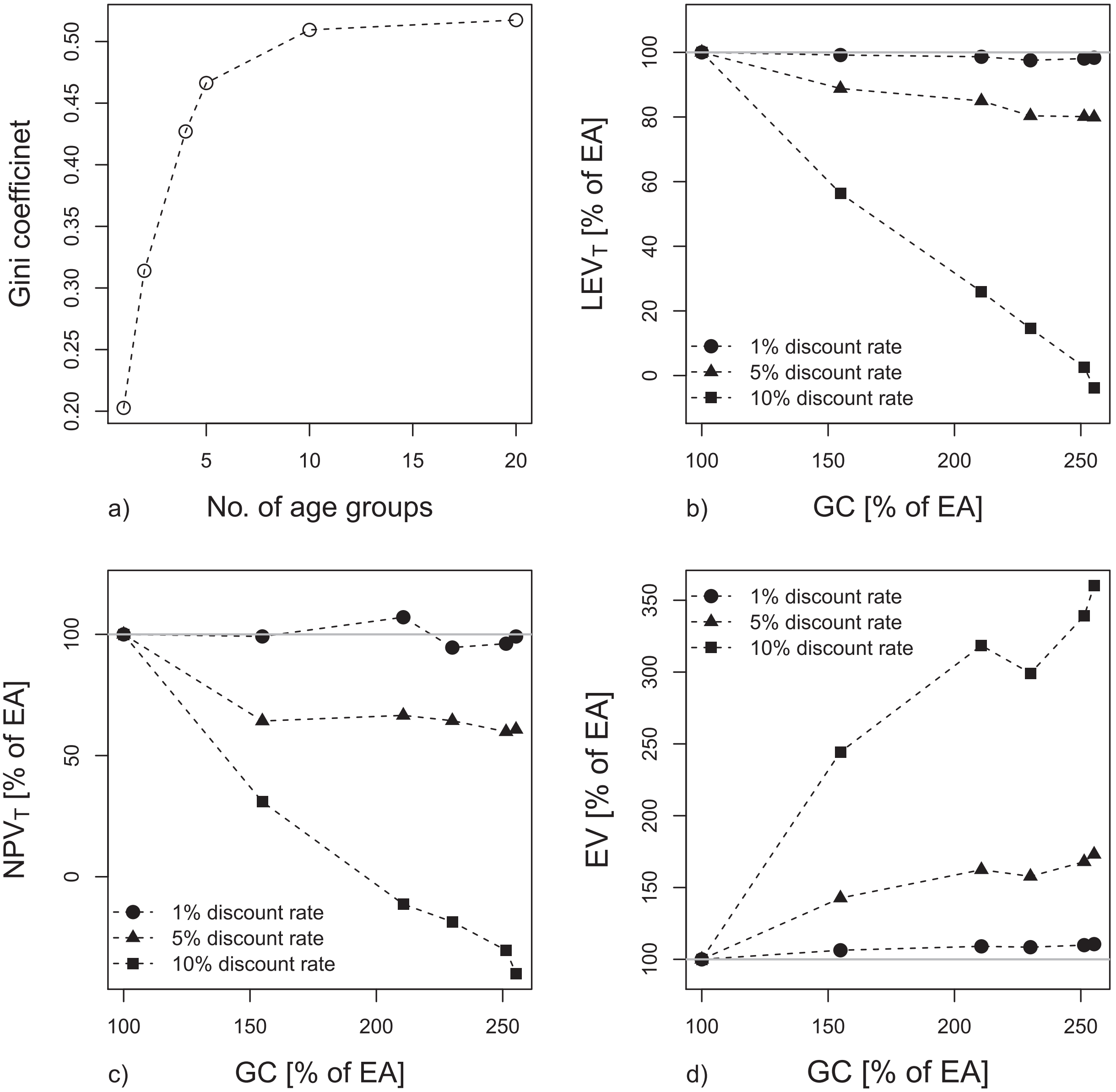

Fig. 6. (a) Stand structural diversity expressed as Gini coefficient (GC) calculated with basal areas vs. age diversity and b) – d) Economic return from timber harvest in % of even-aged (EA) vs. Gini Coefficient (GC) in% of even-aged. (b) Transformation LEV (LEV$_T$); (c) NPV of the transformation phase (NPV$_T$); (d) Expectation value (EV) after transformation at steady state. From left to right: A1, A2, A4, A5, A10, A20. The grey line represents 100% (even-aged).

areas in non-thinned control treatments did not exceed 28 $m^2 ha^{-1}$.

Our results support findings of Clark et al. (2010), who predicted a general decrease in wood production in the lowland rainforest of North-Eastern Costa Rica due to climate change. According to the sensitivity analysis, the main driver for growth reduction was an increase in temperature. This was reflected by the relatively higher losses in yield under climate change, when comparing Upala to San Rafael. For Upala, current and future temperatures were on average 0.6 °C higher than for San Rafael. It should be noted that for 3PG, an increase in temperature leads to elevated vapor pressure deficit (VPD), since VPD is calculated on the basis of minimum and maximum temperatures. Elevated VPD is hypothesized to limit growth by reducing stomatal opening time. The negligible effect of changes in precipitation might be explained by the rather high amount of rainfall and the short dry season. Pandey and Brown (2000) postulate that teak grows best with annual rainfall of 1250–3750 mm. Even under rcp 8.5 this condition will still be met for all analyzed sites in Costa Rica.

It should be kept in mind that the decline in growth could be partly reversed by CO_2 fertilization effects, which were not included in this simulation. Gopalakrishnan et al. (2011), who simulated effects of climate change on teak productivity in India, actually reported an increase in net primary production based on elevated CO_2 concentrations.

4.2. Climate change mitigation

Results for accumulated mean carbon storage in biomass were 10% higher than reports from Kraenzel et al. (2003), who analyzed carbon storage of unmanaged teak plantations in Panama. This difference might be explained by the very fertile growth conditions assumed in our simulation study. Kaul et al. (2010) found even lower carbon storage for teak plantations in India. They calculated 64 $Mg ha^{-1}$ of carbon for plantations with 30 year rotation length. These differences can probably partly be attributed to the treatment of timber harvests from thinning. We calculated carbon storage of accumulated biomass (including timber from thinnings), whereas Kaul et al. (2010) directly allocated biomass from thinning to wood products. Nevertheless, they also

Table 2
Gini coefficient and economic returns for the transformation into uneven-aged forest stands. Economic returns are calculated for discount rates of 1, 5 and 10%. Column headings A1 to A20 refer to the number of different age groups present in a stand. A1 = even-aged.

	A1	A2	A4	A5	A10	A20
Gini coefficient	0.21	0.31	0.43	0.47	0.51	0.52
	At 1% discount rate					
Transformation start ages [years]	20	17	17	14	13	13
Transformation end ages [years]	20	27	32	30	31	32
NPV_T [$\text{US\$ ha}^{-1}$]	89,541	88,694	95,772	84,592	86,019	88,673
EV after transformation at steady state [$\text{US\$ ha}^{-1}$]	495,696	527,110	540,612	537,712	544,747	548,279
EV discounted to the plantation establishment [$\text{US\$ ha}^{-1}$]	406,245	402,925	393,189	398,941	400,158	398,765
LEV_T [$\text{US\$ ha}^{-1}$]	495,696	491,619	488,961	483,534	486,176	487,438
	At 5% discount rate					
Transformation start ages [years]	20	12	12	12	10	10
Transformation end ages [years]	20	22	27	28	28	29
NPV_T [$\text{US\$ ha}^{-1}$]	39,482	25,367	26,282	25,420	23,621	24,004
EV after transformation at steady state [$\text{US\$ ha}^{-1}$]	63,363	90,403	102,892	99,969	106,396	109,686
EV discounted to the plantation establishment [$\text{US\$ ha}^{-1}$]	23,880	30,904	27,559	25,501	27,141	26,647
LEV_T [$\text{US\$ ha}^{-1}$]	63,363	56,272	53,842	50,922	50,762	50,652
	At 10% discount rate					
Transformation start ages [years]	20	12	8	8	8	7
Transformation end ages [years]	20	20	23	24	26	26
NPV_T [$\text{US\$ ha}^{-1}$]	12,972	4013	−1467	−2410	−3941	−5182
EV after transformation at steady state [$\text{US\$ ha}^{-1}$]	15,237	37,234	48,533	45,589	51,673	54,865
EV discounted to the plantation establishment [$\text{US\$ ha}^{-1}$]	2264	4574	5420	4628	4335	4603
LEV_T [$\text{US\$ ha}^{-1}$]	15,237	8587	3952	2218	393	−578

observed an increase in carbon storage with reducing thinning intensity. With regard to extension of rotations, we observed an increase of 29.7% in mean carbon storage in biomass for a 50% increase in rotation length. Kaul et al. (2010), who also modelled carbon storage of tropical Sal (*Shorea robusta*) forests obtained similar results. They found an increase in overall carbon storage when increasing the rotation length from 120 to 150 years, where carbon storage in biomass increased by 15 Mg ha^{-1} (18%), carbon storage in soil increased very slightly and carbon storage in wood products decreased by 4 Mg ha^{-1} (23%).

Kraenzel et al. (2003) further estimated that teak plantations in Panama store on average about 225 Mg ha^{-1} of C in 1.3 m deep soil, yet most of this soil carbon was probably already present before the plantation establishment. Silver et al. (2000) reported an average soil carbon accumulation rate of 1.3 Mg ha^{-1} year^{-1} during the first 20 years after reforestation. They further reported 90 ± 9 Mg ha^{-1} of average soil carbon in forest plantations, which was significantly higher than for secondary forests (61 ± 3 Mg ha^{-1}). In a comparative study of tropical tree plantations and secondary forests of similar age and site conditions, Lugo (1992) also found aboveground biomass of plantations to be higher than of secondary forests. Poorter et al. (2016) found net carbon uptake of secondary, neotropical forests to be 3.05 Mg ha^{-1} year^{-1} during the first twenty years. Reforestation with teak can therefore offer an important contribution to carbon sequestration. Since the permanence of forest is a key element for long-term carbon storage, we suggest incentives for ensuring the permanence of forest cover.

4.3. *Biodiversity conservation*

Evaluating to what extent uneven-aged forest management contributes to biodiversity conservation was one of the major difficulties of this study. We used the Gini Coefficient to monitor the transformation into an uneven-aged forest system and to quantify stand structural diversity, since stand structural diversity is considered to promote forest biodiversity (Ishii et al., 2004; Kuuluvainen, 2002; Lindenmayer et al., 2000). Yet, the relationship between forest structure and forest biodiversity is very complex and operates on a range of spatial and temporal scales (Kuuluvainen, 2002). Consequently, structural diversity indices are insufficient to describe most aspects of forest biodiversity. Neumann and Starlinger (2001), for example found a weak, negative relationship between stand structural diversity and vascular plant diversity of temperate forests. In relation to this debate, we lack experimental studies from tropical regions. More research on functional relationships between uneven-aged forests and forest biodiversity is thus urgently needed.

For thorough biodiversity conservation, uneven-aged forest management would need to go along with other measures, such as the retention of old trees and dead wood and the use of native and mixed species (Carnus et al., 2006; Hartley, 2002; Lindenmayer et al., 2006). Several studies have shown that forest plantations with native and exotic species can enhance regeneration of degraded, deforested lands in Costa Rica (Cusack and Montagnini, 2004; Guariguta et al., 1995; Haggar et al., 1997; Powers et al., 1997). Teak plantations have in fact shown to reduce colonialization with native, woody regeneration compared to unmanaged, abandoned pasture land (Healey and Gara, 2003). This might be partly explained by the general habit to clean understory vegetation in teak plantations (Healey and Gara, 2003). Although cleaning is important during the first three years of plantation establishment (Craven et al., 2009), it should be considered to cease this practice during later stages. Other factors that have been reported to influence colonization with woody, native species are the distance to seed sources and light incidence after canopy closure (Cusack and Montagnini, 2004). Teak plantations with closed canopies have shown to effectively shade out and thus to control the invasive grass species *Saccharum spontaneum* in Panama (Craven et al., 2009). And although natural regeneration was lower for teak plantations than for abandoned pasture land (Healey and Gara, 2003), it did not impede natural regeneration completely. Therefore, teak plantations could be said to contribute to biodiversity conservation when compared to agricultural land uses, such as active cattle farming. Due to stable markets and high prices, teak plantations grown under good conditions might actually be able to compete with this land use form (Stefanski et al., 2015). Although much more valuable for biodiversity conservation, native tree species plantations sometimes face problems of very low demand and highly uncertain prices (personal communication, Griess and Knoke, 2011).

4.4. *Economic implications*

Our study suggested a net present value of almost 40,000 $\text{US\$ ha}^{-1}$.

We want to stress that this is only valid for assumptions of perfect conditions, including the best fertility rating (FR = 1). Under medium fertility conditions (FR = 0.7) NPV was only about a third (12,669 US\$ ha^{-1}). Griess and Knoke (2011) reported a NPV of 13,267 US\$ ha^{-1} for teak plantations in Panama, when using a 5% discount rate.

We observed that economically optimal rotation lengths differed depending whether one or more rotations were considered, displaying a trend towards longer periods when considering only one rotation. Once the economically optimal rotation length was exceeded, we observed a marked trade-off between carbon storage and economic return. Buongiorno et al. (2012) found payment for carbon to compensate effectively for such losses, but this does not seem to work for teak plantations, where carbon credits only contribute about 1% to overall revenues (Derwisch et al., 2009). The same could be said about payments for reforestation (PES) paid by the Costa Rican government, which contributed by about 3–4% to overall revenues. Thus if PES or carbon credits should stimulate a management for carbon sequestration, the payments need to be increased and special incentives for longer rotation periods and low thinning management need to be developed.

Our analysis further showed that the transformation into an uneven-aged forest would deliver economic returns very similar to even-aged systems at 1% discount rate, but notably lower returns at 5% and 10% discount rate. Losses are either caused by a quick and early transformation that leads to lower economic returns from timber harvest or by a postponed transformation that causes a delay in timber harvests of future generations. Hanewinkel (2002) found that consideration of risk strongly influences the profitability of silvicultural systems, where uneven-aged systems have advantages over even-aged management at high levels of risk. This finding is supported by Roessiger et al. (2011), who found this effect to be especially relevant for small forest properties, since these are exposed to greater risk of severe damage on a major proportion of their land. A large part of the economic advantages of uneven-aged forestry is attributed to selection cutting, since this management system makes it possible to harvest trees depending on their diameter rather than their age (Tahvonen et al., 2010). The group selection system modelled in this study does not display this advantage. Theoretically, the group harvesting modelled in this study could be replaced by selection cutting. Yet, since teak is a light demanding species, selection cutting might not be a suitable option. Field experiments on teak growth in a system with selection cutting would be needed to make more precise estimations of the economic consequences of this management system. Uneven-aged forests are moreover thought to provide higher forest resilience and stability in a changing climate, since they can recover quicker from disturbances and adapt faster to changing climate conditions (Diaci et al., 2011; Guldin, 2011). This does apply to the group harvesting modelled in this study. The inclusion of a risk component into the economic analysis that takes into account risks caused by climate change related disturbance events should thus be considered.

4.5. Potential synergies between carbon sequestration and biodiversity conservation

In addition to enhanced carbon storage, longer rotation periods are assumed to be directly linked to higher species richness and diversity (Mang and Brodie, 2015; Styring et al., 2011). An increase in carbon storage could moreover indirectly benefit biodiversity by reducing the risk of species extinction resulting from climate change (Pounds et al., 2006). An uneven-aged forest system could moreover benefit the forest's carbon balance. Seidl et al. (2008) for example found that transition to continuous cover forestry with selection harvest has considerable potential to increase carbon storage of managed forests.

5. Conclusions

Calibration of 3PG led to acceptable predictions for teak plantations in Costa Rica and made the model suitable for further investigations. Extension of rotations and variation in thinning intensity are management strategies that can be used to increase carbon storage of teak plantations, but they are associated with economic losses. If this should be compensated by PES, the amount paid for carbon storage needs to be increased and special incentives for longer rotation periods and low thinning management need to be developed. Transformation into uneven-aged forest stands requires an active investment at discount rates higher than 1%. Further studies are needed to assess whether this investment could be compensated by increased forest resilience or through selection cutting. Impacts of continuously-covered, uneven-aged forest plantations on tropical biodiversity need evaluation in the field. Other measures of biodiversity conservation, such as the use of native and mixed tree species and the retention of old trees and deadwood are moreover necessary.

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Appendix A

3PG parameter table for teak in Costa Rica. Calibration and implementation were made in the R environment and results may differ if the parameters are implemented in a different environment. The R code can be supplied on request.

Parameter description	3PG name	Value	Unit	Method	Reference
Allocation					
Foliage:stem partitioning ratio at DBH = 2 cm	pFS2	0.7		Fitted	
Foliage:stem partitioning ratio at DBH = 20 cm	pFS20	0.007		Fitted	
Constant in the stem mass vs. DBH relationship	aWs	0.18		Fitted	
Power in the stem mass vs. DBH relationship	nWS	2.31		Fitted	
Maximum root biomass partitioning	pRx	0.23		Literature	Kraenzel et al. (2003)
Minimum root biomass partitioning	pRn	0.11		Literature	Kraenzel et al. (2003)
Litterfall and root turnover			month^{-1}		
Litterfall rate for mature trees	gammaF1	0.00823		Literature	Kraenzel et al. (2003)
Litterfall rate at t = 0	gammaF0	0.001	month^{-1}	Default	Sands (2010)
Age at which litterfall rate has median value	tgammaF	12	month	Default	Sands (2010)
Average monthly root turnover	gammaR	0.015	month^{-1}	Literature	Pontes (2011)
NPP and conductance modifiers					

Temperature			C°		
Minimum temperature for growth	Tmin	13		Literature	Pandey and Brown (2000)
Maximum temperature for growth	Tmax	43	C°	Literature	Pandey and Brown (2000)
Optimal temperature for growth	Topt	26	C°	Literature	Martínez (2015)
Modifier for production loss due to frost	kF	0	days	No Frost	
CO2 modifier					
assimilation enhancement factor for 700 ppm atmospheric CO2	fCalpha700	1.4		Default	Sands (2010)
canopy conductance enhancement factor at 700 ppm atmospheric CO2	fCg700	0.7		Default	Sands (2010)
Fertility effects					
Value of m when FR = 0	m0	0		Default	Sands (2010)
Nutrient availability if FR = 0	fN0	0.3		Fitted	
Shape of the response curve	fNn	0.5		Fitted	
Age modifier					
Maximum stand age	MaxAge	50	Years	Defined	Weaver (1993)
Relative age when forest growth is reduced to 50%	rAge	0.08		fitted	
Shape of the growth reduction curve	nAge	3		Fitted	
Self-thinning			year^{-1}		
Mortality rate for large t	gammaN1	0		Default	Sands (2010)
Seedling mortality rate (t = 0)	gammaN0	0	Year^{-1}	Default	Sands (2010)
Age at which mortality rate has median value	tgammaN	2	Years	Default	Sands (2010)
Shape of mortality response	ngammaN	1		Default	Sands (2010)
Maximum stem mass per tree @ 1000 trees/ha	wS × 1000	120	kg tree^{-1}	Fitted	
Power in self-thinning law	thinpower	1.5		Default	Sands (2010)
Leaf mortality fraction	mF	0.5		Fitted	
Root mortality fraction	mR	0.8		Fitted	
Stem mortality fraction	mS	0.8		Fitted	
Canopy structure and processes					
Specific Leaf Area					
Specific leaf area young	SLA0	7.78	m^2 kg^{-1}	Literature	Pontes (2011)
Specific leaf area adult	SLA1	13.79	m^2 kg^{-1}	Literature	Pontes (2011)
Age when SLA = (SLA0 + SLA1)/2	tSLA	4.667	years	Literature	Pontes (2011)
Light Interception					
Radiation extinction coefficient	k	0.47		Literature	Pontes (2011)
Stand age when full canopy cover is reached in years	fullCanAge	3	years	Literature	Pontes (2011)
Rain interception					
Max. proportion of rainfall intercepted by canopy	MaxIntcptn	0.15		Literature	Pontes (2011)
LAI required for maximum rainfall interception	LAImaxIntcptn	3.33	m^2 m^{-2}	Literature	Pontes (2011)
Production and respiration					
Maximum canopy quantum efficiency	alphaCx	0.06	molC/molPAR	Fitted	
Assimilation use efficiency/respiration	y	0.47		Default	Sands (2010)
Conductance					
Response of canopy conductance to VPD	CoeffCond	0.05	mbar	Fitted	
Minimum canopy conductance	MinCond	0	m s^{-1}	Default	Sands (2010)
Maximum canopy conductance	MaxCond	0.2	m s^{-1}	Literature	Pontes (2011)
Canopy boundary layer conductance	BLCond	0.2	m s^{-1}	Default	Sands (2010)
LAI required for maximum canopy conductance	LAIgcx	3.3	m^2 m^{-2}	Literature	Pontes (2011)
Wood and stand properties					
Stem height					
Constant in the stem height relationship	aH	1.65		Fitted	
Power of DBH in the stem height relationship	nHB	0.73		Fitted	
Power of stocking in the stem height relationship	nHN	0.02		Fitted	
Stand volume					
Constant in the stem volume relationship	aV	0.000043		Fitted	
Power of DBH in the stem volume relationship	nVB	2.55		Fitted	
Power of stocking in the stem volume relationship	nVN	1.16		Fitted	

Appendix B

Formula used for calculating NPV of even-aged plantations:

$$NPV = \frac{\sum_{t=0}^{R} v_t}{(1+r)^t} \tag{1}$$

where v = a cost or revenue in US$/ha, t = time after plantation establishment when the cost or revenue occurred in years, R = rotation length in years, r = yearly discount rate.

Formula used for calculating LEV of even-aged plantations:

$$LEV = \frac{\sum_{t=0}^{R} v_t(1+r)^{R-t}}{(1+r)^R - 1} \tag{2}$$

where symbols are as explained above.

NPV_T was calculated using a modified version of the standard NPV formula (Eq. (1)):

$$NPV_T = \sum_{n=1}^{N}\sum_{t=0}^{T} \frac{v_{nt} * a_n}{(1+r)^t} \tag{3}$$

where n = a particular age group, N = total number of age groups, t = time after plantation establishment when a cost or revenue occurred in years, T = transformation end in years, v = cost of revenue of a particular age group in a particular year, a = area of a particular age group and r = yearly discount rate. If the patches of a certain age group had a second generation growing before the transformation ended, costs and revenues from the second generation were also considered.

The EV at steady state was calculated using a modified version of the LEV formula (Eq. (2)):

$$EV = \frac{\sum_{n=1}^{N}\sum_{\tau=0}^{R} v_{n\tau}(1+r)^{R-\tau} * a_n}{(1+r)^R - 1} \tag{4}$$

where τ = time after transformation end when a cost or revenue occurred in years; all other variables are as specified above. Rotation age of the uneven-aged systems was also 20 years. Note that EV calculation was not a bare land situation (in contrast to LEV and NPV calculation) and thus discounting times could differ from the trees' ages.

Harvest costs were 30 US$ m^{-3} and stumpage price (P; in US$ m^{-3}) was calculated with a price function, that was fitted based on data from the Costa Rican national forestry office (OFN, 2013):

$$P_{age} = -146.14 + 16.01 * DBH_{age} \tag{5}$$

with $P_{age} = 0$, if $DBH_{age} < 13$ cm.

Establishment costs were 580 US$ ha^{-1} for soil preparation, planning and planting. Maintenance costs, including weeding and pruning during the first years, were 2270 US$ ha^{-1} in the first year, 1030 US$ ha^{-1} in the second and third year, 830 US$ ha^{-1} in the fourth year and 430 US$ ha^{-1} $year^{-1}$ from year five until the rotation end. Administration costs were 400 US$ ha^{-1} $year^{-1}$.

References

Amichev, B.Y., Bentham, M.J., Kurz, W.A., Laroque, C.P., Kulshreshtha, S., Piwowar, J.M., et al., 2016. Carbon sequestration by white spruce shelterbelts in Saskatchewan, Canada: 3PG and CBM-CFS3 model simulations. Ecol. Model. 325, 35–46. http://dx.doi.org/10.1016/j.ecolmodel.2016.01.003.

Augustynczik, A.L., Hartig, F., Minunno, F., Kahle, H.-P., Diaconu, D., Hanewinkel, M., et al., 2017. Productivity of Fagus sylvatica under climate change – A Bayesian analysis of risk and uncertainty using the model 3-PG. For. Ecol. Manage. 401, 192–206. http://dx.doi.org/10.1016/j.foreco.2017.06.061.

Barlow, J., Gardner, T.A., Araujo, I.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., et al., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. PNAS 104, 18555. http://dx.doi.org/10.1073/pnas.0703333104.

Behling, M., 2009. Nutrição, partição de biomassa e crescimento de povoamentos de teca em Tangará da Serra-MT. PhD Thesis, Minas Gerais.

Bermejo, I., Cañellas, I., Miguel, A.S., 2004. Growth and yield models for teak plantations in Costa Rica. For. Ecol. Manage. 189, 97–110. http://dx.doi.org/10.1016/j.foreco.2003.07.031.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17, 925–951. http://dx.doi.org/10.1007/s10531-008-9380-x.

Buongiorno, J., Halvorsen, E.A., Bollandsås, O.M., Gobakken, T., Hofstad, O., 2012. Optimizing management regimes for carbon storage and other benefits in uneven-aged stands dominated by Norway spruce, with a derivation of the economic supply of carbon storage. Scand. J. For. Res. 27, 460–473. http://dx.doi.org/10.1080/02827581.2012.657671.

Carnus, J.-M., Parotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., et al., 2006. Planted forests and biodiversity. J. Forest. 104, 65–77. http://dx.doi.org/10.1093/jof/104.2.65.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., Zambrano, A.M.A., Aide, T.M., et al., 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Sci. Adv. 2, e1501639. http://dx.doi.org/10.1126/sciadv.1501639.

Clark, D.B., Clark, D.A., Oberbauer, S.F., 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO_2. Glob. Change Biol. 16, 747–759. http://dx.doi.org/10.1111/j.1365-2486.2009.02004.x.

Craven, D., Hall, J., Verjans, J.-M., 2009. Impacts of herbicide application and mechanical cleanings on growth and mortality of two timber species in saccharum spontaneum grasslands of the panama canal watershed. Restor. Ecol. 17, 751–761. http://dx.doi.org/10.1111/j.1526-100X.2008.00408.x.

Cusack, D., Montagnini, F., 2004. The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. For. Ecol. Manage. 188, 1–15. http://dx.doi.org/10.1016/S0378-1127(03)00302-5.

de Camino Velozo R, Villalobos R, Morales Aymerich JP, 2016. Costa Rica Case Study: Prepared for FAO as part of the State of the World's Forests 2016 (SOFO). http://www.fao.org/3/a-C0180e.pdf, 21 November 2016.

Derwisch, S., Schwendenmann, L., Olschewski, R., Hölscher, D., 2009. Estimation and economic evaluation of aboveground carbon storage of Tectona grandis plantations in Western Panama. New Forest. 37, 227–240. http://dx.doi.org/10.1007/s11056-008-9119-2.

Diaci, J., Kerr, G., O'hara, K., 2011. Twenty-first century forestry: Integrating ecologically based, uneven-aged silviculture with increased demands on forests. Forestry 84, 463–465. http://dx.doi.org/10.1093/forestry/cpr053.

Dirzo, R., Raven, P.H., 2003. Global State of biodiversity and loss. Annu. Rev. Environ. Resour. 28, 137–167. http://dx.doi.org/10.1146/annurev.energy.28.050302.105532.

FAO, 2010. Global Forest Resources Assessment 2010: Main report. http://www.fao.org/docrep/013/i1757e/i1757e.pdf, 12 October 2017.

FAO, 2015. Global teak trade in the aftermath of Myanmar's log export ban: by Kollert, W., Walotek, P.J. Planted Forests and Trees Working Paper FP/49/E. Rome, Italy. http://www.fao.org/forestry/plantedforests/67508@170537/en/, 1 December

2016.

FAO, 2016. State of the world's forests. Forests and agriculture: land-use challenges and opportunities. http://www.fao.org/publications/sofo/2016/en/, 16 May 2017.

Gopalakrishnan, R., Jayaraman, M., Swarnim, S., Chaturvedi, R.K., Bala, G., Ravindranath, N.H., 2011. Impact of climate change at species level: a case study of teak in India. Mitig Adapt Strateg Glob Change 16, 199–209. http://dx.doi.org/10.1007/s11027-010-9258-6.

Griess, V.C., Knoke, T., 2011. Can native tree species plantations in Panama compete with Teak plantations?: an economic estimation. New Forest. 41, 13–39. http://dx.doi.org/10.1007/s11056-010-9207-y.

Guariguta, M.R., Rheingans, R., Montagini, F., 1995. Early woody invasion under tree plantations in costa rica: implications for forest restoration. Restor Ecol. 3, 252–260. http://dx.doi.org/10.1111/j.1526-100X.1995.tb00092.x.

Guldin, J.M., 2011. Experience with the selection method in pine stands in the southern United States, with implications for future application. Forestry 84, 539–546. http://dx.doi.org/10.1093/forestry/cpr035.

Haggar, J., Wightman, K., Fisher, R., 1997. The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. For. Ecol. Manage. 99, 55–64. http://dx.doi.org/10.1016/S0378-1127(97)00194-1.

Hallet, J.T., Díaz-Calvo, J., Villa-Castillo, J., Wagner, M.R., 2011. Teak plantations: economic bonanza or environmental disaster? J. Forest. 109, 288–292.

Hanewinkel, M., 2002. Comparative economic investigations of even-aged and uneven-aged silvicultural systems: a critical analysis of different methods. Forestry 75, 473–481. http://dx.doi.org/10.1093/forestry/75.4.473.

Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155, 81–95. http://dx.doi.org/10.1016/S0378-1127(01)00549-7.

Healey, S.P., Gara, R.I., 2003. The effect of a teak (Tectona grandis) plantation on the establishment of native species in an abandoned pasture in Costa Rica. For. Ecol. Manage. 176, 497–507. http://dx.doi.org/10.1016/S0378-1127(02)00235-9.

Hidalgo, H.G., Alfaro, E.J., 2015. Skill of CMIP5 climate models in reproducing 20th century basic climate features in Central America. Int. J. Climatol. 35, 3397–3421. http://dx.doi.org/10.1002/joc.4216.

Ishii, H.T., Tanabe, S.-I., Hiura, T., 2004. Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. Forest Sci. 50, 342–355.

Jégo, G., Thibodeau, F., Morissette, R., Crépeau, M., Claessens, A., Savoie, P., 2017. Estimating the yield potential of short-rotation willow in Canada using the 3PG model. Can. J. For. Res. 47, 636–647. http://dx.doi.org/10.1139/cjfr-2016-0353.

Kanninen, M., Pérez, D., Montero, M., Víquez, E., 2004. Intensity and timing of the first thinning of Tectona grandis plantations in Costa Rica: results of a thinning trial. For. Ecol. Manage. 203, 89–99. http://dx.doi.org/10.1016/j.foreco.2004.07.054.

Kaul, M., Mohren, G.M.J., Dadhwal, V.K., 2010. Carbon storage and sequestration potential of selected tree species in India. Mitig. Adapt. Strat. Glob. Change 15, 489–510. http://dx.doi.org/10.1007/s11027-010-9230-5.

Keogh, R.M., 1979. Teak (Tectona grandis) provisional site classification chart for the Caribbean, Central America. Venezuela and Colombia. Unpublished, Original document at FAO head-quarters, Rome.

Kollert W, Cherubini L, 2012. Teak Resources and Market Assessment 2010. FAO Planted Forests and Trees Working Paper FP/47/E, Rome. http://www.fao.org/forestry/plantedforests/67508@170537/en/, 2 February 2017.

Kraenzel, M., Castillo, A., Moore, T., Potvin, C., 2003. Carbon storage of harvest-age teak (Tectona grandis) plantations, Panama. For. Ecol. Manage. 173, 213–255. http://dx.doi.org/10.1016/S0378-1127(02)00002-6.

Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fennica 36, 97–125. http://dx.doi.org/10.14214/sf.552.

Kuuluvainen, T., Tahvonen, O., Aakala, T., 2012. Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. Ambio 41, 720–737. http://dx.doi.org/10.1007/s13280-012-0289-y.

Landsberg, J., Waring, R., Coops, N., 2003. Performance of the forest productivity model 3-PG applied to a wide range of forest types. For. Ecol. Manage. 172, 199–214. http://dx.doi.org/10.1016/S0378-1127(01)00804-0.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manage. 95, 209–228. http://dx.doi.org/10.1016/S0378-1127(97)00026-1.

Lawton, R.O., Nair, U.S., Pielke Sr., R.A., Welch, R.M., 2001. Climatic impact of tropical lowland deforestation on nearby montane cloud forests. Science 294, 584–587. http://dx.doi.org/10.1126/science.1062459.

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland et al., G., Le Quéré et al., C., Marland, G. et al., 2009. Trends in the sources and sinks of carbon dioxide. Nature Geoscience 2, pp. 831–836. http://doi.org/10.1038/ngeo689.

Lexerød, N.L., Eid, T., 2006. An evaluation of different diameter diversity indices based on criteria related to forest management planning. For. Ecol. Manage. 222, 17–28. http://dx.doi.org/10.1016/j.foreco.2005.10.046.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol. Conserv. 131, 433–445. http://dx.doi.org/10.1016/j.biocon.2006.02.019.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14, 941–950. http://dx.doi.org/10.1046/j.1523-1739.2000.98533.x.

Lugo, A.E., 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecol. Monogr. 62, 1–41. http://dx.doi.org/10.2307/2937169.

Mang, S.L., Brodie, J.F., 2015. Impacts of non-oil tree plantations on biodiversity in Southeast Asia. Biodivers. Conserv. 24, 3431–3447. http://dx.doi.org/10.1007/s10531-015-1022-5.

Martínez HA, 2015. Teca (Tectona grandis L. f.): condiciones para su cultivo “Fomento de la reforestación comercial para la mejora y conservación de las reservas de carbono”. Fondo Nacional de Financiamiento Forestal Costa Rica. http://www.fonafifo.go.cr/documentacion/biblioteca/consultorias_investigaciones/FF_5_Teca.pdf, 23 November 2016.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. https://www.millenniumassessment.org/documents/document.354.aspx.pdf, 20 November 2017.

Ministerio de Ambiente y Energia, 2015. La Gaceta N°143: PAGOS DE SERVICIOS AMBIENTALES PARA EL AÑO 2015. Articulo 2°. http://www.fonafifo.go.cr/psa/estadisticas/gePSA-decreto2015.pdf, 30 March 2018.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. http://dx.doi.org/10.1038/35002501.

Nasi R, Wunder S, Campos A. JJ, 2002. Forest ecosystem services: Can they pay our way out of deforestation? https://vtechworks.lib.vt.edu/handle/10919/66870, 9 November 2017.

Neumann, M., Starlinger, F., 2001. The significance of different indices for stand structure and diversity in forests. For. Ecol. Manage. 145, 91–106. http://dx.doi.org/10.1016/S0378-1127(00)00577-6.

Niemelä, J., Koivula, M., Kotze, D.J., 2007. The effects of forestry on carabid beetles (Coleoptera Carabidae) in boreal forests. J Insect Conserv 11, 5–18. http://dx.doi.org/10.1007/s10841-006-9014-0.

NOAA. Trends in Atmospheric Carbon Dioxide. https://www.esrl.noaa.gov/gmd/ccgg/trends/full.html, 1 December 2017.

Nyland, R.D., 2003. Even- to uneven-aged: the challenges of conversion. For. Ecol. Manage. 172, 291–300. http://dx.doi.org/10.1016/S0378-1127(01)00797-6.

O’Hara, K.L., 2001. The silviculture of transformation — a commentary. For. Ecol. Manage. 151, 81–86. http://dx.doi.org/10.1016/S0378-1127(00)00698-8.

OFN, 2013. Precios de la Madera: Costa Rica, Primer Semestre, 2013. https://www.onfcr.org/publicaciones-tecnicas-onf/precios-de-la-madera, 3 April 2017.

OFN, 2015. Usos y aportes de la madera. Costa Rica - Estadísticas 2015. https://www.onfcr.org/article/usos-y-aportes-de-la-madera-en-costa-rica/, 16 May 2017.

Pan, Y., 2011. A large and persistent carbon sink in the world’s forests. Science 333, 988–993. http://dx.doi.org/10.1126/science.1204588.

Pandey, D., Brown, C., 2000. Teak: a global overview: an overview of global teak resources and issues affecting their future outlook. Unasylva 201 (51), 3–13.

Pawson, S.M., Brockerhoff, E.G., Meenken, E.D., Didham, R.K., 2008. Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodivers. Conserv. 17, 1127–1148. http://dx.doi.org/10.1007/s10531-008-9363-y.

Pawson, S.M., Brockerhoff, E.G., Norton, D.A., Didham, R.K., 2006. Clear-fell harvest impacts on biodiversity: past research and the search for harvest size thresholds. Can. J. For. Res. 36, 1035–1046. http://dx.doi.org/10.1139/x05-304.

Pawson, S.M., Brockerhoff, E.G., Watt, M.S., Didham, R.K., 2011. Maximising biodiversity in plantation forests: Insights from long-term changes in clearfell-sensitive beetles in a Pinus radiata plantation. Biol. Conserv. 144, 2842–2850. http://dx.doi.org/10.1016/j.biocon.2011.08.001.

Payn, T., Carnus, J.-M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., et al., 2015. Changes in planted forests and future global implications. For. Ecol. Manage. 352, 57–67. http://dx.doi.org/10.1016/j.foreco.2015.06.021.

Pérez, D., 2005. Stand growth scenarios for Tectona grandis plantations in Costa Rica. Academic dissertation 2005.

Pérez, D., 2008. Growth and volume equations developed from stem analysis for Tectona Grandis in Costa Rica. J. Trop. For. Sci. 20, 66–75.

Pérez, D., Kanninen, M., 2003a. Aboveground biomass of Tectona grandis plantations in Costa Rica. J. Trop. For. Sci. 15, 199–213.

Pérez, D., Kanninen, M., 2003b. Provisional equations for estimating total and merchantable volume of Tectona grandis trees in Costa Rica. Forest Trees Livelihoods 13, 345–359.

Pérez, D., Kanninen, M., 2005. Stand growth scenarios for Tectona grandis plantations in Costa Rica. For. Ecol. Manage. 210, 425–441. http://dx.doi.org/10.1016/j.foreco.2005.02.037.

Pontes, M.d.S., 2011. Parametrização do modelo 3-PG para teca (Tectona grandis L.f.) e dos sistemas FERTI-UFV e NUTRI-UFV para subsidiar o seu manejo nutricional. Master Thesis, Minas Gerais.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., et al., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. http://dx.doi.org/10.1038/nature16512.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., et al., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161–167. http://dx.doi.org/10.1038/nature04246.

Powers, J.S., Haggar, J.P., Fisher, R.F., 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. For. Ecol. Manage. 99, 43–54. http://dx.doi.org/10.1016/S0378-1127(97)00193-X.

Rockström, J., Steffen, W., Noone, K., Persson, A., Chapin, S.F., Lambin, E.F., et al., 2009. A safe operating space for humanity. Nature 461, 472–475. http://dx.doi.org/10.

1038/461472a.

Roessiger, J., Griess, V.C., Knoke, T., 2011. May risk aversion lead to near-natural forestry?: A simulation study. Forestry: An Int. J. Forest Res. 84, 527–537. http://dx.doi.org/10.1093/forestry/cpr017.

Sands P, 2010. 3PG-PJS User Manual, 26 April 2017.

Schroeder, P., 1992. Carbon storage potential of short rotation tropical tree plantations. For. Ecol. Manage. 50, 31–41. http://dx.doi.org/10.1016/0378-1127(92)90312-W.

Seidl, R., Rammer, W., Lasch, P., Badeck, F.-W., Lexer, M.J., 2008. Does conversion of even-aged, secondary coniferous forests affect carbon sequestration? A simulation study under changing environmental conditions. Silva Fennica 42, 369–386.

Silver, W.L., Ostertag, R., Lugo, A.E., 2000. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor Ecol. 8, 394–407. http://dx.doi.org/10.1046/j.1526-100x.2000.80054.x.

Stefanski, S.F., Shi, X., Hall, J.S., Hernandez, A., Fenichel, E.P., 2015. Teak–cattle production tradeoffs for Panama Canal Watershed small scale producers. Forest Policy Econ. 56, 48–56. http://dx.doi.org/10.1016/j.forpol.2015.04.001.

Styring, A.R., Ragai, R., Unggang, J., Stuebing, R., Hosner, P.A., Sheldon, F.H., 2011. Bird community assembly in Bornean industrial tree plantations: effects of forest age and structure. For. Ecol. Manage. 261, 531–544. http://dx.doi.org/10.1016/j.foreco.2010.11.003.

Tahvonen, O., Pukkala, T., Laiho, O., Lähde, E., Niinimäki, S., 2010. Optimal management of uneven-aged Norway spruce stands. For. Ecol. Manage. 260, 106–115. http://dx.doi.org/10.1016/j.foreco.2010.04.006.

Weaver PL, 1993. Tectona Grandis L.f. Teak: Verbenaceae. Verbena Family. http://www.fs.fed.us/global/iitf/pubs/sm_iitf064%20%20(18).pdf, 4 November 2016.