

Growing biodiverse carbon-rich forests

JEAN-BAPTISTE PICHANCOURT*, JENNIFER FIRN*†, IADINE CHADÈS* and TARA G. MARTIN*

*CSIRO Ecosystem Sciences, Conservation Decision Team, Ecosciences Precinct, 41 Boggo road, Dutton Park, QLD 4102 Australia, †Faculty of Science and Technology, Queensland University of Technology, Brisbane, QLD 4001 Australia

Abstract

Regrowing forests on cleared land is a key strategy to achieve both biodiversity conservation and climate change mitigation globally. Maximizing these co-benefits, however, remains theoretically and technically challenging because of the complex relationship between carbon sequestration and biodiversity in forests, the strong influence of climate variability and landscape position on forest development, the large number of restoration strategies possible, and long time-frames needed to declare success. Through the synthesis of three decades of knowledge on forest dynamics and plant functional traits combined with decision science, we demonstrate that we cannot always maximize carbon sequestration by simply increasing the functional trait diversity of trees planted. The relationships between plant functional diversity, carbon sequestration rates above ground and in the soil are dependent on climate and landscape positions. We show how to manage ‘identities’ and ‘complementarities’ between plant functional traits to achieve systematically maximal cobenefits in various climate and landscape contexts. We provide examples of optimal planting and thinning rules that satisfy this ecological strategy and guide the restoration of forests that are rich in both carbon and plant functional diversity. Our framework provides the first mechanistic approach for generating decision-making rules that can be used to manage forests for multiple objectives, and supports joined carbon credit and biodiversity conservation initiatives, such as Reducing Emissions from Deforestation and forest Degradation REDD+. The decision framework can also be linked to species distribution models and socio-economic models to find restoration solutions that maximize simultaneously biodiversity, carbon stocks, and other ecosystem services across landscapes. Our study provides the foundation for developing and testing cost-effective and adaptable forest management rules to achieve biodiversity, carbon sequestration, and other socio-economic co-benefits under global change.

Keywords: biodiversity conservation, carbon sequestration, co-benefits, decision theory, ecosystem services, forest restoration, Optimal Control, plant functional diversity, plant functional traits

Received 18 April 2013; revised version received 22 July 2013 and accepted 25 July 2013

Introduction

Taxing, buying, and selling ‘bio-carbon credits’ are emerging worldwide as a key policy tool for mitigating climate change impacts (Venter *et al.*, 2009; Agrawal *et al.*, 2011; Phelps *et al.*, 2012). Large carbon sinks can be created by reforesting cleared land, as vegetation and soil microbes sequester carbon from the atmosphere. To date, most scientific research and efforts to reforest land for bio-sequestration have focused on establishing fast-growing single species plantations (i.e., monocultures) and agro-forestry crops for timber production (Diaz *et al.*, 2009; Agrawal *et al.*, 2011; Phelps *et al.*, 2012), which maximize above ground carbon sequestration in the short term. The problem with this approach is that adopting a monoculture strategy for regrowing forests limits the potentially large number of environmental and socio-economic cobenefits that more diverse forests can provide. Less biodiverse

forests can decrease soil carbon stocks, possibly a more stable sink of carbon over the long term than above ground biomass (Diaz *et al.*, 2009). Monocultures can also be more susceptible to disease and insect attack, provide little benefit for biodiversity conservation, and have poor nutrient retention that reduces plant species recruitment in the understorey (Hobbs & Suding, 2009). For these reasons, finding evidence and technical solutions for building larger and more stable stocks of carbon in biodiverse forests have attracted much attention from global initiatives (Diaz *et al.*, 2009; Venter *et al.*, 2009; Agrawal *et al.*, 2011; Phelps *et al.*, 2012), such as Reducing Emissions from Deforestation and Forest Degradation (REDD+), the Billion Tree Campaign, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) and the International Partnership for Satoyama Initiative (IPSI).

Responding to the need for guidance on how to balance biodiversity and carbon sequestration, research has turned to decision theory (Venter *et al.*, 2009; Wilson *et al.*, 2009; Crossman *et al.*, 2011). These studies

Correspondence: Jean-Baptiste Pichancourt, tel. +61 07 3833 5680, fax +61 07 3833 5504, e-mail: jean-baptiste.pichancourt@csiro.au

explore the large-scale spatial trade-offs of planning for carbon sequestration and biodiversity conservation but do not provide any detailed guidelines on what to plant and how to manage these plantings to achieve cobenefits given environmental conditions. Practitioners need a decision support system to provide such guidelines.

At present, our capacity to build such decision support systems to help regrow forests for both carbon and plant biodiversity simultaneously is limited by our knowledge of the relationship between these two objectives. Studies that have found a positive correlation between biodiversity and productivity in the past (measured as biomass: a surrogate of carbon sequestration) were generally conducted in grasslands and experimental communities (Adler *et al.*, 2011). Studies within forests are fewer and results are equivocal (Erskine *et al.*, 2006; Firn *et al.*, 2007; Vilà *et al.*, 2007; Whittaker, 2010; Ruiz-Jaen & Potvin, 2011; Nguyen *et al.*, 2012). Much of the controversy in the nature of the relationship involves the extent to which diversity effects are driven by single, highly productive species (known as the ‘selection effect hypothesis’: Cardinale *et al.*, 2012) vs. some form of ‘complementarity’ among species (known as the ‘complementarity hypothesis’: Cardinale *et al.*, 2012) (Fig. 1). Recently, a comparison of more than 200 studies found that species identity (‘selection effect’) and species diversity (‘complementarity’) contributed equally to explaining the relationship between biodiversity and productivity (Cardinale *et al.*, 2011). However, the relative extent to which these two mechanisms broadly contribute to productivity and carbon sequestration remains uncertain (Cardinale *et al.*, 2011). In parallel, forest management science is also

debating the most efficient methods for manipulating either species identities (known as the ‘framework species method’) or complementarities between species (known as the ‘maximum species diversity method’ (Florentine & Westbrooke, 2004) Fig. 1). The controversy lies in the fact that productivity and carbon sequestration are influenced more by the identities or complementarities between the plant functional traits that characterize species than by the identities or complementarities between species themselves (e.g., Bunker *et al.*, 2005; Mayfield *et al.*, 2010), that is, the ‘morpho-physio-phenological traits which impact fitness (and the role species play in the ecosystem) indirectly via their effects on growth, reproduction and survival (Violle *et al.* (2007). Furthermore, the relationship between carbon sequestration and the diversity of species plant functional traits (called plant functional diversity) depends on the environmental conditions where these species grow (e.g., soil, and position in the landscape or catchment, climate), and the disturbance regimes which are driven by natural and/or human processes (Molino & Sabatier, 2001; Ruiz-Jaen & Potvin, 2011).

As research and management agencies grapple with how to regrow forests that are rich in both carbon and plant functional diversity (Diaz *et al.*, 2009; Secretariat (Convention on Biological Diversity), 2011), in practice forests are being planted to maximize a single predictable objective, that is, forests for carbon or for some biodiversity metric like plant functional diversity (Diaz *et al.*, 2009; Secretariat (Convention on Biological Diversity), 2011), rather than for maximizing these two objectives simultaneously (Phelps *et al.*, 2012). Because

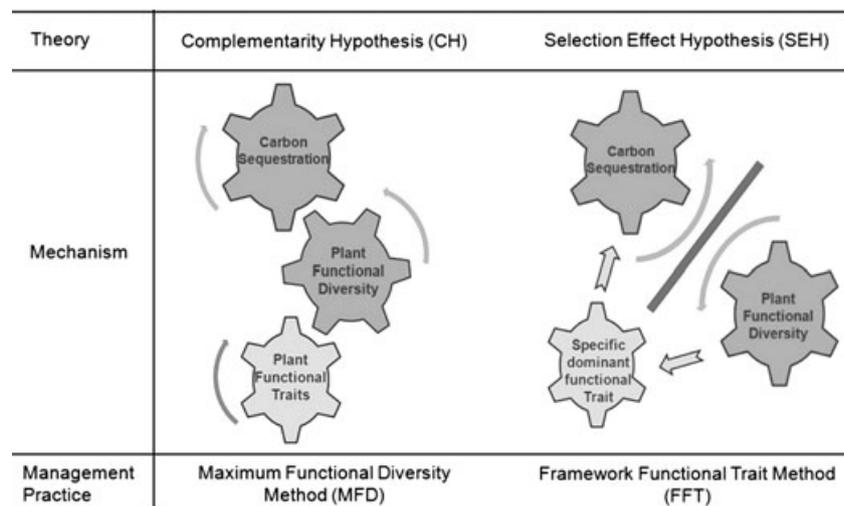


Fig. 1 Two hypotheses and practices to explain and restore carbon/biodiversity cobenefits: The ‘complementarity hypothesis’ (CH) and associated ‘maximum functional diversity’ method (MFD), suggest that high plant functional diversity (PFD) provides high trait complementarities, which in turn drive carbon sequestration. The ‘selection effect hypothesis’ (SEH) and associated ‘framework functional trait’ method (FFT) predict that functional traits drive carbon sequestration independently of the local PFD. We illustrate the mechanistic relationship between interlocking factors using cogs, where the turning of one can influence the turning of another.

regrowing forests for multiple benefits is a long-term investment where success is subject to changing climate and disturbance regimes, there is an urgent need to develop decision support systems to generate simple and testable rules to guide the decision process throughout the different phases of forest regrowth.

We present here a decision support system based on a mechanistic model of forest ecosystem dynamics, to identify forest regrowth strategies that cobenefit long-term total organic carbon sequestration and plant functional diversity. Applying the decision support system, we develop cobenefit management rules of thumb tailored for a region of Australia, Southeast Queensland; soils (i.e., medium grain, 2 m depth of A–B horizon), landscape position (i.e., upland and lowland), future climate scenarios (i.e., subtropical climate becoming drier or wetter). We focus on a situation where forests have been cleared, soil nitrogen is not a limiting factor, and the diversity of plant functional traits is still

present within surrounding remnant forests in the landscape. Our decision framework can be adjusted to generate other specific rules for different world locations and for landscapes characterized by different soil limitations, topographic, and climate contexts.

Materials and methods

We propose a decision model for identifying forest regrowth strategies that cobenefit the rate of total organic carbon sequestration over the long term and plant functional diversity. We form this model through the integration of a series of mathematical models that have been developed and previously tested independently elsewhere (see details in Data S1). We provide in the main text a summary of the model structure and implementation. Details of the equations and parameters are describes in the Data S1. Our model comprised three sub-models (see Fig. 2): (i) a model of the management decisions that includes choices available to practitioners on how to regenerate and maintain forests (Hobbs & Suding, 2009; see

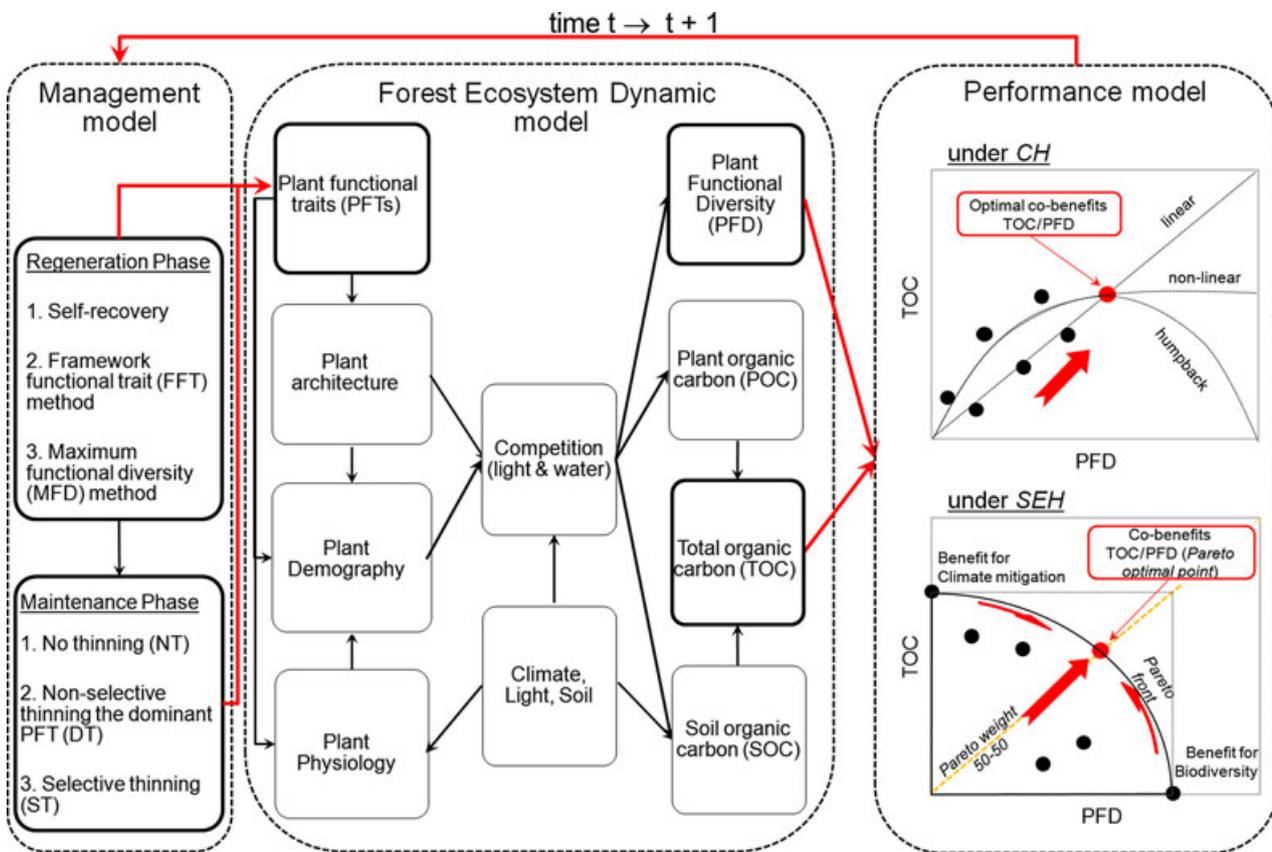


Fig. 2 General decision framework for managing cobenefits like Total organic carbon sequestration rate (TOC) and plant functional diversity (PFD). The restoration practitioner first defines the different options for manipulating the plant functional traits during the regeneration and maintenance phases, through the decision model. The consequences of these manipulations on forest TOC and PFD will be determined through a forest ecosystem dynamic model, which includes submodels of plant architecture, physiology, demography, competition, environment, and plant organic carbon and soil organic carbon sequestration. Depending on the TOC/PFD relationship, a performance model helps practitioners evaluate the optimal management strategy that maximizes the TOC/PFD cobenefits under ‘complementarity hypothesis’ or under ‘selection effect hypothesis’. See Data S1 for details of the models.

details in Data S1, section 1); (ii) a model of the forest ecosystem dynamics that synthesizes a series of mathematical equations that have been developed, and that simulates the realistic growth of a forest over different time periods depending on the functional traits of species chosen, management decisions, climate, landscape position, and soil conditions (Moorcroft *et al.*, 2001; Purves & Pacala, 2008; Medvigy *et al.*, 2009; Falster *et al.*, 2011; see details in Data S1, section 2); and (iii) a performance model that ranks the best set of decisions for the cobenefits of carbon sequestration and biodiversity (Gatto & De Leo, 2000; see details in Data S1, section 3). Our objective is to maximize both the total organic carbon sequestration rate and plant functional diversity across different climate projections and positions in the landscape (Table S1). By simulating and evaluating the growth of forests through time under two extreme climatic conditions (arid vs. wet), two landscape positions in a catchment (lowland vs. upland) and management strategies, we then identify rules of thumb to guide management (Fig. 2). Uplands were characterized in the model by climate-dependent soil-moisture variables, whereas lowlands were characterized by fully saturated soil-moisture conditions [see Data S1, section 2.2 Eqn (35)]. We used a partitioning method approach to select the two most relevant models of climate change among 23 possible coupled ocean-atmosphere models of climate change (CMIP3) for Australia (see Table S1 for details and reference of the method).

Management decision model

In the management decision model (Fig. 2 and Data S1, section 1), the manager is faced with important decisions that

need to be evaluated during two phases of forest regrowth (Prach & Pysek, 2001; Florentine & Westbrooke, 2004; Lamb *et al.*, 2005; Hobbs & Suding, 2009; Kanowski & Catterall, 2010): (i) regeneration – whether and which plant functional traits to choose when planting trees, and (ii) stand maintenance – whether, and how to maintain the stand by thinning. The decision model assumes first that the trees available to plant and thin in forests have a limited range of plant functional trait values (Lamb *et al.*, 2005; Falster *et al.*, 2011). We reduced the possible set of independent plant functional traits to three well studied and easily measured traits namely seed mass, leaf mass per area, and wood density (often called ‘soft traits’ (Diaz *et al.*, 2004)). These three functional traits have been shown to scale with most of the important plant functional traits that determine the plant architecture, plant physiology, plant competitive demography, and therefore have a strong influence on ecosystem functions (Falster *et al.*, 2008, 2011). As specified by Falster *et al.* (2008), we assumed in this study the seed size(mass) produced by a tree was correlated with tree size at maturity, but this constraint can be relaxed for trees that do not fit this relationship (Falster *et al.*, 2011). Different combinations of values for these three independent plant functional traits are called plant functional trait syndromes. We also assume that practitioners can choose between eleven possible management strategies (Table 1) involving planting or thinning trees with different plant functional trait syndromes during the regeneration and maintenance phases.

During the regeneration phase, practitioners must decide whether to allow for natural regeneration, hereafter self-recovery (Prach *et al.*, 2001), or initiate regeneration by

Table 1 Summary of the eleven actions used during the two management phases. δ , σ and ϕ are the three plant functional traits used to characterize the trees and, respectively, refer to timber density, seed mass, and leaf mass per area

Management phase	Action	Definition of the action
Regeneration	Self	Self-recovery without planting
	FFT ₁	Framework functional trait method by planting fast-growing tree species under full light (i.e., with low leaf mass per area ϕ) and with small size at maturity (i.e., small seeds* σ)
	FFT ₂	Framework functional trait method fast-growing tree species under full light (low ϕ) and with tall size at maturity (i.e., heavy seeds*)
	MFD δ	Maximum functional diversity method by planting late successional trees having the densest wood (δ) but with varying σ and ϕ
	MFD σ	Maximum functional diversity method by planting late successional trees producing the heaviest seeds but with varying δ and ϕ
	MFD ϕ	Maximum functional diversity method by planting late successional trees having with the highest leaf per area but with varying σ and δ
Maintenance	NT	No thinning
	DT	Thinning the species from the dominant plant functional trait syndrome ω
	ST δ	Selectively thinning the dominant ω to accelerate succession toward denser wood for long-lived and more resistant trees
	ST σ	Selectively thinning the dominant ω to accelerate succession toward greater seed mass for taller trees at maturity*
	ST ϕ	Selectively thinning the dominant ω toward more productive and shade tolerant understory with higher leaf mass per area

See details of actions in Data S1, section 1. * see Data S1, section 2.

planting trees with selected functional traits syndromes, hereafter enrichment planting. When choosing to initiate regeneration, planting fast-growing trees (i.e., characterized by low values of leaf mass per area) can provide increased canopy cover or 'framework' to aid in the suppression of undesirable weed species and promote shade-tolerant species in the understorey (Lugo, 1992; Florentine & Westbrooke, 2004). We refer to this option as the 'framework functional trait' method. The 'framework functional trait' method supports the 'selection effect hypothesis' (Fig. 1) and can be achieved in the model with two possible strategies [Table 1: 'framework functional trait' (FFT)]. The second option to initiate regeneration involves more complex and expensive strategies that plant a maximum diversity of species (Florentine & Westbrooke, 2004), each having a unique combination of plant functional traits. We refer to this option as the 'maximum functional diversity' method. The 'maximum functional diversity' method supports the 'complementarity hypothesis' and three different strategies are possible in the model [Table 1: 'maximum functional diversity' (MFD)]. Once the initial regeneration phase is chosen, the next phase is to decide what and how often to thin to reduce competition.

During the maintenance phase, practitioners have to decide whether they need to accelerate or maintain productivity of the stand over time, enhance desirable target species with specific sets of plant functional traits, or eradicate species with undesirable sets of traits (Florentine & Westbrooke, 2004; Lamb *et al.*, 2005; Chazdon, 2008; Dwyer *et al.*, 2010; Kanowski & Catterall, 2010; Paquette & Messier, 2010). We consider that practitioners have the choice between five thinning actions (Table 1). We also assume the practitioner can implement these thinning strategies at different frequencies: annually, every 5 years, 10 years, and 50 years. Each initial stand planted was defined in the model by one combination of planting and thinning strategy. As such, we have defined 126 unique combinations of planting and thinning strategies (and therefore 126 unique stands) that can be evaluated against our objectives over time under different climate, landscape position, and soil scenarios.

Forest ecosystem dynamic model

In the forest ecosystem dynamics model (Fig. 2), forests grow depending on the functional traits of the species planted, and competition for essential resources through a set of biological submodels (Data S1, section 2). As predicted by plant scaling relationships synthesized across many tree species in different climate and landscape conditions around the world, the model assumes that species with similar plant functional trait syndromes have very similar architecture, physiology, and demography (e.g., Nikolov *et al.*, 1995; Niklas, 2004; Moles & Westoby, 2006; Kattge *et al.*, 2011; and additional references in Data S1). Models based on these syntheses have already been developed and tested with success for forests characterized by species with a single functional trait syndrome (Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009; Falster *et al.*, 2011). This approach has never been considered for the management of forests characterized by a wide range of functional trait

diversity values. Given the extreme range of diversity of functional traits we consider in our study and the resulting long computation time, we did not include in the model the standard errors of the average scaling parameters estimated across tree species from referenced meta-analyses (see Table S2 for average values and associated references), which represent the unexplained intra- and interspecific variation of the scaling relationship between trees characterized by similar plant functional traits (Kattge *et al.*, 2011; Osnas *et al.*, 2013). However, for real-world management applications more likely characterized by a low range of plant functional configurations, we suggest these sources of error should be included when exact species-specific scaling relationships are unknown.

In this type of dynamic plant functional trait forest model, each syndrome of plant functional trait values ω is first used to define the allometric relationship between biomass and plant architecture (e.g., plant height, canopy area, root length, mass of fine roots, leaf length, bark density; see Data S1, section 2.1). Combined with the climate and soil conditions, we then derived from the values of the syndrome of plant functional trait, the physiological characteristics of trees (i.e., photosynthetic carbon assimilation, respiration, V_{\max} , J_{\max} , biomass turn-over, water absorption, carbon biomass production: see Data S1, section 2.2 and 2.3) and tree and seed vital rates (tree growth, survival, fertility, and seed survival and germination; see Data S1, section 2.4). All the vital rates from individuals within each syndrome of plant functional traits, size and life-stage (seed, plant) are then integrated into macroscopic equations to scale correctly from the parameters governing individual trees to the dynamics of tree community within the stand (Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009; Purves & Pacala, 2008; Falster *et al.*, 2011; see Data S1, section 2.4). The organic carbon sequestration of the trees above ground and in the roots can then be calculated per meter square (see Data S1, section 2.5). The carbon from the dead biomass (i.e., litter and dead individuals) is then processed and stocked in the soil using a carbon sequestration model. Practitioners can then measure the total carbon sequestration rate of the forest per meter square as the sum of the plant organic carbon and soil organic carbon to evaluate the performance of a management strategy. We defined a Shannon index representing the diversity of plant functional traits of a forest per meter square, based on the number of trees belonging to different unique plant functional trait syndromes. The index was built using a reduced set of plant functional traits that are known to be statistically independent: seed mass (σ), leaf mass per area (ϕ), and wood density (δ).

Performance model

In the performance model (Fig. 2 and Data S1, section 3), practitioners can compare and rank the effectiveness of alternative management strategies. This ranking depends on the relationship between the total carbon sequestration rate and plant functional diversity of the forest for the different climate and landscape contexts. If the relationship between the total carbon sequestration rate and plant functional diversity is found to follow the 'complementarity hypothesis', then the best

strategy will be the one that maximizes the cobenefits simultaneously the total carbon sequestration rate and plant functional diversity. In this case, the cobenefit relationship can be in theory positive linear, log-linear or unimodal (humpback) (Mittelbach *et al.*, 2001). If the relationship between the total carbon sequestration rate and the plant functional diversity follows the 'selection effect hypothesis', then the total carbon sequestration rate and plant functional diversity have no a-priori relationship and different strategies can occupy a space of solutions bounded by a Pareto front (Fig. 2). The Pareto formulation falls into the multi-objective decision problem, which consists of ranking the management strategies according to their geometric distance with the optimal cobenefit solution found along the Pareto front (Gatto & De Leo, 2000). To help rank the management strategies, we assumed the plant functional diversity and the total carbon sequestration rate of the forest are equally important and thus have the same weights (50/50). Therefore, the maximal Pareto cobenefit solution is the one that maximizes the sum of weighted carbon and weighted biodiversity benefits compared to the minimum possible cobenefit obtained from the range of possible management scenarios.

Results

The forest biodiversity–carbon relationship

Our model results suggest that we cannot simply maximize the annual rate of organic carbon sequestration above ground, in the soil, or the resulting total organic carbon sequestration rate by maximizing the plant functional diversity in a particular climate or landscape context. By simulating 126 combinations of decisions during the two restoration phases, across four climate-by-landscape scenarios over 100 years, we found context-specific relationships between the plant functional diversity and the above ground carbon sequestration rate (Fig. 3a), the soil carbon sequestration rate (Fig. 3b) and the total carbon sequestration rate (Fig. 3c). In arid/hot uplands (e.g., tropical semi-arid forests), increasing plant functional diversity does not change significantly the above ground carbon sequestration rate (Fig. 3a red data points), but changes the soil carbon sequestration rate and the total carbon sequestration rate nonlinearly (Fig. 3b and c), whereas the total carbon sequestration rate log-linearly decreases in wet/hot uplands (Fig. 3c light-blue data points). Forests that are regrown on lowlands (e.g., riparian or flood plain tropical rainforests) are not significantly sensitive to change in climate and have similar cobenefits for the scenarios considered, such that increasing plant functional diversity linearly increases the above ground carbon sequestration rate (Fig. 3a dark-blue data points), decreases the soil carbon sequestration rate (Fig. 3b), and increases by up to 100% the total carbon sequestration rate (Fig. 3c).

As a consequence, three context-specific Pareto spaces solutions emerge for the relationship between the total carbon sequestration rate and plant functional diversity (Fig. 3c and d). Each Pareto space is bounded by four forest states: a state where the total carbon sequestration rate and plant functional diversity are both low (a nondesirable state); a state where the total carbon sequestration rate is maximal but plant functional diversity is minimal, that is, beneficial for climate mitigation only; a state where the total carbon sequestration rate is minimal but plant functional diversity is maximal, that is, beneficial for biodiversity only; and an optimal state that cobenefits the total carbon sequestration rate and plant functional diversity, that is, the Pareto optimal point. Changing the climate or landscape position changed the Pareto-optimal solution (Fig. 3d). Therefore, the optimal management solution that maximizes simultaneously the total carbon sequestration/plant functional diversity must be adjusted to the climate and habitat context.

Decision rules that optimize cobenefits

Decisions in the regeneration phase of forest development matter most in wet/hot uplands (Fig. 4a, light-blue data points) and lowlands (Fig. 4a, dark-blue data points) regardless of the climate scenario. Under these climate and landscape conditions, enrichment planting using the 'maximum functional diversity' planting technique (MFD) is closer to the Pareto optimal trade-off than the 'framework functional trait' (FFT) or 'self-recovery' (Self) techniques. Furthermore on lowlands, 'self-recovery' provided higher plant functional diversity benefits than the 'framework functional trait method' (FFT), but lower total carbon sequestration rate benefits than planting a diversity of tree species that have a high wood density (MFD δ) or high seed mass (MFD σ). Within arid-hot uplands, however, there is no significant difference between 'self-recovery' and enrichment planting via either of the 'framework functional trait' methods (Fig. 4a, red data points).

Thinning trees after regeneration results in higher cobenefits than no thinning (NT) irrespective of climate and landscape context (Fig. 4b), with maximum average cobenefits provided when thinning for denser wood (Fig. 4b). The NT option was never beneficial for both the total carbon sequestration rate and plant functional diversity. In arid-hot uplands (red data points, Fig. 4b), thinning nonselectively the dominant species (DT) or thinning selectively for increasing seed mass (ST σ) provide similar optimal total carbon sequestration/plant functional diversity cobenefits, but higher plant functional diversity in wet/hot climate on

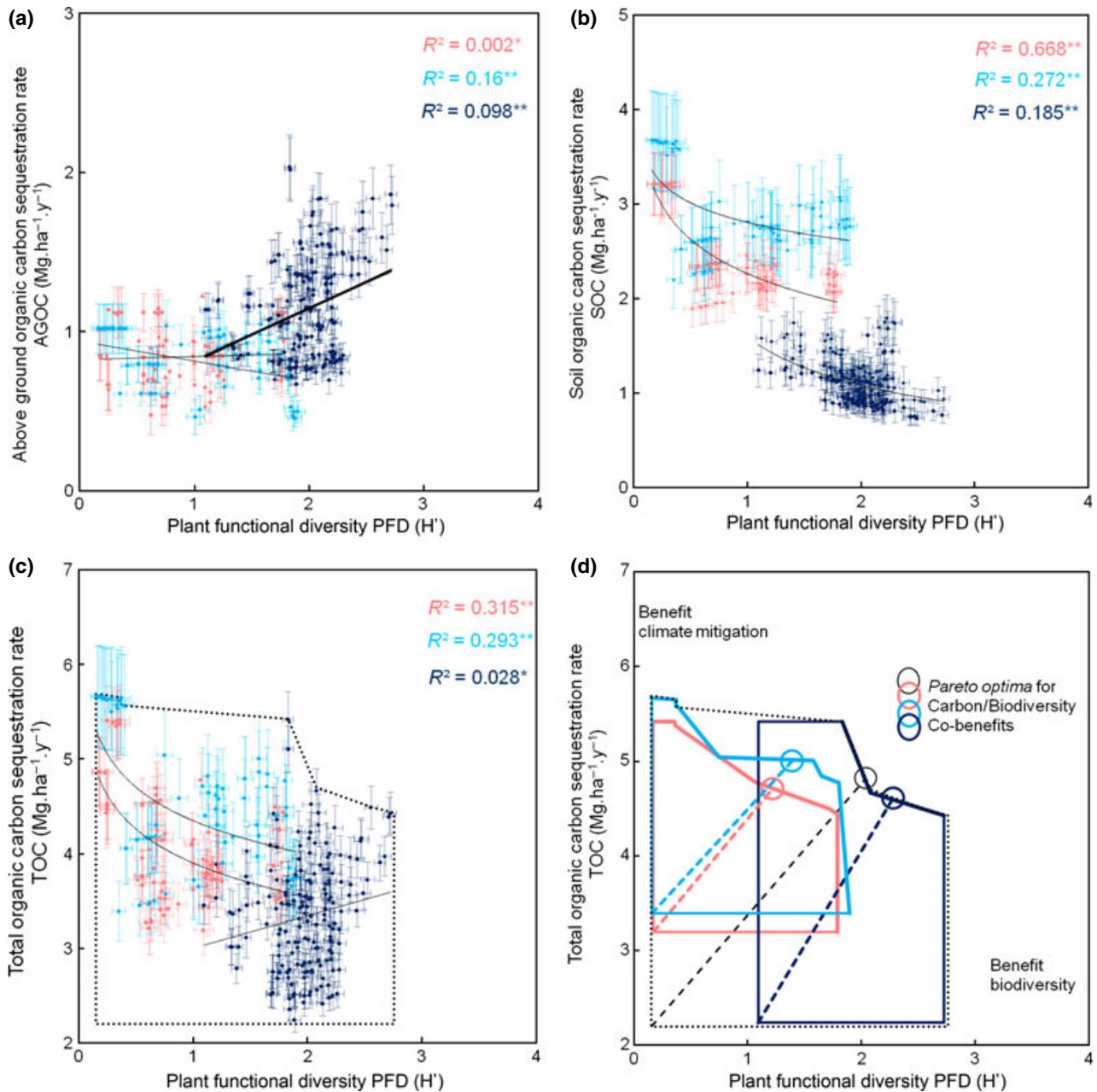


Fig. 3 Relationship between plant functional diversity (PFD) and carbon sequestration rates in various compartment of the forest. Relationship between PFD and (a) the above ground organic carbon sequestration rate (AGOC), (b) the soil organic carbon sequestration rate (SOC), (c) the total organic carbon sequestration rate (TOC), and (d) TOC with associated Pareto spaces, Pareto 50–50 weight vector and Pareto optimal solutions (large circles) for each of the climate-by-landscape scenarios (Table S1). Red and light blue colors indicate, respectively, the arid/hot climate scenario on uplands, the wet/hot climate scenario on upland. Dark blue indicates the two arid/hot or wet/hot climate scenarios on lowlands. Large circles represent the optimal solution as determined by Pareto optimization. In panel a–c, the 126 points represent the 126 combinations of planting/thinning scenarios, where each data point represents the average value over 100 years of restoration for AGOC, SOC, and TOC. Error bars represent SEM. TOC is the sum of the carbon sequestration rate of the soil, of the above ground biomass and of the root biomass (see details in Data S1). Linear, exponential, log-linear, log-log, and quadratic regressions were performed and compared between climate-by-landscape scenarios. Only the functions with the best fit are presented. $*P < 0.05$, $**P < 0.01$.

uplands (light-blue data points, Fig. 4b). Whereas thinning selectively for higher leaf mass area ($ST\phi$) on uplands, irrespectively of the climate scenario, provides

a very unbalanced solution leading to highly simplified forests useful for maximizing carbon sequestration only.

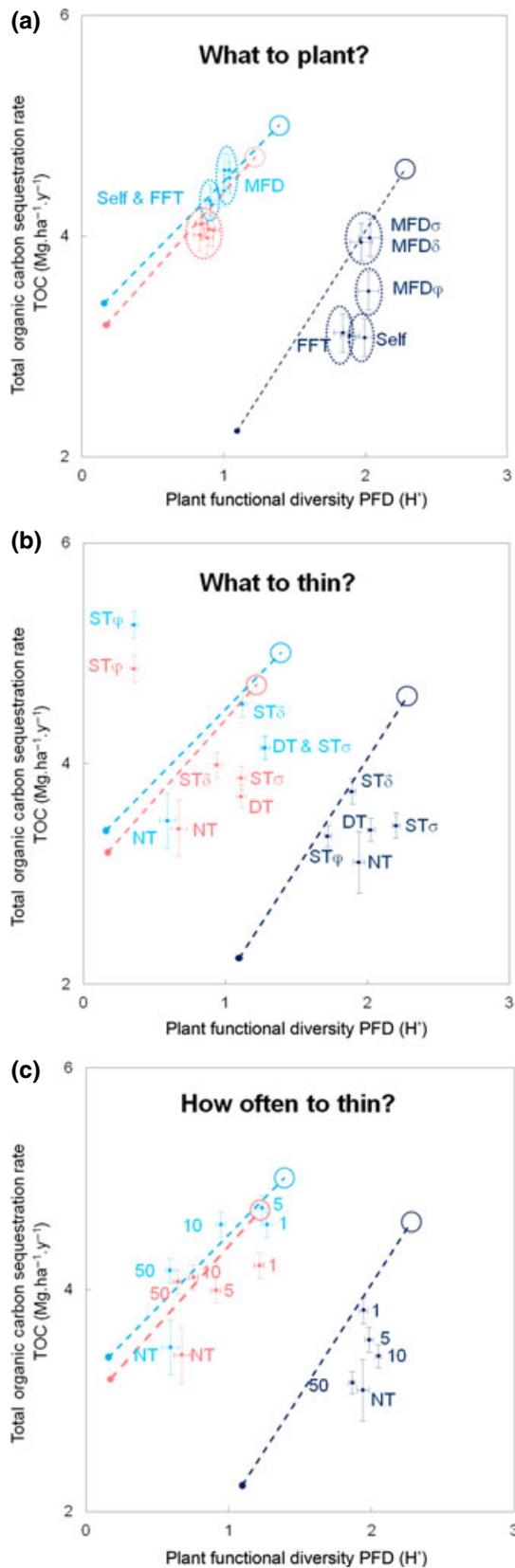


Fig. 4 Decision rules that maximize simultaneously the total organic carbon sequestration rate (TOC) and plant functional diversity (PFD). (a) Regeneration phase: What to plant? Self-recovery (Self), framework functional trait method (FFT), or maximum functional diversity method (MFD); (b) Maintenance phase: What to thin? (c) Maintenance phase: how often to thin? every year (1), five (5), ten (10), and 50 years (50). Shannon index H' of plant functional diversity. In panels a–c, values represent averages over 100 years for each combinations of planting and thinning. Error bars represent SEM. Red, and light blue colors indicate, respectively, the arid/hot climate scenario on uplands, the wet/hot climate scenario on upland. Dark blue indicates the two arid/hot or wet/hot climate scenarios on lowlands. The dashed lines indicate the linear function relating the expected least optimal solution (small solid points) to the best Pareto optimal solution (large circles) found in panel 4a. nomenclature of actions can be found in Table 1.

Changing the frequency of the thinning regime also influences cobenefit objectives (Fig. 3c). Within wet-hot uplands, intermediate thinning frequency (every 5 years) on one of the dominant plant functional traits results in high total carbon sequestration/plant functional diversity cobenefits, whereas on arid-hot uplands or on lowlands regardless of climate, thinning every year one of the dominant traits will provide higher and more balanced cobenefits.

Discussion

Turning the trade-off debate into a cobenefit opportunity

Despite more than three decades of theory and practice, managing ecosystems for cobenefits like carbon sequestration and biodiversity on the same land remain problematic (Hobbs & Suding, 2009; Phelps *et al.*, 2012). Most of the decision models developed in the past have mainly been designed for solving spatial allocation between forests biodiversity and carbon objectives (Venter *et al.*, 2009; Wilson *et al.*, 2009; Crossman *et al.*, 2011). For this reason, investing in fast-growing monocultures that maximize carbon benefits, while sparing other forest lands for biodiversity benefits, has long been seen as a more convenient strategy than sharing forest lands for cobenefits (Phelps *et al.*, 2012). The basis for promoting land-sharing and cobenefits within the same forest land rests on the strength of the correlation between biodiversity and carbon in relation to management and natural disturbances, plant functional traits and environmental conditions (Diaz *et al.*, 2009; Cardinale *et al.*, 2011). Studies that have found a positive correlation between biodiversity and carbon sequestration in the past were generally conducted in grasslands and experimental communities (Adler *et al.*, 2011). Studies within forests are few and results are

equivocal (Erskine *et al.*, 2006; Firn *et al.*, 2007; Vilà *et al.*, 2007; Whittaker, 2010; Ruiz-Jaen & Potvin, 2011; Nguyen *et al.*, 2012). Here, using a detailed model that synthesizes biological knowledge of forest dynamics, we find that the relationships between plant functional diversity and the above ground carbon sequestration rate, the soil carbon sequestration rate or the total carbon sequestration rate are context specific across a range of climate, landscape position, and management scenarios (Fig. 3). We do find that some combinations of planting and thinning rules can synergistically produce high biodiversity forests with high carbon stocks, but that management has to be adapted to landscape position and changing climates over the long term, in response to the difference of successional trajectories of the plant functional traits in a given environmental context (Fig. S1).

Biodiversity, above ground and soil carbon sequestration are not always correlated

Most work on the relationship between forest carbon sequestration and biodiversity has focused on above ground carbon sequestration (Bunker *et al.*, 2005; Ruiz-Jaen & Potvin, 2010; Potvin *et al.*, 2011) and consequently forms the basis for, forest management decisions and recommendations delivered under REDD+ and other carbon credit initiatives (Venter *et al.*, 2009; Wilson *et al.*, 2009; Agrawal *et al.*, 2011; Crossman *et al.*, 2011; Phelps *et al.*, 2012). By combining the results of all of our decision scenarios, we show that biodiversity, above ground and soil carbon sequestration rates are not always correlated; and that the degree of correlation depends on landscape and climate context (Fig. 3). Under water-limited conditions (i.e., uplands), the establishment of tall and heavy trees fail (i.e., tall trees producing heavy seeds and dense canopy and trunk with high leaf mass per area: see Data S1, section 2) and result in a fast turn-over of dead organic biomass accumulating in the soil (Fig. 3b). Forests end up

trapped in a state with low diversity of functional trait syndromes, mostly dominated by small trees that are fast-growing, shade intolerant with low-water requirements and producing many small seeds (i.e., low leaf mass per area, light seeds and high wood density syndrome: see Figure S1 for results and Data S1, section 2). Under conditions where water is not limiting (i.e., lowlands), a higher diversity of tree species with 'functional complementarities' can coexist (Fig. 3; Cardinale *et al.*, 2012), including tall and heavy water-demanding trees (i.e., producing large seeds, with high leaf mass per area and high wood density: see Data S1, section 2) that can contribute to increases in above ground carbon stocks (Fig. 3a, Fig. S1).

Planting rules and their associated cobenefits

There is much debate around the most efficient methods for regrowing biodiverse carbon-rich forests (Lugo, 1992; Lamb *et al.*, 2005; Hector *et al.*, 2011). Practitioners must decide whether to allow self-regeneration, or plant fast-growing species that will provide the overstorey needed to recruit an understory of diverse shade-tolerant species ('framework functional trait' method), or plant a diversity of species with complementary functional trait syndromes ('maximum functional diversity' method) (Florentine & Westbrooke, 2004; Fig. 1; Table 2). Here, we show that investing more in regeneration, using technical enrichment planting (i.e., 'maximum functional diversity' method: Fig. 4a), delivers substantial cobenefits, irrespective of the climate on lowlands or in wet-hot uplands.

Co-benefits accrue because management removes the barriers to colonization, and promotes the persistence of the plant functional traits that increase total organic carbon sequestration rate (mostly leaf mass area: Fig. S1c) and increases plant functional diversity (mostly seed mass and wood density Fig. 4b, Fig. S1b, f). However, enrichment planting provides little extra benefit in arid-hot uplands, where natural regeneration is

Table 2 Key management recommendations based on the management of plant functional trait syndromes (ω) for achieving maximal cobenefits in selected climate and landscape contexts, for specific soil and forest conditions. Management are compared and ranked according to their impact on carbon and plant functional diversity cobenefit-values. For instance, MFD > Self = FFT means that maximum functional diversity planting methods (MFD) perform better than self-regeneration (Self) and the framework functional trait methods (FFT), and that FFT and Self methods perform equally in term carbon plant functional diversity cobenefits

Climate scenario	Landscape position	What to ω Plant?	What type of dominant ω to thin?	How often the dominant ω should be thinned?
Arid	Upland	MFD σ = MFD δ = MFD ϕ = Self = FFT	ST δ > ST σ > DT > ST ϕ > NT	1 year > 5 y \approx 10 y > 50 y > NT
	Lowland	MFD σ = MFD δ > MFD ϕ > Self > FFT	ST δ > ST σ > DT > ST ϕ > NT	1 year > 5 y > 10 y > 50 y > NT
Wet	Upland	MFD σ = MFD δ = MFD ϕ > Self = FFT	ST δ > ST σ = DT > ST ϕ > NT	5 years \approx 1 y > 10 y > 50 y > NT
	Lowland	MFD σ = MFD δ > MFD ϕ > Self > FFT	ST δ > ST σ > DT > ST ϕ > NT	1 year > 5 y > 10 y > 50 y > NT

See definitions of acronyms in Table 1.

equally effective. In this case, natural regeneration is expected to result in a steady state scenario where the forest is dominated by short, drought tolerant species that produce small seeds (see Figure S1 for results and Data S1, section 2). The long-term effect of enriching the forest with the 'maximum functional diversity' method (including tall water-demanding trees producing heavy seeds, high leaf mass per area producing heavy canopy, and high wood density: see Data S1, section 2) is quickly lost after the soil water limit is reached, and the planted water-demanding trees are not capable of surviving.

Maximum diversity planting method (MFD) and framework planting method (FFT) are two competing management practices that match the competing ecological concepts of complementarity hypothesis (CH) and selection effect hypotheses (SEH), respectively, for understanding the relationship between carbon and biodiversity. Therefore, our decision framework not only provides a way to rank the performance of different planting practices, but also provides a way to test which of the CH/SEH hypotheses (through MFD/FFT hypotheses) are more likely to explain the carbon biodiversity relationship (see synthesis of results in Table 2).

Maintenance thinning rules and their associated cobenefits

The most efficient method to maintain and thin to produce biodiverse carbon-rich forest is also a topic debate (Erskine *et al.*, 2006; Firm *et al.*, 2007; Nguyen *et al.*, 2012). Here, we considered a subset of different thinning strategies that can be used: no maintenance thinning, thinning selectively the species belonging to the dominant functional trait syndrome, or selectively thinning the dominant species to increase shade-tolerant trees (i.e., high leaf mass per area) or to get taller trees (i.e., producing heavier seeds) or to get denser wood/timber (Fig. 1; Table 2). Our results suggest that without maintenance thinning of growing forests, competition for limiting water and light resources decreases considerably recruitment of new species in the understorey and thus decreases above ground carbon sequestration and plant functional diversity, regardless of the climate on uplands (see Fig. 4b, but also Hobbs & Suding, 2009; Muller-Landau *et al.*, 2006). We found practitioners can optimally remove competitive barriers to stimulate colonization by a more productive and higher diversity of species functional trait syndromes using one of three strategies: (i) Selectively thinning the trees with the dominant functional trait syndrome, (ii) Thinning dominant trees with low density wood, and (iii) retain after thinning taller trees that produce larger seeds (Fig. 4b, more frequent thinning in wet

conditions than in dry condition Fig. 4c), These three selective thinning strategies cobenefit the total organic carbon sequestration rate regardless of the landscape and climate context considered (summary results in Table 2).

In contrast, other selective thinning strategies give different cobenefit relationships in dry and wet conditions. For instance, we show that thinning for more shade-tolerant trees will maximize carbon sequestration (Fig. S1c), but at the expense of plant functional diversity (Fig. 3c and 4b). Furthermore, thinning in water-limited conditions for taller trees with bigger seeds is rarely possible given water limitations (Fig. S1e). These results suggest that maximizing both carbon and biodiversity is not always possible in dry conditions, as opposed to our results in wet conditions that support what others have observed in the wet tropics (e.g., Erskine *et al.*, 2006; Firm *et al.*, 2007; Nguyen *et al.*, 2012). Our results also confirm that thinning rules have to be adapted to the climate and landscape context (Fig. 4c; e.g., Erskine *et al.*, 2006; Firm *et al.*, 2007; Nguyen *et al.*, 2012).

Using the model for restoring biodiversity, ecosystem services, and other socio-economic cobenefits

Our model and derived management rules require simple measures of plant traits and environmental variables (Diaz *et al.*, 2004), and predict realistic carbon sequestration rates in tropical forests (0.2–7 Mg [C] ha⁻¹ yr⁻¹, Lehmann *et al.*, 2003). The components of the model are based on tried and tested plant scaling relationships and mechanistic models of forest ecosystem dynamics where trees are characterized by a single functional trait syndrome (Purves & Pacala, 2008; Falster *et al.*, 2011). We extended these models to include forests with trees characterized by multiple functional trait syndromes, and the trait syndromes can be manipulated depending on management objectives. Providing that the variation within plant functional traits is included in this type of model (Kattge *et al.*, 2011) and that the model results are field tested, decision makers can use our decision framework to systematically design context-specific rules that can guide the choice of what species to plant and thin (i.e., by matching species with functional trait syndromes), to achieve results when managing biodiversity and carbon sequestration as cobenefits. The region-specific costs of planting and thinning and soil nitrogen limitations have not been considered and, if integrated, may change the rules presented here. Cost of plantation establishment is an important factor but will depend on the intended management objective of the forest. For example, in the tropics plantations with trees characterized by different

functional trait syndromes may be more expensive to establish, but preferable and over the long-term more cost-effective for small landholders, as they can provide multiple forest products overtime including fruits, fuelwood, timber, medicine, and carbon credits (Lugo, 1992; Lamb *et al.*, 2005). Therefore, optimal planting designs and thinning regimes are context specific, depending on environmental but also social, economic, and cultural factors. In this regard, our model can be linked to social network and econometric models that account for the governance structures of forests (e.g., community-owned forests, state forests, nonindustrial private forests, or more polycentric cooperation arrangements) and the associated collective behaviors of stakeholders under socio-economic incentives (e.g., models that predict the probability of harvesting timber and nontimber forest products, the probability of cooperation between stakeholders, of conservation actions). Our model can also be combined with species distribution models to predict across landscapes the management rules that will help tree communities adapt to climate change or other disturbances (e.g., invasion by undesirable species, overexploitation, and altered fire regimes). Going further in these directions is essential if we want to build integrative decision support systems that will help turning debates around biodiversity, carbon, ecosystem services, governance, and livelihoods into cobenefit opportunities in socio-ecological production landscapes (e.g., REDD+; Bélair *et al.*, 2010; Agrawal *et al.*, 2011).

Managing the restoration of simultaneously biodiverse and carbon-rich forests on cleared and degraded land is a complex task with many contributing factors determining success. Arguably never before have policy makers, practitioners and scientists been as concerned about how to most efficiently grow forests for benefits other than traditional forest products like timber and pulp. Opportunities for reforestation and plantation establishment have increased greatly with the emerging carbon market and international institutions designed to provide guidelines for the management of ecosystem services in social-ecological forest systems (e.g., REDD+, IPBES, IPSI). However, previous findings showed that we need more effective strategies for cobenefiting biodiversity and carbon sequestration objectives on the same land, otherwise perceptions that fast-growing monocultures (which are known to continuously encroach on biodiverse forests) are the best option will continue (Phelps *et al.*, 2012). Our results suggest that maximizing carbon sequestration and the associated carbon credits through biodiversity planting cannot be achieved with a 'one size fits all solution' and involves more complex planning than just planting trees characterized by a diversity of plant functional

traits. Climate and landscape position are key drivers for predicting the best strategies, and forest stakeholders may have to monitor cobenefits to actively adapt strategies to climate change projections. Our decision framework offers a step toward predicting and developing detailed, site specific adaptive management guidelines and fruitful opportunities for achieving simultaneously carbon sequestration, biodiversity conservation and socio-economic development objectives.

Acknowledgements

J-B.P. was supported by a CSIRO OCE PDF. T.G.M. acknowledges support of the Julius Career Award and the Australian Government's National Environmental Research Program and the Australian Research Council Centre of Excellence for Environmental Decisions (I.C., T.G.M.). We are grateful to D. Falster, M. Westoby, Y. Buckley, S. Nicol and two anonymous reviewers for discussions and comments on earlier versions of this manuscript. We thank J. Ricketts, D. Bruget, and the Queensland Climate Change Centre of Excellence for the climate scenarios.

Author contributions

J-B.P. and T.G.M. conceived the project. J-B.P. constructed the model and performed the analysis. All authors wrote the manuscript, discussed results, and edited the manuscript.

The Authors declare no conflict of interest.

References

- Adler PB, Seabloom EW, Borer ET *et al.* (2011) Productivity is a poor predictor of plant species richness. *Science*, **333**, 1750–1753.
- Agrawal A, Nepstad D, Chhatre A (2011) Reducing emissions from deforestation and forest degradation. *Annual Review of Environment and Resources*, **36**, 373–396.
- Bélair C, Ichikawa K, Wong BYL, Mulongoy KJ (2010) *Sustainable Use of Biological Diversity in Socio-ecological Production Landscapes*. In *Background to the 'Satoyama Initiative for the Benefit of Biodiversity and Human Well-being'*. Secretariat of the Convention on Biological Diversity, Technical Series No. 52, Montreal.
- Bunker DE, DeClerck F, Bradford JC *et al.* (2005) Species loss and aboveground carbon storage in a tropical forest. *Science*, **310**, 1029–1031.
- Cardinale BJ, Matulich KL, Hooper DU *et al.* (2011) The functional role of producer diversity in ecosystems. *American Journal of Botany*, **98**, 572–592.
- Cardinale BJ, Duffy JE, Gonzalez A *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.
- Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, **320**, 1458–1460.
- Crossman ND, Bryan BA, Summers DM (2011) Carbon payments and low-cost conservation. *Conservation Biology*, **25**, 835–845.
- Diaz S, Hodgson JG, Thompson K *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.
- Diaz S, Hector A, Wardle DA (2009) Biodiversity in forest carbon sequestration initiatives: not just a side benefit. *Current Opinion in Environmental Sustainability*, **1**, 55–60.
- Dwyer JM, Fensham R, Buckley YM (2010) Restoration thinning accelerates structural development and carbon sequestration in an endangered Australian ecosystem. *Journal of Applied Ecology*, **47**, 681–691.
- Erskine PD, Lamb D, Bristow M (2006) Tree species diversity and ecosystem function: can tropical multi-species plantations generate greater productivity? *Forest Ecology and Management*, **233**, 205–210.
- Falster DS, Moles AT, Westoby M (2008) A general model for the scaling of offspring size and adult size. *American Naturalist*, **172**, 299–317.
- Falster DS, Brannstrom A, Dieckmann U, Westoby M (2011) Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and

- biomass density in single-species forests: a theoretical investigation. *Journal of Ecology*, **99**, 148–164.
- Firn J, Erskine PD, Lamb D (2007) Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia*, **154**, 521–533.
- Florentine SK, Westbrooke ME (2004) Evaluation of alternative approaches to rainforest restoration on abandoned pasturelands in tropical north Queensland, Australia. *Land Degradation & Development*, **15**, 1–13.
- Gatto M, De Leo GA (2000) Pricing biodiversity and ecosystem services: the never-ending story. *BioScience*, **50**, 347–355.
- Hector A, Philipson C, Saner P, et al. (2011) The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 3303–3315.
- Hobbs RJ, Suding KN (ed.) (2009) *New Models for Ecosystem Dynamics and Restoration*. Island Press, Washington D.C.
- Kanowski J, Catterall CP (2010) Carbon stocks in above ground biomass of monoculture plantations, mixed species plantations and environmental restoration plantings in north east Australia. *Ecological Management & Restoration*, **11**, 119–126.
- Kattge J, Diaz S, Lavorel S, Prentice IC, Leadley P, Bönsch G, Ford H (2011) TRY—a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.
- Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. *Science*, **310**, 1628–1632.
- Lehmann J, Kern DC, Glaser B, Woods WI (eds) (2003) *Amazonian Dark Earths: Origin, Properties, Management*. Springer, New York.
- Lugo AE (1992) Comparison of tropical tree plantations with secondary forests of similar age. *Ecological Monographs*, **62**, 1–41. (also cite for framework species method)
- Mayfield MM, Bonser SP, Morgan JW, Aubin I, McNamara S, Vesik PA (2010) What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, **19**, 423–431.
- Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research Biogeosciences*, **114**, G01002. doi:10.1029/2008JG000812.
- Mittelbach GG, Steiner CF, Scheiner SM et al. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. *Oikos*, **113**, 91–105.
- Molino JF, Sabatier D (2001) Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science*, **294**, 1702–1704.
- Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs*, **71**, 557–585.
- Muller-Landau HC, Condit RS, Chave J, Thomas SC, Bohlman SA, Bunyavechewin S, Ashton P (2006) Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecology Letters*, **9**, 575–588.
- Nguyen H, Herbohn J, Firn J, Lamb D (2012) Biodiversity-productivity relationships in small-scale mixed-species plantations using native species in Leyte province, Philippines. *Forest Ecology and Management*, **274**, 81–90.
- Niklas KJ (2004) Plant allometry: is there a grand unifying theory? *Biological Reviews*, **79**, 871–889. doi: 10.1017/S1464793104006499.
- Nikolov NT, Massman WJ, Schoettle AW (1995) Coupling biochemical and biophysical processes at the leaf level - an equilibrium photosynthesis model for leaves of C-3 plants. *Ecological Modelling*, **80**, 205–235.
- Osnas JL, Lichstein JW, Reich PB, Pacala SW (2013) Global leaf trait relationships: mass, area, and the leaf economics spectrum. *Science*, **340**, 741–744.
- Paquette A, Messier C (2010) The role of plantations in managing the world's forests in the Anthropocene. *Frontiers in Ecology and the Environment*, **8**, 27–34.
- Phelps J, Webb EL, Adams WM (2012) Biodiversity co-benefits of policies to reduce forest-carbon emissions. *Nature Climate Change*, **2**, 497–503.
- Potvin C, Mancilla L, Buchmann N et al. (2011) An ecosystem approach to biodiversity effects: carbon pools in a tropical tree plantation. *Forest Ecology and Management*, **261**, 1614–1624.
- Prach K, Pysek P (2001) Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. *Ecological Engineering*, **17**, 55–62.
- Prach K, Pysek P, Bastl M (2001) Spontaneous vegetation succession in human-disturbed habitats: a pattern across seres. *Applied Vegetation Science*, **4**, 83–88.
- Purves D, Pacala S (2008) Predictive models of forest dynamics. *Science*, **320**, 1452–1453.
- Ruiz-Jaen MC, Potvin C (2010) Tree diversity explains variation in ecosystem function in a neotropical forest in Panama. *Biotropica*, **42**, 638–646.
- Ruiz-Jaen MC, Potvin C (2011) Can we predict carbon stocks in tropical ecosystems from tree diversity? Comparing species and functional diversity in a plantation and a natural forest. *New Phytologist*, **189**, 978–987.
- Secretariat (Convention on Biological Diversity) (2011) REDD-Plus and Biodiversity, CBD Technical Series No. 59 <http://www.cbd.int/doc/publications/cbd-ts-59-en.pdf>
- Venter O, Laurance WF, Iwamura T, Wilson KA, Fuller RA, Possingham HP (2009) Harnessing carbon payments to protect biodiversity. *Science*, **326**, 1368.
- Vilà M, Vayreda J, Comas L, Ibáñez JJ, Mata T, Obón B (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters*, **10**, 241–250. doi:10.1111/j.1461-0248.2007.01016.x.
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.
- Whittaker RJ (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness-productivity relationship. *Ecology*, **91**, 2522–2533.
- Wilson KA, Carwardine J, Possingham HP (2009) Setting conservation priorities. *Annals of the New York Academy of Sciences*, **1162**, 237–264. doi:10.1111/j.1749-6632.2009.04149.x.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. The role of successional trajectories of the plant functional traits on plant functional diversity PFD and the total organic sequestration rate TOC.

Data S1. Methods.

Table S1. Scenarios of climate change.

Table S2. Parameters used in the forest ecosystem dynamic model.