Theoretical exploration of how a greater and more equitable access to forest commons by a diversity of tree resource users can impact biodiversity, carbon and livelihood outcomes: (1) non-trivial differences between wetter and drier conditions (#53609)

First revision

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Theoretical exploration of how a greater and more equitable access to forest commons by a diversity of tree resource users can impact biodiversity, carbon and livelihood outcomes: (1) non-trivial differences between wetter and drier conditions

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ny societies have for millennia tried to provide an equitable access to common pools of biological resources, in a way that users could sustain their livelihoods through the extraction of a diversity of competing species. One particular problem is to assess whether, why, how, when and where an equitable access to these commons for livelihood outcomes can be compatible with biodiverse and carbon outcomes. Several studies have attempted to evaluate empirically this complex multi-dimensional problem, but without exploring the extent to which it could be true, and understanding it in relation with existing ecological and governance theories.

The study presents a social-ecological model of multi-species forest dynamics, built on the foundation of theoretical ecology (i.e. the life-history theory, Chesson's species coexistence theory, and the forest successional theory), constrained by Ostrom design principles of good governance of common pool resources (CPR), and parametrised based on a selection of fixed and plausible forest management parameters.

The exploration of numerical projections across a wide range of scenarios confirms first that opening the forest access to resource users, for harvesting living biomass for timber and deadwood for household energy, should lead to suboptimal biodiversity outcomes, but not for aboveground carbon stocks. But once opened to varying levels of resource users, it is possible to predict that a first dimension, wetter vs drier forests, should impact the success of combining these objectives. In wetter forest commons, opening up to as many diverse and co-vulnerable resource users as there are competing tree species managed for wood biomass, produces a greater diversity of disturbances. These disturbances are acting as an "equalising mechanism" on the structure and dynamics of tree assemblages, which are predicted to benefit species coexistence, biological diversity, carbon sequestration, collective economic benefits from timber harvesting. Our understanding of the results is greatly improved as we uncover the underpinning laws with and between plant functional trait dimensions (specific leaf area index SLA, seed size SS, specific wood density SWD) along the forest vertical niche space, and during forest successions. Reversely, drier forest commons are not expected to benefit from this same human induced equalising mechanism, vertically in the forest and along the forest succession. This is due to the greatly reduced functional niche space and partitioning, ultimately constraining species that can coexist with greater SWD, lower SLA and SS.

Altogether, the model and results of this study suggests that some pure ecological theories, combined Peer reviewing PDF (2020:10:53609:1:1:NEW 12 Oct 2022)



with carefully thought through methodological guidelines, can be of great help to generate novel hypotheses for understanding human-nature dilemmas and solutions in complex social-ecological systems.

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Abstract

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Many societies have for millennia tried to provide an equitable access to common pools of biological resources, in a way that users could sustain their livelihoods through the extraction of a diversity of competing species. One particular problem is to assess whether, why, how, when and where an equitable access to these commons for livelihood outcomes can be compatible with biodiverse and carbon outcomes. Several studies have attempted to evaluate empirically this complex multi-dimensional problem, but without exploring the extent to which it could be true, and understanding it in relation with existing ecological and governance theories.

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44 Keywords: Social-ecological system, coupled-infrastructure system, forest commons, carbon
 45 sequestration, biodiversity, species coexistence theory, disturbance theory, life-history traits,
 46 mathematical modelling.



Introduction





Socio-ecological context

An estimated 1.6 billion people depend on forests for their livelihoods, of which 350 million, including 60 million indigenous peoples, live in or adjacent to forests and are almost wholly dependent on forest biological resources for their subsistence and income needs. Among these people, many are collectively managing forests as commons, i.e. where a diversity of resource users can access the common pool of a diversity of tree resources, and compete (under stated constraints) for the extraction essential products and services based on timber and non-timber biomass (McKean, 1992; Agrawal & Gibson, 1999; Kijima et al., 2000; Klosowski et al., 2001; Gebremedhin, Pender & Tesfay, 2003; Lemos & Agrawal, 2006; Antinori & Rausse, 2007, 2008; Chhatre & Agrawal, 2008, 2009). Under these conditions, one particular challenge is to determine how the complexity of the social-ecological conditions (e.g. the size and diversity of competing resource users and of species assemblages, and the rules governing the access and relationship) can affect the sustainability and equity of the collective livelihood objectives, as well as of a variety of other less tangible services provided by these forests, e.g. the protection of biodiversity, the sequestration of carbon for mitigating climate change (Poteete & Ostrom, 2004; Naidu, 2009; Saunders, 2014; Betts et al., 2021)?

To balance these social, economic and ecological objectives, the dominant post-World War II development pathway has been for many countries to reduce livelihood options, by incentivising the specialisation of local economies around few cost efficient high-yield species forming mono-specific stands, preferably based on local tree species (Lamb et al., 2005; Brockerhoff et al., 2008). This has been the case for instance in Malaysia, Australia, Costa Rica, Vietnam and other South-East Asian countries (SOM of Lamb et al., 2005). These stands were then efficiently marketed to secure the provisioning of a few essential forest goo and services for human livelihoods. This approach, coupled with comprehensive conservation approaches, is now known to have had in certain cases contributed to free lands to protest surrounding biodiversity, and successfully alleviated poverty in some rural communities (Lamb et al., 2005; Brockerhoff et al., 2008; Betts et al., 2021). However in others, people have struggled to protect

biodiversity and carbon stocks (Westoby 1987; Toledo et al. 2003; Fisher et al., 2011).



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Furthermore many people were locked away from harvesting other resources, in order to reduce the transformation of biodiverse carbon-rich forests into mono-specific stands. This led to inequitable access to a diversity of other products and services directly essential for their livelihoods, or indirectly through the perpetuation of essential social exchanges, e.g. related to gift economy (Ellis & Allison 2004). The negative impacts of this development pathway has particularly been serious, during boom-bust cycles associated with single crop economies, and when in response to growing demand in food, fibre and timber.

Drawing from these experiences, especially since the mid-1980s, more and more international and local government agencies are promoting novel resource management policies. They are designed to adapt local economies towards more biodiverse, climate resilient, productive and equitable targets (Lamb et al., 2005). When applied to mono-sectoral/-ecological systems like forestry, they consist in instituting the collective governance and management of forests as common pool resources, or CPR for short (Ostrom, 1990; Chhattre & Agrawal, 2009; Persha, Agrawal & Chhatre, 2011). There, theory suggests that a greater diversity of resource users could have access to a greater diversity of species used for timber, fuelwood, food, fibres, REDD+ carbon credits etc ..., but under strict collective rules of good governance, and preferably nurtured by local collective knowledge (Ostrom, 1990, 2009; Parrotta & Trosper, 2012). These forms were not uncommonly observed in the past in forest commons (e.g. Hegde et al., 1996; Murali et al., 1996; Agrawal and Gibson, 1999; Ambrose-Oii, 2003; Toledo et al., 2003; Kimengsi et al., 2019). But now, existing organisation are supposed to also abide to post-World War II principles of efficiency and outcome focus for the economy, the conservation of carbon stocks and of biodiversity (Ostrom, 1990; Ellis & Allison, 2004; Chhatre & Agrawal, 2008, 2009). The problem is that regular syntheses on the success and failures of such CPR policies are still raising the need to understand the reasons for these success and failures (Ellis & Allison 2004; Cox et al., 2010; Saunders, 2014).

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Scientific problem

The studies that have successfully demonstrated the why, how, when and where-about of the social-ecological consequences of letting complex human communities freely manage,



harvest, re-plant and sell a more diverse portfolio of tree species, are few and results are at best equivocal. Understanding the reasons for this ambiguity requires world scale evidences that are rarely available, probably due to the long-time frame for detecting a response to these drivers, but also the time and money required to get enough social-ecological data to understand these complex multifactorial systems. But more broadly, it is suit difficult to comprehend the type of scientific framework that would be best for assessing the long term sustainability of social-ecological systems, where complex human organisations need to equitably access common pool resources that are themselves biologically complex, (Ostrom, 1990; Poteete & Ostrom, 2004; Naidu, 2009; Ostrom, 2009; Saunders, 2014; Betts et al., 2021). In this study we will see that this problem is in fact connected to a more specific ecological one, i.e. how the diversification of management disturbances imposed on species by a diversity of resource users, is predicted to impact the coexistence of entire pool of competing tree species, with some or all of them having livelihood and carbon benefits? We will see that framing the problem this way can be of great use for exploring this problem in a more efficient way using mathematics and existing theories.

Objective and structure of the paper

Given this re-framing, the objective of this paper is to explore the social and ecological conditions under which opening the access to as many diverse and co-vulnerable resource users as there are competing tree species managed for wood biomass, is likely to impact positively or negatively the long-term species coexistence, biological diversity, carbon sequestration and collective economic benefits from timber harvesting.

To achieve this, the paper presents a mathematical model of social-ecological system (SES) dynamics based on existing work. In a previous paper, Pichancourt et al. (2014) developed a mathematical model of multi-species forest ecosystem dynamics and forestry management, that was used to explore the relationship between carbon, biodiversity and a wide range of combination of planting and thinning/harvesting rates, across a wide range of species assemblages. In the model species were characterised by their combinations of life-history trait values (specific leaf per area: SLA [m².kg⁻¹], specific wood density: SWD [kg.m⁻³], seed size SS [kg]) that are known to be of great use to understand the dynamics of species populations and



assemblages (van Bodegom et al., 2014). Now based on this model and results, the present study extended this model to constrain the management actions, based on plausible forestry processes, and grounded in Ostrom's theory and modelling frameworks for studying the sustainable governance of CPR (Ostrom, 1990; Anderies, Janssen & Ostrom, 2004). The main control variable of the model is the access rate to the forest common by more resource users. By increasing it, the odel assumes that opening the forest common to a greater coexistence of resource users produces a greater diversity of management disturbances on a greater proportion of competing tree species (through independent harvesting and post-harvesting planting on each species). Then numerical solutions are produced to explore their impact on the Shannon index of tree life-history trait (aka. plant functional trait) diversity, on above-ground carbon biomass carbon stock, and on the collective economic return of timber supply from a greater diversity of species based on international market prices. Finally, the relationship is decomposed and analysed to emphasise the functional role of a reduced set of tree life-history traits.

The mathematical model presented in this paper can be considered of an intermediate complexity, and thus the numerical results obtained across a wide range of situations covered here were quite long to produce. Given the high dimensions of the problem, there was a need to strategise the exploration.

The first way to strategise the exploration was to design the modelling protocol by proceeding *Ceteris Paribus*, i.e. by assuming in this paper some fixed social-ecological constraints (collective governance of the common pool resources), that are detailed in the method section. Rather than fixing them in an ad-hoc fashion, the model used a mixture of empirical forestry behavioural models found in the literature, in order to provide a primer for a range of realistic values of parameters (harvesting, replanting, weeding maintenance, governance). The goal of this paper was, in no case, to test the verisimilitude of incorporating these specific models in relation with the social-ecological contexts defined with these behavioural models. Rather, by setting plausible parameters of forestry management from models, it was possible to reduce the dimension of the general problem, and focus on the exploration of the opening of the forest access on forest outcomes, and studying its sensitivity in response first to two ecological conditions (wetter and drier forest commons), and then analyse the underpinning ecological structure and processes that drive these difference of results.



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The choice to focus first on these limited aspects was intentional. Based on it, it was decided that a series of following papers will successively explore the sensitivity of this relationship to changes of other specific constraints, with the major ones are introduced in the last part of the discussion section.

A final strategy was to focus on this paper on the terministic model. This strategy is appropriate given the objective of first broad exploration, which also facilitates the understanding and logical criticism of the results. Nevertheless, this provides the details of the behavioural equations, the standard errors of their parameters, and the computer code to generate bootstrap confidence intervals (see link in the supplementary attachment). Some of the studies that will follow this one will justify the use of these bootstrapped uncertainty analyses for testing more targeted social-ecological hypotheses based on existing contexts of interest (see last part of the discussion section). The behavioural models and their errors can also be replaced by other context specific ones, for he who plans to challenge parts of the general predictions of this model, based on their specific social-ecological and physical data.

For all these reasons, the general social-ecological model and results presented hereafter can only be considered as a stepping stone for the development of a future more general, analytical and simpler theory for the type of general problem presented in this paper.

2. Methods

2.1. Model summary



The structure of the SES model is based on how governance of common pool resources (CPR) is actually practised and can be modelled (Ostrom, 1990). It is particularly following modelling guidelines of the Couple Infrastructure System Framework (CIS), initially created by Anderies, Jansen and Ostrom (2004), and further developed qualitatively and mathematically in a following series of articles (Anderies & Janssen, 2013; Anderies, 2015; Anderies et al., 2016; Anderies, 2019; Bernstein et al., 2019). This modelling framework is now becoming the de-facto



standard for constructing mathematical models of social-ecological dynamics, and investigate the sustainability of governance choices on common pool resources (Muneepeerakul and Anderies, 2017; Homayounfar et al., 2018; Houballah et al., 2021). The qualitative CIS representation of our problem is summarised in Figure 1.

Figure 1 approximately here

In the most complex situation of governance, a CIS would be represented as four interacting infrastructures. However, not all of them are present in all the social-ecological systems SES (see Anderies et al., 2019). Here the SES model uses only three of these interacting infrastructures: the resource infrastructure (RI, i.e. the forest containing an assemblage of eight tree species for this study), the resource users (RU, i.e. the actors accessing the forest to harvest and manage tree species for their biomass), the public infrastructure (PI, e.g. the collective association, material, rules, finance by and for the RU). The model does not define any governance infrastructure (GI), as in this study there is no need to define providers of institutional rules and budget for the PI or RU.

Under this CIS representation, the model first defines the boundaries of livelihood diversification, by setting the maximal diversity of resource users that can access the RI to harvest and replant independently their tree species of interest. In the model the RU is limited to eight species, for computational reasons (the species are presented in the method section 2.2). Therefore, the maximal number of RU is eight (1 species-actor pairing). Within those constraints, the model defines that RU access the RI to harvest (link 1a in Figure 1) independently and sustainably their species under a predefined rate. The latter is defined by econometric equations (eqn 1-15) that depend on the forest, species and tree size and life-history characteristics, also on other socio-economic and physical factors. Similarly RU are imposing post-harvesting rates, that follow specific planting behaviours (link 1b, equations 16-18), and harvesting of dead/firewood for individual heaters (link 1a, equation 19).

The harvesting and replanting rates of one species by one RU is performed independently of the demographic consequences on other species, through competition. However, all these activities are assumed perfectly performed on each species, in the sense e.g. that harvesting of



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one species is not damaging other species directly, like through logging damage, infrastructure building or transportation). Now because in the model coexisting species (managed or not) compete for the same resource (light, soil water), they can potentially all be indirectly impacted by management disturbances. Consequently all the RU are a-priori co-vulnerable in term of biomass outcome from harvesting, potentially affecting collective economic outcomes from harvesting, on top of potentially impacting tree forest biodiversity and carbon. In this situation, empirical observations show that co-vulnerable resource users usually form association and cooperate (link 6b) in order to share public infrastructures (PI), e.g. rules of good conduct, in order to avoid the tragedy of the commons (Cox et al., 2010). As a consequence, PI in the model sets that RU collectively monitor the ecological state of RI (link 4a: levels of biodiversity, organic carbon biomass) and the economic state of resource users from harvesting (link 6a: effective firewood supply, timber supply and revenues). It also also assumed that the association of RU can monitor and control the RI access by a collectively accepted quantity of RU, and thus avoid free riding (monitor: link 5a, control: link 5b). The PI model assumes that RU collectively support the RI state through the control of invasive species (link 4b, equations 20-23). In order to focus on the impact of environmental context, this first paper considers that all the resource users form a perfect association (probability P(6a) = 1 [on a 0-1 scale]) leading to the best possible monitoring efforts (P(4a)=1, P(5a)=1), control effort $P(4b) \rightarrow max$ (of equations 20-23). These constraints will be relaxed and their effect explored in a following paper.

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This hybrid individual/community strategy of managing resources is found in various parts of the world and is known to be frequently more cost-effective than when silvicultural practices are operated solely at a community level (Kijima, Sakurai & Otsuka 2000; Gebremedhin, Pender & Tesfay 2003; Rana and Chhatre, 2017). However, the model carefully considered the possibility to modulate and extend the forest governance and collective behaviour of resource users in the PI. This way, the model can be used to also explore a variety of forest institutional arrangements, econometric behaviours, and of ecological contexts encountered across the planet. This will be presented in following papers. The code of the model can be found in the supplementary material, for he who plan to test it as is, or by modifying some of the equations, based on their own data from other social-ecological contexts. For instance, the equations of the model could easily be replaced to account for traditional or modern community forest management such as



the community forest enterprises (CFE) found in Mexico (Antinori & Rausser, 2007, 2008), mixed state-community forms of joint forest management (JFM) found in India, South-East Asia, Nepal or Africa (Baker, 1998; Sakurai et al., 2004; Lokina et al., 2008; Arifin et al., 2009; Naidu, 2011), for the iriaichi-yamawari mixed community-private system of Japan (Totman, 1985; McKean, 1992; Kijima et al., 2000; Shimada, 2014), for the mixed association-private agreement system like found in many European and especially Scandinavian countries (Korhonen et al, 2012), or the informal communities between non-industrial private neighbours (with or without state or NGO agreements) found in the USA (Klosowski et al., 2001; Vokoun et al., 2010; Ma & Kittredge, 2011). All of them would ultimately provide a different range of PI values for the regulation and support parameters on the RI (equations from links 4b, 5b ...)

The consequences of these management practices on the forest is determined through a mathematical model of multi-species forest ecosystem dynamics (RI detailed in Fig. 2), which includes sub-models of life-history traits, architecture, physiology, demography, competition for resources, and above-ground organic carbon biomass, in relation to climate, soil and landscape contexts (Pichancourt et al., 2014).

2.2. Model of Resource infrastructure (RI) and its dynamics (link 7a in CIS Figure 1)

The RI uses the model developed by Pichancourt et al. (2014), with the same parametrisation (see http://onlinelibrary.wiley.com/doi/10.1111/gcb.12345/suppinfo). This model was used because it is still as of today one of the only mathematical model to be able to correctly scale up the dynamics of single to complex tree species assemblages, and make predictions on their structure and dynamics the under a diversity of forestry or restoration practices. Because of its underpinnings are important to interpret the results, this part of the method section presents a summary of its structure and basic assumptions.

2.2.1. Model of life-history traits and population dynamics at a species level

Pichancourt et al. (2014)'s model is primarily based on the Life-history theory, i.e. the constraining bio-physical laws and fitness consequences of allocating energy to reproduction,



growth and self-maintenance across the life-cycle of an organism. Under this theory, biophysical constraints and natural selection are viewed as the primary explanans of why species do not possess arbitrary combinations of life-history traits (LHTs), why they are subject to inner trade-offs in relocating energy between organs and life-stages, which ultimately drive the population growth rate of species, to adapt to their environmental conditions. To reflect this principle, the model is structured according to a multiple-tiers approach of LHTs (Figure 2).

Figure 2 approximately here

The 1st tier LHTs represents the stage and size specific vital rates along the life-cycle of a tree species (i.e., seed survival, germination, tree growth, survival and fertility). These traits are constrained by allometric traits that are assumed optimally defined by natural selection (2^{nd} tier LHTs, as outlined by the Scaling theory of ecology). Finally 2^{nd} tier LHTs are themselves constrained by 3^{rd} tier metabolic LHTs from different intra-cellular and organs of the tree, e.g. photosynthetic carbon assimilation, respiration, V_{max} , J_{max} , biomass turn-over, water absorption, carbon biomass production (as outlined e.g. by the Metabolic theory of ecology).

The theory also predicts for plant species, that the ~50% of the variability of most of the tree LHTs on Earth can ultimately be reduced to three (van Bodegom et al., 2014): specific leaf area (SLA) $[m^2.kg^{-1}]$, specific wood density (SWD) $[kg.m^{-3}]$, seed size (SS) [kg]). Under this realistic assumption, species with similar values of these three LHTs share other similar tier 1, 2 and 3 LHTs and life-cycle. By organising this way, mathematical models can be developed to create a wide range of unique tree species life-cycles and life-history trade-offs (Purves & Pacala, 2008; Pichancourt et al., 2014; van Bodegom et al., 2014; Falster et al., 2017). In this paper, computational capabilities limited our exploration to eight species, representing all the combinations between these extreme values of LHTs found in the literature (see Pichancourt et al., 2014): SLA (2.5 and 20 $m^2.kg^{-1}$), SWD (400 and 1000 $kg.m^{-3}$) and SS (10⁻⁷ and 10⁻³ kg per seed).

2.2.2. Model of species competition



This type of model can mathematically be generalised to correctly scale up the dynamics of tree community within the stand. Vertical competition in relation with light is simply modelled from the principle of perfect plasticity (PPA), used in all modern terrestrial biosphere models. Competition for water in the soil is also simply modelled using a soil water bucket model that depends on soil characteristics. In the present study, the RI model was parametrised as in Pichancourt et al. (2014) to match forests where the soil is 2 m depth loam A-B horizon composed of 50% sand, 20% clay, 30% silt, which is the most common soil found on Earth.

2.2.3. Indicator of the forest state

Forest-level variables were then calculated per meter square and re-scaled to account for the forest area considered (1 ha). This study focused on the Shannon index of the diversity of life-history traits (based on the relative density of trees belonging to every combination of LHTs values: SLA/SWD/SS), the organic above-ground carbon sequestration of the trees (MgC/ha/y), the live biomass and deadwood in the forest (t/ha/y), and finally average forest level of LHTs (SLA, SWD, SS). Similar to Pichancourt et al. (2014), the model exemplified the projected state of the forest RI under 100 year climate scenarios where sub-tropical forests were parametrised based on the Latitude around Brisbane in Queensland, Australia, and were subject to one of the predicted scenario of hotter and drier climate change (CSIRO mk3.5 using CMIP3 model: see details in Pichancourt et al., 2014: supplementary table S1).

2.3. Model of resource User Infrastructure (UI)

2.3.1. Model of timber harvesting (link 1a in CIS)

There is a large spectrum of harvesting behaviours in forest systems on Earth. But in the absence of global data and a model to describe harvesting behaviour in various types of forest institutional agreements, the choice was made to use Canham et al. (2013)'s dataset and model. This model represents to date the most accomplished effort to predict the probability of individual resource users of harvesting trees in forests in the united states. It describes a succession of decisions emerging at three scales of observation: at a stand level (biomass and



basal area), at species level (21 species with a wide spectrum of LHTs), and at an individual tree level (size). The main interest of this dataset and model is that the harvesting rates are expected to match every species' ecological state and biological characteristics considered in the RI model. For this reason, any harvesting model combined with the multi-species forest model is expected to apply sustainable harvesting rates independently on every species, but without making any a-priori on their impact on the demographic structure and dynamics of other competing species not directly impacted by each specific harvesting rate. Therefore, applying a diversity of species-specific harvesting rates, simultaneously or as a temporal succession, is expected to impact in a complex way the coexistence of tree species within the forest.

Following Canham et al. (2013), the harvesting behaviour of individual resource users can be modelled as a hierarchical chain of four decisions:

- 1. Decision 2.3.1.1 (stand level): resource users decide whether or not to harvest given the biomass state of the forest and the average timber density of the trees
- Decision 2.3.1.2 (stand level): resource users decide of the average basal area harvested,
 given the average timber density of the trees
 - 3. Decision 2.3.1.3 (species level): resource users decide of the probability for every tree species to be harvested, based on its life history traits (SWD, SS/maximal height of the tree species, SLA)
 - 4. Decision 2.3.1.4 (individual tree level): resource users decide of the probability for every tree to be harvested given its size (diameter at breast height *dbh*).

Using this approach it becomes possible to predict the supply of timber for every species at a given year of harvest. These four decision are now explained in details.

- 373 Decision 2.3.1.1 Stand level preference: what is the probability that the plot is logged?
- 374 If resource users decide to harvest in a life-time, the decision to harvest depends on the time T
- 375 since the last decision, and the above-ground biomass B of the adult trees in the stand, such that
- 376 the greater the biomass and the time since last harvest, the greater is the probability P_{harvest}.
- Following Canham et al. (2013), this process can simply be modelled as follow:



 $P_{\text{harvest}} = 1 - a_1 e^{(-m_1 B^b)^T} \text{ with } a_1 = 1$ eqn 1

where coefficients a_I , b_I and m_I were measured per forest type. P_{harvest} is a function bounded between 0 and 1, that asymptotically reaches 1. By following Cunham, resource users harvest the plot when the forest biomass reaches $P_{\text{harvest}} \ge 95\%$.

From Canham et al. (2013)'s original dataset, the dominant species mentioned is associated to the forest type. Therefore, using reported species-level specific wood density (SWD) found in the US Forest Services (http://www.feis-crs.org/beta/) and other sources when not accessible on the site (Table S1), it is possible to estimate the average forest-type level SWD_{mean}. By doing so, we can easily predict from Canham et al. (2013)'s original dataset that SWD_{mean} of a stand is a good predictor of the Canham's coefficients b_1 and m_1 from eqn 1 (Table S1, eqn. 2), and thus of how RU made their first decision at that level:

393
$$b_1 = -0.0016 \pm 0.002 \text{ SWD}_{\text{mean}} + 1.61 \pm 1.36 \quad (R^2 = 0.84)$$
 eqn 2

 $m_1 = 1.21^{-5} \pm 1.11^{-5} \text{SWD}_{\text{mean}} - 0.0046 \pm 0.007$ (R² = 0.92)

- 396 Decision 2.3.1.2 stand level preference: how much basal area is harvested per stand?
- Once the harvesting decision of the forest is made, the RU decide of the percentage of basal area removed (RBA), given the above ground biomass of the stand (or stand basal area):

400 RBA=
$$a_2 e^{(-m_2 B^{b^2})}$$
 eqn 4

Like in Canham et al. (2013), coefficients a_2 , b_2 and m_2 are measured per forest type, the same way as in Decision 1 (Table S2). By doing so, it is again trivial to detect that b_1 and m_1 can be predicted again from SWD_{mean} (Table S1), such that:

406
$$b_2 = -0.003 \pm 0.003 SWD_{mean} + 2.44 \pm 2.25$$
 (R² = 0.87) eqn 5

407
$$m_2 = 0.0007 \pm 0.002 SWD_{mean} - 0.33 \pm 1.35$$
 (R² = 0.51) eqn 6



408 $a_2 = 114.5 \pm 156 \ m_2 + 40.9 \pm 25.2 \ (R^2 = 0.84)$ eqn 7

409

comforting the fact that SWD is the main factor for timber pricing at international level (Fig. S1) and thus the driving force for deciding to harvest at a stand level (decisions 1 & 2).

412

- 413 Decision 2.3.1.3 Species-level preference: which species is harvested?
- 414 After RU decide of the basal area to harvest, they choose the tree species to harvest. Canham et
- al. (2013) predicted that the probability of a given species to be harvested depends on the basal
- 416 area removed (RBA):

417

418
$$P_{hs} = 1 - \gamma e^{(-\beta RBA)^{\alpha}}$$
 eqn 8

419

- 420 where coefficients α , β and γ are measured at a species level. Using the same original data,
- 421 combined with general information found from http://www.feis-crs.org/beta/ and other sources
- 422 when not accessible on the site (Table S3), it was possible to perform a simple analysis of how
- 423 RU made their decision based on specific LHTs (SWD, SLA, and/or SS that is highly correlated
- with tree size at maturity: Falster et al., 2008). This time, α and β from eqn. 8 could also be
- reasonably well predicted from the species-specific SS, i.e. maximal height of the tree species
- 426 (Fig. S1), such that:

427

428
$$\alpha = 0.12 \pm 0.08 \ logSS + 2.98 \pm 0.85 \ (R^2 = 0.35)$$
 eqn 9

429
$$\beta = 0.5 \pm 0.45 \text{ e}^{(-3.45 \pm 0.37\alpha)} (R^2 = 0.82)$$
 eqn 10

430
$$\gamma = -0.095 \pm 0.03 \ \alpha + 1.1 \pm 0.05 \ (R^2 = 0.74)$$
 eqn 11

431

- These relations define that at this step, after SWD, that RU now consider for harvest the maximal
- 433 height of a tree species (as on average larger seeded species grow into taller tree species, and
- 434 vice versa, Falster et al., 2008). By doing so, we show we can simplify the harvesting model
- from our knowledge of the tree LHTs, at least when using Canham et al.'s data.

436

437 Decision 2.3.1.4 – Tree-level preference: which size-class is harvested?



Once the proportion of a species is selected, RU decide whether each tree should be logged based on the diameter at breast height of the tree (*dbh*), that depends on tree height:

440

441
$$P_{\rm ht} = e^{\frac{-1}{2} \left(\frac{{\rm dbh} - \mu}{\sigma}\right)^2}$$
 with eqn 12

$$442 \quad \sigma = a_2 + b_2 RBA^c \qquad \text{eqn } 13$$

443 c = 1

444
$$\mu = 1.058 \pm 0.77 \log(SS) + 54.78 \pm 3.68 (R^2 = 0.345)$$
 eqn 14

445

446

Combination of harvesting decisions

- Once we have the models for the four decisions, we can combine them to predict the probability
- 448 that any tree of any species i is harvested in the forest given the biomass of trees in the forest,
- 449 *SWD* and SS values:

Kijima et al., 2000).

450

451
$$P_{i,SWD,SS} = \left(1 - \gamma e^{(-\beta RBA)^{\alpha}}\right) e^{\frac{-1}{2} \left(\frac{\text{dbh} - \mu}{\sigma}\right)^2}$$
 eqn 15

452

This model significantly predicts the supplied timber biomass for each species at a given year of 453 harvest, when excluding the Mahogany tree. From this prediction, we can deduce the expected 454 revenue from timber harvesting (\$/ha/y), as the international price for timber is highly based on 455 456 the SWD value of species (Ahmed & Ewers, 2012, Figure S3). Here, the model assumes a constant price for this analysis, which can be changed in the model. Furthermore, the model 457 assumes that all RU have the material for cutting appropriately their species, and that the costs of 458 increasing the number of RU and thus of species harvested is not increasing, by assuming the 459 460 community-level marginal return on labour for each RU represented only a small fraction of the 461 value of the marginal product of labour to manage more species (Agrawal & Gibson, 1999,

463

462

2.3.2. Model of fuel-wood harvesting (link 1a' in CIS)

465

464

Fuelwood is a crucial resource for rural livelihoods in many developing countries, and is still of importance in developed countries (Parikka, 2004). The model considers fuelwood harvesting as



a constraint on timber harvesting. It assumes that the harvesting of fuelwood starts with deadwood first and then supplement with live trees if deadwood is not available (Foley, 1985; Webb & Dhakal, 2011). At a world scale, fuelwood demand can vary from 200 kg to more than 2000 kg per person per year (Foley, 1985; Webb & Dhakal, 2011). The model defines the main need in fuelwood as a function of the size of the household (HH_{size}) and the density of households per hectare (HH_{density}), following Webb & Dhakal (2011), but the model can be changed and adapted to the local context:

475

476 $B_{fuelwood} = HH_{density} HH_{size} (899.24 - HH_{size} 34.68)$ eqn 16

477

For this study, population density was simply defined as one household per hectare with five members per household.

480

- 481 Decision 2.3.2.1 Preference in species collection
- 482 Fuelwood preference by RU has been found to be positively correlated with the Fuelwood value
- 483 index (FVI) of the tree species, which depends on SWD (Ramos et al., 2008), such that:

484

485 $FVI = 0.0475 \pm 0.008 SWD - 11.424 \pm 4.8 \quad (R^2 = 0.82, n = 38)$ eqn 17

486

The model assumes a perfect relation between FVI and harvesting choice, such that the probability of harvesting a given timber species (dead or alive) is considered as the FVI rank of the given species divided by the sum of all the FVI ranks of all the species present in the forest.

490

- 491 Decision 2.3.2.2 Preference in tree size collection
- 492 Once the RU select a species to collect based on SWD, we can simply predict from Thapa &
- 493 Chapman (2010)'s free data and Nguyen et al (2014) that the collection of deadwood is also
- 494 based on the tree *dbh*:

495

496
$$P_{\text{fwt}} = 12.43 \frac{1}{1.23 \sqrt{2\pi}} (100 \,\text{dbh} - 4.106) e^{\left(\frac{-(\log(100 \,\text{dbh} - 4.106) - 3.381)^2}{2 \times 1.23^2}\right)} \quad (R^2 = 0.94)$$
 eqn 18



The combination of these models determines how much trees are harvested. The model then considers harvesting once a year, and that live trees are harvested if the total annual quantity of dead fuelwood for the household (defined in eqn. 16) is not fulfilled. In all our simulations, this level was never reached as the number of households was low (one per hectare). Changing this aspect will be tested in a following paper (see last discussion section).

503

504

2.3.3. Behavioural model for individual post-harvesting planting (link 1b)

The model considers that resource users who are harvesting trees for timber are engaged in 505 individual post-harvesting planting. For instance, Sakurai et al. (2004) show that the density of 506 tree replanted can simply be modelled from few variables; from whether the parcel is managed 507 privately, as an association or publicly (PRIVATE: binary 0-1, if 0: then resource users are 508 509 organised as community or state for post-harvesting practices), from the walking time to the forest T_{wt}, from the soil quality (with sand: S_{sandy} [binary 0-1], gravels S_{gravel} [binary 0-1]). Given 510 that the soil considered is loam, and the time to walk to the forest is 18.5mn, the planting density 511 after harvest D_{planting} [given as 1000 seedlings/ha] is defined as follow: 512

513

- 514 $D_{planting} = 10.2 \pm 3.32 \ PRIVATE log(T_{wt}) 1.85 \pm 0.93 \ S_{gravel} 2.03 \pm 1.31 \ S_{sandy} \sim 7$ eqn
- 515 19

516

The variable PRIVATE = 1, given it is assumed that the resource users individually replant according to their harvesting preferences defined in section B.2 and B.3. The impact of changing these variables will be tested in following papers (see last part of the discussion section).

520

521

2.4. Model of Public infrastructure (PI)

522

523 2.4.1. Collective weeding and thinning model (arrow 4a in CIS)

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Weeding and thinning efforts are considered in the model collective supporting activities that are engaged by the association of resource users to free space, provide light gaps, water and nutrients for the tree species of livelihood interest. The model is not considering invasive/alien species coming from outside the predefined mix of species or grass or animal species. The econometric

model of thinning and weeding developed by Sakurai et al. (2004) was used as it is simple, replicable, and considers that weeding is not a separate effort on different target species, but rather an extra collective effort of thinning the dominant tree species that is not of use for timber harvesting and the least interesting for fuel-wood. The model also assumes a two-step decision process for thinning/weeding. It considers first that a global effort is allocated at a stand level, which depends on the governance system, the distance to the forest and size of the forest (Sakurai et al., 2004: Decision 1). Then the model considers that the association of RU in the PI allocate collectively the weeding/thinning effort at a species-level. This effort depends on the capabilities of RU and time to detect collectively the most dominant species among others (Garrard et al., 2013: Decision 2). In this study, these variables are considered fixed and parametrised based on the most common or average values found in the literature. The effect of changing some of them on the forest outcomes will also be tested in a following paper (see details in last part of the discussion section).

Decision 2.4.1.1 – Weeding and thinning effort at a forest stand level

- The collective weeding/thinning effort depends in the model on a series of factors (Sakurai et al.,
- 545 2004; Joshi and Arano, 2009): the governance of forestry practices (PRIVATE: binary variable
- 546 0-1, so 0 in our case), the walking time to reach the forest (Twt), the size of the forest parcel
- 547 (F_{area}), and the presence of gravel (S_{gravel} : binay 0-1) and loam (S_{loam} : binay 0-1):

549 Thinning =
$$6.09\pm2.23$$
 PRIVATE -2.34 ± 1.2 $F_{area}-4.37\pm1.79$ $S_{gravel}-3.33\pm1.71$ $S_{loamy}\sim0.4$

550 eqn 20

Then, as previously mentioned, an extra effort was applied as weeding, to control the same invasive species that is not of any use for timber and fuelwood. The target of this weeding effort can be changed if an invasive species is identified and taken into account. Considering the distance to the forest, Sakurai et al. (2004)'s simple model of weeding effort [man-day/ha/yr] is defined as follow:

558
$$Weeding = 30.9 \pm 12.2 - 2.79 \pm 1.35 log(T_{wt})$$
 eqn 21



560 Decision 2.4.1.2 – Weeding/thinning effort at a species level

Once the man-day effort is defined, the association of resource users is faced with the problem of 561 562 detecting and controlling the dominant species with specific set of LHTs, among various other species with other LHTs (Garrard et al., 2013). The complexity of this multi-species/trait 563 problem has a cost that translates into increase in time to detect the dominant species (Garrard et 564 al., 2013). Garrard et al. (2013)'s model gives a first approximation of the time to detection 565 between plant species, but of course this model should be updated once more general rules are 566 known for trees. Assuming that all RU are experienced observers (EXPERT: binary variable 0-567 1), and that the density of individual per square/m is equal to the frequency of occurrence at one 568 hectare, Garrard et al.'s (2013) model gives a good primer to define the time in minutes to detect 569 one individual of the dominant species: 570

571

572
$$t_{mean} = e^{(4.27\pm0.58 - 0.17\pm0.39 \text{ EXPERT} - 0.28\pm0.12 \text{ log}(- \log(1 - Nsurvey) + 0.34\pm0.17 + 0.27\pm0.2 + 0.89\pm0.2))}$$

573 eqn 22

574

Finally, to predict the actual number of trees detected and weeded/thinned ($N_{thinned}$), the model simply makes, like Garrard et al. (2013), the reasonable assumption of a spatial random distribution of the trees, and a 8 hours per man-day and 60 mn/hour (i.e., t = 480 minutes), such that:

579

$$N_{\text{thinned}} = \frac{480 \text{ (Weeding+Thinning)}}{t_{\text{mean}}}$$
eqn 23

581 582

2.4.2. Control of the access for individual harvesting and post-harvesting replanting to a diversity of resource users (link 5b and 5b' in CIS)

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For this paper, resource users possess the right of harvesting timber and enough deadwood for household heaters (fuelwood). Given that harvesting more timber can impact fuelwood availability and that fuelwood is critical for livelihood, resource users need to respect basic rules collectively defined: rules on the access rate for timber harvesting (link 5b) and for fuelwood (link 5b'). The effect of changing links 5b and 5b' is symmetrical and explored in this paper,



which means that one RU who harvest live tree for timber, can collect deadwood for his own household heater. On the other hand, the impact of link 5b' is defined as a fixed constraint in the model, where timber harvesting must stop if fuelwood harvesting cannot reach at least the minimal livelihood threshold (see eqn. 16). However as it was mentioned before, this was never reached in the simulations that we explored, and will be studied in a following paper.

2.5. Scenarios, outputs and sensitivity analysis



For computational reasons, the forest model was constrained to height types of species, corresponding to all the combinations between two values for each of the three LHTs (see section 2.2.): SLA (2.85 and 20 m⁻².kg), SWD (400 and 1000 kg.m⁻³) and SS (10⁻⁷ and 10⁻³ kg). With the eight types of tree species considered, the effect of the 2⁸ = 256 combinations of tree species management were explored, over 100 years projections of the composition, structure and dynamics of the forest and its outcomes.

The model calculated every year various outcomes (see details of the calculation in Pichancourt et al., 2014): the expected Shannon index of LHT diversity, the above-ground carbon biomass (MgC/ha/y), and the revenue generated from timber harvested (\$/ha/y). The model also estimated every year the average forest-level values of the three LHTs.

To facilitate generalisation, criticism and comparison with future studies, the gradient of increased access is presented as a percentage/proportion of species managed for biomass (timber) extraction. In the caption of figures, the actual number of species is notified (i.e. 1 species = 12.5% managed, 2 species = 25% managed, ..., 8 species = 100% managed).

Following salient results from Pichancourt et al. 2014, a similar sensitivity analysis was performed by focusing on the comparison of the impact of opening the access rates between two types of ecological factors: between wetter forest commons (that assumes water saturation in the soil bucket model from Pichancourt et al. 2014) and drier forest commons (that assumes no water saturation and depends only on the rainfall pattern of the climate model from Pichancourt et al., 2014). Bootstrapping, e.g. 1000 times, is incorporated in the code based on error margins of the behavioural model parameters from equations 1 to 23. But as explained in the end of the introduction section, given the size of the entire social-ecological model and the objective of the present paper, this method could not be computed in a reasonable time for all the 512 scenarios



(8 species, $2^8 = 256$ combinations of harvesting, times two types of forests: wetter and drier). Proper code optimisation associated with super computing capabilities and parallel programming would be necessary. Nevertheless, bootstrapping will be implemented in a following paper when testing the effect of changing targetted parameters of governance and number of species in the forest. As the code is open sourced, potential model users can already use bootstrapping and test the current model based on their own social-ecological data.

3. Results

3.1. Impact of opening the access to resource users on the forest-level outcomes in wetter and drier forest commons

Figure 3 approximately here

Compared to non-harvested forests (in fig. 3 "no access", equivalent to an exclusive conservation zone), opening the access to resource users, who are disturbing species to supply timber and fuelwood in wetter forest commons, is predicted to bring long-term economic benefits (fig. 3a), stimulate regrowth and thus increase above-ground forest carbon biomass (fig. 3d). However there, it is reducing by \sim 50% the long-term average Shannon index of biodiversity (fig. 3c). In drier forest commons, the Shannon index of biological diversity is predicted to reduce even by \sim 90%, without bringing much economic value.

In term of life-history traits (LHTs), opening the access is increasing in wetter forests the average community-level SLA (fig. 3d), whereas it is decreasing on average in drier forests. The average specific wood density (SWD) is predicted to decrease both in wetter and drier forests with opening the access (fig. 3e). Reversely, the average community-level seed size SS (and thus the average maximal size of tree species) produced in wetter forests is expected to increase, whereas it is no predicted to be affected in drier forest commons (Fig. 3f).

3.2. Impact of increasing the access to a greater diversity of resource users on forest outcomes in wetter and drier forest commons



3.2.1. Average and variance of the impact

Figure 4 approximately here

Opening the access of the forest to a greater diversity of resource users, each specialised on harvesting and replanting a different species, is expected to impact the three main forest outcomes in both drier and wetter forest commons. The Shannon index of LHT diversity is expected to reach its maximum level at different proportions of species targeted by management disturbances in drier (fig. 4a) and wetter (fig. 4b) forest commons. In drier ones, this maximum level is low on average, very variable and reached at intermediate levels (~37.5%); whereas in wetter ones, it is expected to reach a much greater maximum value and when most species are controlled by management disturbances.

Forest carbon storage is expected to be less impacted in drier forests (fig. 4c) than in wetter forests (fig. 4d), even though the variability of the results is greater in drier than in wetter ones. In wetter forests, increasing the proportion of species targeted by management disturbances is always leading to greater long-term level of living above-ground carbon storage than in non harvested forest. Nevertheless it still leads to an expected reduction in carbon.

Profit generated from harvesting obviously is expected to increase with the number of species targeted by management disturbances for timber harvesting. However, profits are expected to be much greater in more productive wetter forests (fig. 4f) than in drier ones (fig. 4e).

Detailed impacts on the equilibrium dynamics between the three forest outcomes can be seen in fig. S3 (S3.1 for drier forests and S3.2 for wetter ones).

3.3. Understanding with the life-history traits, the sensitivity of the impact between drier and wetter forests



The impact was then decomposed, by emphasizing the role of the three main life-history traits measured at a forest-level. This impact is highly predictable and is very sensitive to the forest wetness. The results are decomposed into three analytical steps.

3.3.1. Impact of opening to a greater diversity of species resource users on the average value of forest-level life-history traits (LHTs).

Figure 5 approximately here

The relationship was first decomposed to emphasise the impact of changing the access strategy on the dynamics of the three life-history traits. The model predictions were sensitive to whether it was in drier and wetter forests.

In drier forest commons (fig. 5a,c,d), only SWD is predicted to be sensitive to changing the percentage of species managed for timber harvesting (fig. 5c), where the maximum value of SWD is predicted to be obtained for intermediate proportion of species disturbed (~1/3 species harvested, i.e. between 2-3 from 8 species).

In wetter forest commons (fig. 5b,d,f), SWD is predicted to only be slightly sensitive to this change (fig. 5d). Both SLA and SS are predicted to be respectively reduced (fig. 5b) and increased (fig. 5f) in a symmetric fashion, by increasing the proportion of species managed for timber harvesting: the maximum SLA and minimum SS values are predicted to be obtained at minimum proportion of species managed, whereas the minimum SLA and maximum SS values are predicted to be obtained at maximum proportion of species managed.

3.3.2. Relation between average forest-level life-history traits (LHTs).

Figure 6 approximately here

The second step was to focus on how the species assemblages in the forest commons are predicted to evolve in term of the relation between the average LHTs. When plotting all the years, scenarios, and forest wetness classes, we can detect the same non-linear trade-offs, mostly visible between SLA and SS, and between SLA and SWD (Figure 6). In fact, the model predicts



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that forests with on average greater SLA should be composed of trees that also produce on average smaller seeds SS and lighter timber SWD (and vice versa). Decomposition between drier and wetter forests shows that the latter should be sufficient to detect these above-mentioned trade-offs between LHTs.

Fig. S4 (S4.1 in drier and S4.2 in wetter) provides details on how the difference between LHTs trade-offs dynamically change between scenarios decomposed and averaged per classes of proportion of species managed (from 0% to 100% of the 8 species from the forest). For instance in wetter forest commons, opening the access to resource users and then increasing the proportion of species managed is predicted to change the LHT pattern. When there is no access, the model predicts that the domination by shorter trees producing smaller seeds SS should dynamically alternate between trees of different SLA and SWD along the dynamic trade-off between in an unpredicatable way (fig. S4.2: 0%). Then when opening the access to resource users (fig. S4.2: >0\% and <100\%), the model predicts that wetter forest commons should have more complex dynamics between high and low values for the three LHTs; but progressively with greater SS (taller tree species), as the access to a greater diversity of resource users increases. Finally when all species are managed for timber extraction (fig. S4.2: 100%), the tree species are on average dynamically and predicably alterning between different values of SLA and SWD (with stable high SS values), in a way that the complete dynamics gravitates around a stable attractor point (SLA ~ m².kg⁻¹, and SWD ~ kg.m⁻³ : see fig. S5) and form a limit cycle. More details on the temporal trajectories of the individual LHTs can be found in figures S5 (S5.1-S5.6).

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3.3.3. Impact of changing the average value of forest-level life-history traits on the forest level biological diversity, carbon stock and profit

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Figure 7 approximately here

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The second step was to analyse how forest biodiversity, carbon and economic outcomes from timber production were affected by the change in forest-level LHTs. Below is detailed the effect on biodiversity (fig. 7). The effects on carbon and economic outcomes are presented respectively in figures S6.1 and S6.2. It was possible to predicted three laws that related the



Shannon index with the three LHTs. The shape of these laws does not change with wetness. Only the position along this law changes with wetness.

When looking at the average forest-level SLA, the Shannon index is predicted to reach its maximal value at intermediate to low average forest-level values of SLA (~5 m².kg⁻¹), by following a saturating logistic law (fig. 7a,b). The turning point of maximal Shannon index (fig. 7b) could be tracked back in fig. 5b (wetter forest commons) to correspond to ~2/3 of the species managed. There the entire spectrum of values is homogeneously covering the law from low to high average forest-level values of SLA. Therefore the turning point is expected to be detected in these wetter systems. Reversely in drier forest commons (fig. 7a), the lower Shannon index observed in fig. 4 can now be explained by the fact that forest-level average SLA values rarely reach (and even exceed less) the SLA turning point of maximal Shannon index, regardless of the percentage of species managed for timber harvesting.

When looking at the average forest-level SWD, the maximum Shannon index in drier forest commons is expected to be reached roughly half-way along the SWD spectrum. It is following a saturated parabolic law (~700 kg.m-3, Fig 7c), even-though most values fall more frequently into either high or low SWD states, with rarely sustaining in-between SWD states. For this reason, the turning point of maximal Shannon index (~700 kg.m-³, fig. 7c) is rarely reached, and is reduced to a narrow range of percentage of species managed for timber harvesting (~1/3 [17.5%-40%] of the eight species managed, see fig. 5c). In comparison, wetter forest commons (undisturbed and disturbed ones) follow a similar law, but with on the top of the law, much more low SWD values covering any type of Shannon index values (corresponding actually to the varying effect of SLA and SS laws).

Finally when looking at the average forest-level seed size SS, the Shannon diversity index in drier and wetter forest commons follows again the same saturating logistic law. However, compared to the SLA law, the maximal level of Shannon index is reached for forests with on average high seed size values (> 5.10⁻⁵ kg). This level is only reached in wetter forest commons (fig. 7f), on average when ~2/3 of species are managed for timber harvesting (see fig. 5f), eventhough any proportion of species managed (between 12.5% to 100%) can regularly achieve this result. Reversely, drier forest commons contain mostly tree species producing small seeds (10⁻⁷ kg: fig. 7e), which can be reached for any proportion of species harvested for timber (fig. 5e). On top of this law, averagely low seed size forest commons that are only composed of small tree



species producing small seeds (10⁻⁷ kg) can produce any Shannon index values along the possible ones (fig. 7e and f), corresponding to the effect of the SLA law (fig. 7a,b) and SWD law (fig. 7c,d).

4. Discussion

Finding a proper scientific framework for assessing the long term sustainability of social-ecological systems, where complex human organisations need to equitably access common pool resources that are themselves biologically complex, is difficult to comprehend (Ostrom, 1990; Poteete & Ostrom, 2004; Naidu, 2009; Ostrom, 2009; Saunders, 2014; Betts et al., 2021). For this reason, and despite more than a century of ecological theory and practice, it is still difficult for (social)ecologists, conservation biologists and bio-resource managers to imagine precise mechanisms that could explain, e.g. how opening the access of a biodiverse carbon rich ecosystem, ideally to as many diverse resource users as there are species to harvest and manage for biomass resources, may be compatible with an objective of conserving the initial ecosystem's characteristics. The goal of this paper was to offer theoretical arguments to progress on this debate.

Here we can see that this problem is connected to a more specific ecological one, i.e. how the diversification of controlled disturbances imposed on species, is predicted to impact the coexistence of entire pool of competing tree species, with some or all of them having interest for the productivity of the entire ecosystem? By re-framing this way, it was possible to perform purely ecological analyses, and understand this complex (social-)ecological problem in relation with classical ecological theories. Nevertheless based on past experiences, this approach was not a guarantee of success. Indeed, the ecological literature on the topic raised some issues regarding the analysis and use existing theories when there is a large number of species that can be disturbed in a complex way (Barabás et al., 2018). However, this has not stopped various ecologists to independently conjecture the potentially positive role of the diversification of disturbances on the process of biological diversification and the productivity of ecosystems (Calbi et al., 2021; Jones et al., 2022).



4.1. On the causal link between the diversification of resource users and biodiversity

Here the social-ecological system (SES) model predicted that forests with an open access to resource users for timber harvesting can be biodiverse, but never as in protected forests, regardless of whether the forest is in drier or wetter conditions (fig. 3). This result is quite trivial and well documented. A less trivial result however, was that the model predicted that wetter tropical forests, opened to an increased number of timber resource users, who manage and disturb collectively a greater diversity of species, should have greater Shannon index of tree LHTs diversity (compared to forests where only one of the species is harvested by one user, and this regardless of the species). The model also predicted that the above-ground carbon stock, and the expected economics benefits from harvesting should be greater. Reversely in drier forests, this relation was not predicted to be observed. To wrap up, the success of achieving sustainable management of biodiverse common pool forest resources could in theory be achieved, but is predicted to be sensitive to the moisture conditions of the forest common.

These results need to be confronted to more empirical data from a wide range of existing social-ecological contexts, which is obviously hard to get. Nevertheless, the results already corroborate various observations from forestry science. For instance, greater species and functional diversities (especially in the understory) is regularly observed when forests a subject to repeated local selective logging disturbances or other disturbances that are frequent enough to prevent competitive exclusion over an entire area, but not so frequent as to eliminate most species (e.g., Berry et al., 2008; Calbi et al., 2021). Furthermore, forestry science demonstrated that some irregular shelter-wood practices applied to mixed species stands. These practices consist in imposing a diversity of controlled disturbances on different tree species and different cohorts. Experience suggest that they can benefit canopy openings to the requirements and tolerance of a greater diversity of tree species, e.g. especially shade tolerant ones (Daniel et al., 1979), and without sacrificing vigorous small merchantable stems (Raymond et al., 2009).

This complex disturbance patterns are usually thought as a coordinated strategy by a single forestry actor (Berry et al., 2008; Raymond et al., 2009), or as emerging from completely unrelated and uncoordinated natural and human drivers (e.g., fire, wind, diseases, harvesting, ...,



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Calbi et al., 2021). In the extreme latter case, the large diversity of unpredictable and radically different origins of disturbances makes it difficult to predict their impacts. However, this process can equally be thought, like in our case, as an exclusively non-coordinated disturbance process emerging from the practice of a diversity of resource users working in the same forest common. This process is not uncommonly observe and can naturally emerge under certain circumstances. The reason is that in human communities, usually no single member can possess the entire spectrum of knowledge, beliefs and practices (KBP) to sustainably harvest and manage by himself a highly biodiverse common pool of resources with different ecological conditions (Poteete and Ostrom, 2004). Rather human communities are characterised by a diversity of coexisting actors, possessing different socio-economic and cultural attributes, in relation with the independent extraction of different biological resources (Natcher et al., 2005; Lemos and Agrawal, 2006), and in order to secure and equitably share a diversity of livelihood benefits from a variety of forest ecosystem services (Hegde et al., 1996; Murali et al., 1996; Agrawal and Gibson, 1999; Wunder, 2001; Ambrose-Oji, 2003; Toledo et al., 2003; Belcher, Ruíz-Pérez & Achdiawan, 2005; Kimengsi et al., 2019). These institutional diversification processes were well documented, especially in forests, but there were no theoretical studies to help understand the limit of these commonly found practices. As a consequence, the results of this study represents a useful first step for showing how to explore and generate new refutable hypotheses regarding the impact of such complex institutional organisations on the biodiversity and carbon sequestration of CPR.

Now, how can the results be explained? Given the important roles of ecological processes in this study, it is only natural to try to use first well known and powerful classical ecological theories to try to explain these results. The most robust ones are the life-history theory (summarised in Caswell, 2000), the forest successional theory (Lohbeck et al., 2013; Poorter et al., 2019), the Chesson's species coexistence and disturbance theory (Chesson, 2000; Barabás et al., 2018). To use them for interpreting the results, the best way is to start by not separating (i.e. accept to conflate) first the effect of disturbance regimes in our results. Their interpretation in 4.2 will then serve as a baseline for explaining in 4.3 what is happening when we integrate the impact of the diversification of disturbance regimes into the equation.



4.2. On the role of life-history traits to understand this causal link

In the modelling example of wetter tropical rainforest, tree species compete only for light, and respond to eommon climate variabilities. There,—the life-history theory predicts that each tree species possessing combination of LHTs values (SWD, SLA, SS) should have a unique life-cycle capability and demographically respond to specific ranges of light disturbances (Caswell, 2000). Therefore on the long run, only a fraction of the tree species is expected to have exactly the same vertical niche space and respond to the light gradient (see detailed explanation in Pichancourt et al., 2014). For this reason it is trivial to predict from Chesson species coexistence principles, even though it is not well suited for understanding communities with complex dynamics and large number of species (Barabás et al., 2018), that the greater coexistence and vertical partitioning of species along the light gradient should be achieved mostly through first "stabilizing mechanisms": i.e. intra-specific light competition > inter-specific light competition (Chesson, 2000; Barabás et al., 2018).

Translated into a forest system where species are defined by their LHTs values (SWD, SLA, SS) like it is done here, Chesson's *stabilising mechanism* would mean that along the vertical light niche space, species with the same SLA value should compete more than between species with different SLA values. Therefore, Chesson's theory should legitimately predict that the coexistence of species with different SLA should be greater than between species with the same SLA but different SWD and SS. This was highlighted in the wetter forest results, where the variation of light promoting traits like SLA (and SS) played a major role in niche partitioning and positive species coexistence (fig. 5,6,7). Particularly, the model predicted that the Shannon diversity index was greater and more variable in forests that were dominated by tall trees (i.e. producing seeds with greater SS: Falster et al., 2008) and leaves with lower SLA (for irradiation tolerance) (fig. 7b,f). The simple reason is that having a dominant upperstory is not incompatible with having also an understory containing a diversity of tree species characterised, on the one hand by a diversity of lower SS seed traits covering a wider spectrum of small tree height, and on the other hand with a diversity of greater SLA leave traits covering a wider spectrum of shade tolerance.



From the same token along the SWD trait gradient (symptomatic of the wet/drought tolerance dimension: Poorter et al., 2019), the fact that species had similarly low SWD in wetter forests, but greater and more variable values in drier forests, signifies that species coexistence should be respectively lowered in wetter forests and increased in drier forests along this dimension (fig. 5c,d; 6c,d; 7c,d).

The same reasoning can be extended to understand temporal results along the forest dynamical succession of these traits. The model produced predictable successions (fig. S5), that followed the same predicted trade-off laws between community-level SLA (fig. 6), and consequences on species coexistence/diversity (fig. 7), enriching previous empirical results (Lohbeck et al.., 2013; Muscarella et al., 2017). For instance in wetter environments, as forests are transiting to secondary successional stages (with taller species producing bigger seeds and lower SLA), the coexistence of species is expected to increase too (fig. S4.2). Less trivially, standard successional theory also predicts that successions would also proceed from low towards high forest-level SWD in wetter forests (and reversely from high towards lower community-level SWD in drier forests), following again the law that high SWD reflects well drought tolerance in harsh early successional environments (Poorter et al., 2019). This was actually corroborated by our independent theoretical predictions from fig. S5.3a in drier forest and fig. S5.4a in wetter forest commons.

4.3. On the role of disturbance regimes on this causal link



Now we have the main theories, empirical laws and mechanisms right, we can start understanding the the role of the diversification of human-induced disturbances. In the model, once harvesting and replanting disturbances are introduced, the species coexistence mechanisms are changed. Light gaps are created, niche partitioning disappears, and the level and type of species that coexist depend now on the relative competitive abilities of each species to quickly harness light (SLA) as a newly germinated seedling, grow and construct wood to resist drought in harsh early successional environments (SWD), and avoid being trapped into a non viable vertical niche. In our case, the most dominant species is the one with the cheapest leaves, timber and seeds to build, i.e. with the lowest SLA [m².kg⁻¹], lowest SS [kg] (but producing many small



seeds), and lightest SWD [kg.m⁻³] (2.85, 10⁻⁷, 400). This type of species thus with the greatest above-average fitness advantage (in the Darwinian sense) and population growth rate within the community of competing species. Not harvesting this dominant species always leads to suboptimal Shannon biodiversity results (see Pichancourt et al. 2014 for explanation based on detailed thinning results).

In our model, as the access to a greater number of resource users increases, each specialised in the harvesting and replanting of a different species, there is a greater proportion of species managed (and thus more species whose size structure and dynamics are disturbed). Consequently, there is a greater probability that the most abundant and competitive tree species is controlled too. The population of this dominant species occupies a relatively greater basal area than the other species (harvested or not). So harvesting this dominant species (i.e. when the minimal forest biomass threshold is reached, see method section 2.3.1.1) is always freeing relatively greater resources for other species (space, light and soil water) to germinate and grow vertically, leading eventually to greater species coexistence with different LHT combinations in wetter forests (Pichancourt et al., 2014). This corresponds to the second "equalising mechanism", as described by Chesson's species coexistence theory (Chesson, 2000; Barabás et al., 2018). The fact that drier forests would not necessarily lead to greater species coexistence, is due to the selection pressure that favour greater SWD species to resist early successional drought, and thus increasing both inter and intra LHT competition, and thus lower SS and SLA tree species (due to community-level trade-offs between LHTs: see fig. 6).

By following this line of reasoning, it is further trivial to understand that for every new dominant species harvested and replanted on top of the most dominant species, it should be expected to produce an extra *equalisation* benefit on the species assemblage and relative abundance between two time steps, given thus new opportunities for even more species (and eventually the biologically more expensive one to construct: i.e. SLA = 20 m².kg⁻¹, SS = 10⁻³ kg, SWD = 1000 kg.m⁻³) to also compete on a more equal grounds (fig. 5). And because the species LHT dominance can change with environmental context (water, light) and successionnal stage, the *equalizing mechanism* is expected to be more efficient for the tree assemblage, when forest access is opened to as many and diverse resource users than there are species to harvest and replant (obviously under collective governance constraints on sustainable harvesting, replanting



and post harvesting weed management specified in the model which contribution would have to be tested). Conversely, if the forest is opened to homogeneous resource users that are targetting only one species (and especially the less dominant one), then biodiversity is expected to drop drastically, and the tree assemblage will be dominated by mostly the relatively few dominant ones (greater SS and lower SLA and SWD for wetter forests, and lower SS and SLA and greater SWD in drier forests). This is what is predicted in fig. 3 when only one species is randomly selected to be harvested and replanted.

Altogether we see that the relation between some forms of biodiversity and livelihood diversification processes can simply be explained using existing ecological theories, e.g. the life-history, disturbance, succession, and Chesson coexistence theories.

4.4. Toward a research agenda on the topic

This study was limiting the focus to some specific practices of opening the forest access and under specific ecological and management contexts (see method section). So obviously, the theoretical results may surely be highly sensitive to social ecological factors, other than the wetness gradient explored here. For instance we should expect different results under different ecological conditions (climate, soil, forest structure and composition), other governance rules and management behaviours. We can also expect this especially when extending the monosectoral forestry system to a more commonly found pluri-sectoral one containing supplementing activities important for diversifying the livelihoods of resource users (e.g. products from non-timber, hunting, fishing or agricultural origins: Ellis & Allison, 2004). Nevertheless the present model and results can serve as an introduction to an agenda for future studies to advance on this topic. It is the hope of the author here that some of these factors will be explored in a series of following papers in this journal, justifying the mention (1) in the title of this paper. The elements of this agenda are the followings, by order of expected difficulty:

(i) A first type of study should use this model (or another) to explore the sensitivity of the relationship to changes in the maximal number of species in the forest common and to the access



- of the associated number actors (link 5a in Figure 1). The size and complexity of these commons (NB: diversity is an index of complexity) have been mentioned as important factors to guarantee the success of their common pool resources (Ostrom, 1990). Exploring this aspect with such model could thus be a good way to question some of the important CPR hypotheses from Ostrom, particularly as the complex/diversity of the social-ecological systems is perceived as a difficulty for controlling the sustainability of such systems (Ostrom, 2009).
- (ii) A second type of study should explore its sensitivity to changes in the spatial organisation of the diversity of livelihood activities. Indeed, activities in forests can be organised differently, either in the same location (strategy called *land sharing*) or separated between locations (strategy called *land sparing*). The former is based on the belief that synergies between species and activities can be achieved (especially vertically in forests like in this study). The latter is based on the belief that each activity should be separated spatially (carbon, biodiversity conservation, one performing timber species in a monospecific stand, etc ...) in order to better optimise all the outcomes. The model could be used to explore some of the new limits of the *land-sharing* vs *sparing-debate* (Fischer et al., 2011; 2014; Runting et al., 2019), especially in relation with the diversification of livelihood activities based on a diversity of timber species.
- (iii) Then a third type of study should compare the response on biological diversity of the impact of the present disturbance strategy (that we equilibrium) refer to the *diversified disturbances hypothesis*), with other disturbance hypotheses that have been expressed in the past. A first maximalist and popular one assumes that harvesting should be focused always on the most dominant species to the maximal of extent (Chesson, 2000; Pichancourt et al., 2014; Barabás et al., 2018). Another popular one refers to the *intermediate disturbance hypothesis*, which assumes that intermediate frequencies or intensities applied on the entire resource or on specific species should lead to better biodiversity and productivity outcomes. The latter theory is source of debate in the literature (Chesson, 2000; Sheil and Burslem, 2013, Fox, 2013; Barabás et al., 2018) this model could also be used to explore and compare the forest outcomes of these different hypotheses.
- (iv) Finally, a fourth type of study should explore its sensitivity to changes in the management and governance parameters affecting collective actions. These include the CIS parameters from the resource user infrastructures RI (links 1a and 1b) and the from the public infrastructure PI (links 4, 5 and 6). For instance, some strong assumptions were made in this



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study, among which the strong governance with perfect public infrastructure, the legality of timber harvests, the validity of which is debatable, e.g. in many tropical countries (e.g. Agrawal & Gibson, 1999; Chhatre & Agrawal, A., 2008; Phelps, Webb & Agrawal, 2010; Finer et al. 2014; Brancalion et al. 2018). These justify the exploration of the relaxation of some of the strong assumptions, ideally in relation with the eight design principles of good governance specified by Ostrom, 1990. Linking the model and analysis to these famous design principles, as it is suggested in Anderies et al. (2019) or even in Fig. 3 of Guerbois et al. (2019), may be of great help to advance on Ostrom's SES theory. For instance, the experience accumulated on these design principles suggest that some may be less of an importance (Cox et al., 2010). A corroboration or limit of the scope of some of them may be achieved, through the use of broad exploration of a range of values of these links, associated with context-specific targetted sensitivity/uncertainty analyses based on existing contextual data and models.

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Outside these direct extensions of this study, the type of model and results presented here could also indirectly serve as a primer to explore a variety of other important questions that are also in need of novel methodological guidelines. For instance it could first broadly serve to explore a range of potential novel disturbance practices for managing biodiverse and carbon rich social-ecological systems (Newman, E. A., 2019). It could also be used to explore possible explanations for understanding ancient social-ecological systems, where the role of human disturbances on the biodiversity and productivity of ecosystems has been conjectured. This is for instance the case for some ancient agro-ecological systems (Balée, 2006), but more surprisingly for biological hotspots of tropical Amazonian forests where we have now proof of extensive nurturing and use of species resources by ancient indigenous communities (Heckenberger et al. 2007; Mayle et al. 2007; McKey et al. 2010; Maezumi et al., 2018a,b). This type of study could also be of use for foresters who are trying to explore the extent to which complex shelter-wood techniques should be used on mixed species stands, in order to protect biological diversity, and without sacrificing vigorous small merchantable stems (Raymond et al., 2009). However more broadly, this study opens up interesting avenues for exploring how the complexity/diversity in both human and biological dimensions can coexist and even reinforce each other in some conditions. This type of question is associated with the scientific discipline and concept of "biocultural diversity". They are built upon the conjecture that there exists an inextricable link



between the broader processes of biological diversification, the process of diversification of cultural knowledge beliefs and practices (e.g. the local diversity of actors' management and institutional practices like in our study), and the sustainable livelihood outcomes from managing species (Maffi, 2005; Maffi & Woodley, 2012). Past research on the topic mostly focused on anthropological explanations, on the development of indicators, and on positive statistical results using large scale dataset. However, they never offered ways to explore the limits of this concept, provide convincing explanations involving robust ecological theories, nor precise logical and empirical falsifiers.

Altogether, the model and results of this study suggests that some pure ecological theories, combined with carefully thought through methodological guidelines, can be of great help to generate novel hypotheses for understanding human-nature dilemmas and solutions in complex social-ecological systems.

Supplementary Information

Data & Code

Table S1. Coefficient in equations 1-3 for the type of forests and associated dominant species considered in Canham et al., 2013. The average timber density of the species considered were extracted from the US forest services (http://www.feis-crs.org/beta/) and various other relevant official sources when not found on the site.

Table S2. Coefficient in equations 4-7 for the type of forests and associated dominant species considered in Canham et al., 2013. The average timber density of the species considered were extracted from the US forest services (http://www.feis-crs.org/beta/) and various other relevant official sources when not found on the site.

Table S3. Coefficient in eqn & of the species considered in Canham et al., 2013. The average specific wood density (SWD) and the size of seeds (SS) produced of the species considered were extracted from the US forest services (http://www.feis-crs.org/beta/) and from various other relevant official sources when not found on the site.



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1071	Figure S1. Relationships between the size of seeds (SS) produced and a) coefficients α , or b) coefficient
1072	μ used in the model that predicts the household-level tree harvesting probability.
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1074	Figure S2. Relationship between specific wood density (SWD) and average price of timber on
1075	international market.
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1077	Figure S3. 100 years dynamical relationship between three forest-level variables in drier (Fig. S4.1) and
1078	wetter (Fig. S4.2) forest commons: annual biodiversity (Shannon index), carbon (AGOC [tonnes CO2 eq
1079	ha-1]) and the economy (collective profit from timber harvesting [\$]). For each plot, a line represents the
1080	mean trajectories over all the same scenarios with the same proportion of species managed, from 0% to
1081	100%)
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1083	Figure S4: 100 years dynamical relationship between three life-history traits estimated at a forest level in
1084	drier (Fig. S5.1) and wetter (Fig. S5.2) forest commons: specific leaf area SLA [m².kg⁻¹], specific wood
1085	density SWD [kg.m ⁻³], seed size SS [kg] plotted at a log scale. For each plot, the line represents the mean
1086	trajectories over all the same scenarios with the same proportion of species managed, from 0% to 100%)
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1088	Figure S5. Detailed 100 years dynamics (mean and s.e.) of the forest-level specific leaf area SLA (drier
1089	forest commons: Fig. S6.1, wetter forest commons: Fig. S6.2), specific wood density SWD (drier: Fig.
1090	S6.3, wetter: Fig. S6.4), seed size SS (drier: Fig. S6.5, wetter: Fig. S6.6) for different proportions of tree
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1326 Figure legends

Figure 1 – Conceptual model of Coupled Infrastructure System (CIS) framework derived from Ostrom's theory on Common Pool Resources. The model decomposes any social ecological system into various interlinked infrastructures. Here is represented the resource infrastructure (RI), the resource user infrastructure (RU), the public Infrastructure (PI). These four infrastructures are linked through operational and institutional processes specified in the figure (1a to 7a). The model does not define any governance infrastructure (GI), as in this study there is no need to define providers of institutional rules and budget for the PI or RU. For this reason some of the links usually specified in CIS model (links 2a, 2b, 3a and 3b) are not visible in Figure 1. However, as this coding is considered standard when reading CIS, it was decided that the specific CIS system of this study would use the same numbers of the functional links. The mathematical equations and variables associated with these links and infrastructures is described in the method section.

Figure 2 – Structure of the ecological model for the resource Infrastructure. Multiple tier functional model of species life history traits (LHTs) used to estimate the average population growth (r: Darwinian fitness) of every tree species (summary from Pichancourt et al., 2014), based on life-history theory.

Figure 3 – Comparison of average forest-level outcomes between non-harvested and harvested forest commons in both (a, c, e) drier vs (b, d, f) wetter conditions: for (a,b) Shannon index of tree life-history trait diversity, (c,d) above ground organic carbon, and (e,f) collective profit from harvesting timber.

Figure 4 – Predicted relationship between changing the forest access to a greater diversification of species resource users harvesting and replanting a diversity of species, and three forest-level outcomes, in both drier (**a**, **c**, **e**) and in wetter (**b**, **d**, **f**) forest commons: (**a**, **b**) the long-term total revenue from timber harvesting (based on international timber market price), (**c**, **d**) the long-term average Shannon diversity of tree species (defined by their life-history traits), and (**e**, **f**) the long-term average above-ground organic carbon biomass (AGOC). The solid and dotted lines represent the median and mean trend over 100 years of management regime. The dark and light



1357	grey ribbons represent the quantiles [0.025 0.25 0.5 0.75 0.975], i.e. the interquartile range and
1358	95% confidence interval. Here the proportion of species harvested is based on a forest containing
1359	eight species, i.e. 1 species = 12.5% managed, 2 species = 25% managed,, 8 species = 100%
1360	managed).
1361	
1362	Figure 5 – Expected relationship between changing the forest access to a greater diversification
1363	of species resource users harvesting and replanting a diversity of species, and three life-history
1364	traits indexes measured at a forest-level, in both drier (a, c, e) and in wetter (b, d, f) forest
1365	commons: (a, b) the Specific Leaf Area (SLA) index, (c, d) the specific wood density index
1366	(SWD), and (e, f) the seed size index (SS). The solid and dotted lines represent the median and
1367	mean trend over 100 years of management regime. The dark and light grey ribbons represent the
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1370	species = 12.5% managed, 2 species = 25% managed,, 8 species = 100% managed).
1371	
1372	Figure 6 – Expected relationship between three average forest-level indexes of life history traits,
1373	in both drier (a, c, e) and in wetter (b, d, f) forest commons: (a, b) the Specific Leaf Area (SLA)
1374	index, (c, d) the specific wood density index (SWD), and (e, f) the seed size index (SS).
1375	
1376	Figure 7 – Expected relationship between the Shannon index of biological diversity and three
1377	average forest-level indexes of life history traits, in both drier (a, c, e) and in wetter (b, d, f)
1378	forest commons: (a, b) the Specific Leaf Area (SLA) index, (c, d) the specific wood density
1379	index (SWD), and (e, f) the seed size index (SS).



Figure 1 📃

Figure 1: Conceptual model of Coupled Infrastructure System (CIS)

Conceptual model of Coupled Infrastructure System (CIS) framework derived from Ostrom's theory on Common Pool Resources. The model decomposes any social ecological system into various interlinked infrastructures. Here is represented the resource infrastructure (RI), the resource user infrastructure (RU), the public Infrastructure (PI). These four infrastructures are linked through operational and institutional processes specified in the figure (1a to 7a). The model does not define any governance infrastructure (GI), as in this study there is no need to define providers of institutional rules and budget for the PI or RU. For this reason some of the links usually specified in CIS model (links 2a, 2b, 3a and 3b) are not visible in Figure 1. However, as this coding is considered standard when reading CIS, it was decided that the specific CIS system of this study would use the same numbers of the functional links. The mathematical equations and variables associated with these links and infrastructures is described in the method section.



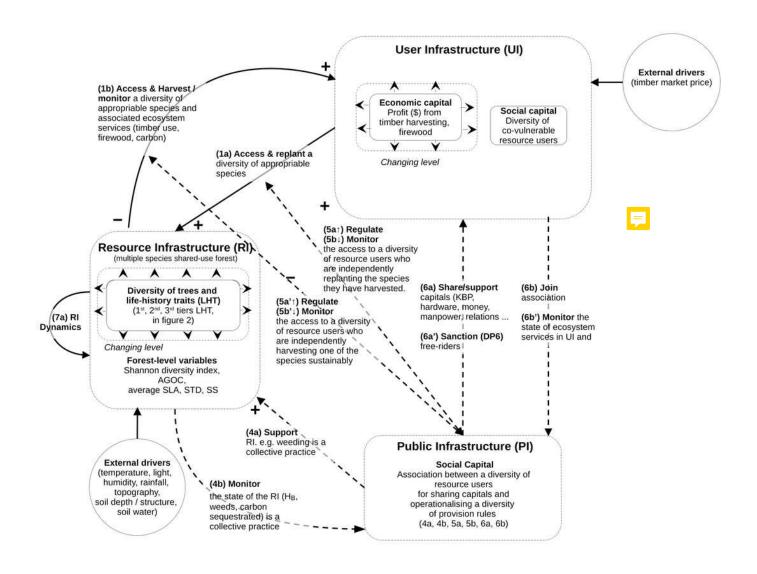


Figure 2: Structure of the ecological model for the resource Infrastructure

Structure of the ecological model for the resource Infrastructure. Multiple tier functional model of species life history traits (LHTs) used to estimate the average population growth (r: Darwinian fitness) of every tree species (summary from Pichancourt et al., 2014), based on life-history theory.

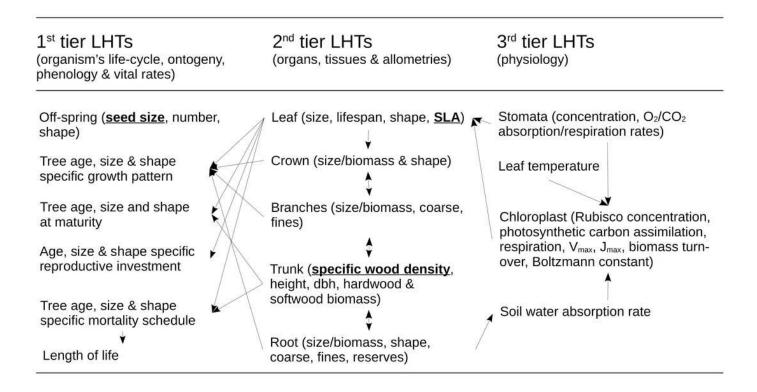




Figure 3: Comparison of average forest-level outcomes between non-harvested and harvested forest commons

Comparison of average forest-level outcomes between non-harvested and harvested forest commons in both (a, c, e) drier vs (b, d, f) wetter conditions: for (a,b) Shannon index of tree life-history trait diversity, (c,d) above ground organic carbon, and (e,f) collective profit from harvesting timber.



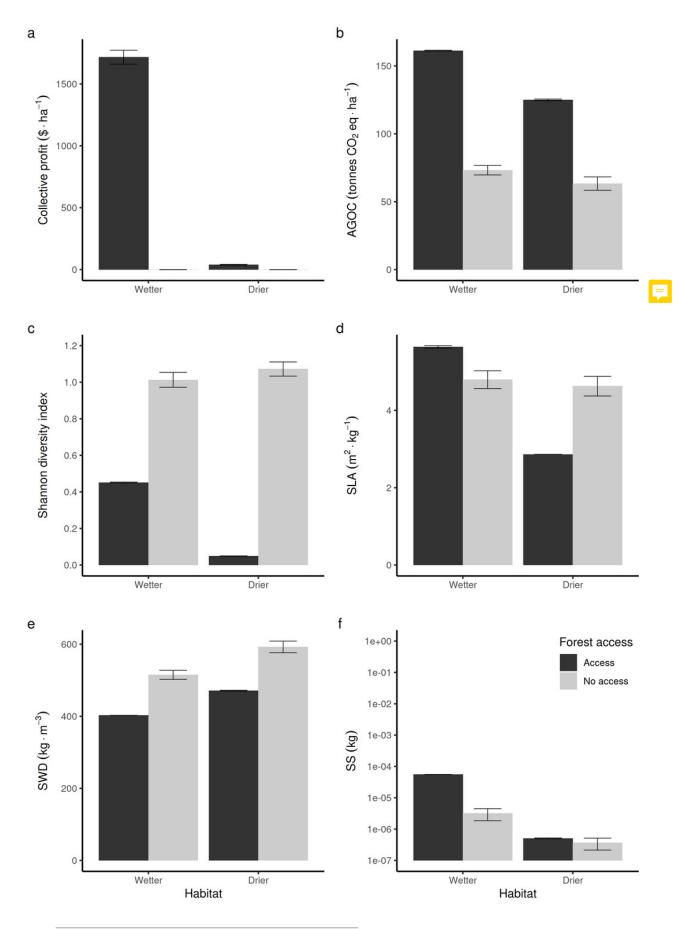


Figure 4: Predicted relationship between changing the forest access to a greater diversification of species resource users harvesting and replanting a diversity of species, and three forest-level outcomes

Predicted relationship between changing the forest access to a greater diversification of species resource users harvesting and replanting a diversity of species, and three forest-level outcomes, in both drier (a, c, e) and in wetter (b, d, f) forest commons: (a, b) the long-term total revenue from timber harvesting (based on international timber market price), (c, d) the long-term average Shannon diversity of tree species (defined by their life-history traits), and (e, f) the long-term average above-ground organic carbon biomass (AGOC). The solid and dotted lines represent the median and mean trend over 100years of management regime. The dark and light grey ribbons represent the quantiles [0.025 0.25 0.5 0.75 0.975], i.e. the interquartile range and 95% confidence interval. Here the proportion of species harvested is based on a forest containing eight species, i.e. 1 species = 12.5% managed, 2 species = 25% managed, ..., 8 species = 100% managed).



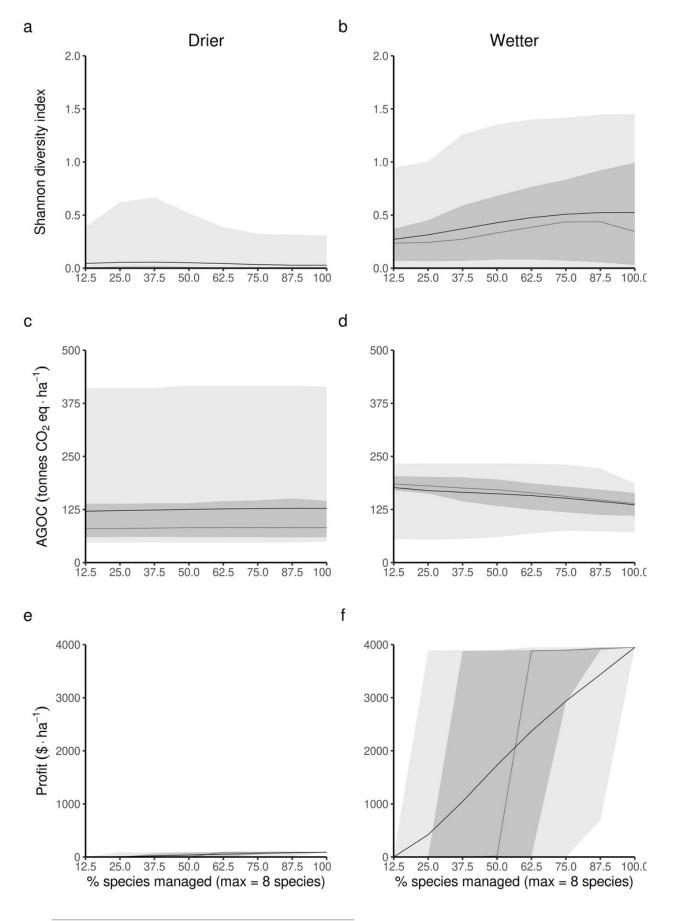


Figure 5: Expected relationship between changing the forest access to a greater diversification of species resource users harvesting and replanting a diversity of species, and three life-history traits indexes measured at a forest-level

Expected relationship between changing the forest access to a greater diversification of species resource users harvesting and replanting a diversity of species, and three life-history traits indexes measured at a forest-level, in both drier (a, c, e) and in wetter (b, d, f) forest commons: (a, b) the Specific Leaf Area (SLA) index, (c, d) the specific wood density index (SWD), and (e, f) the seed size index (SS). The solid and dotted lines represent the median and mean trend over 100years of management regime. The dark and light grey ribbons represent the quantiles [0.025 0.25 0.5 0.75 0.975], i.e. the interquartile range and 95% confidence interval. Here the proportion of species harvested is based on a forest containing eight species, i.e. 1 species = 12.5% managed, 2 species = 25% managed, ..., 8 species = 100% managed).



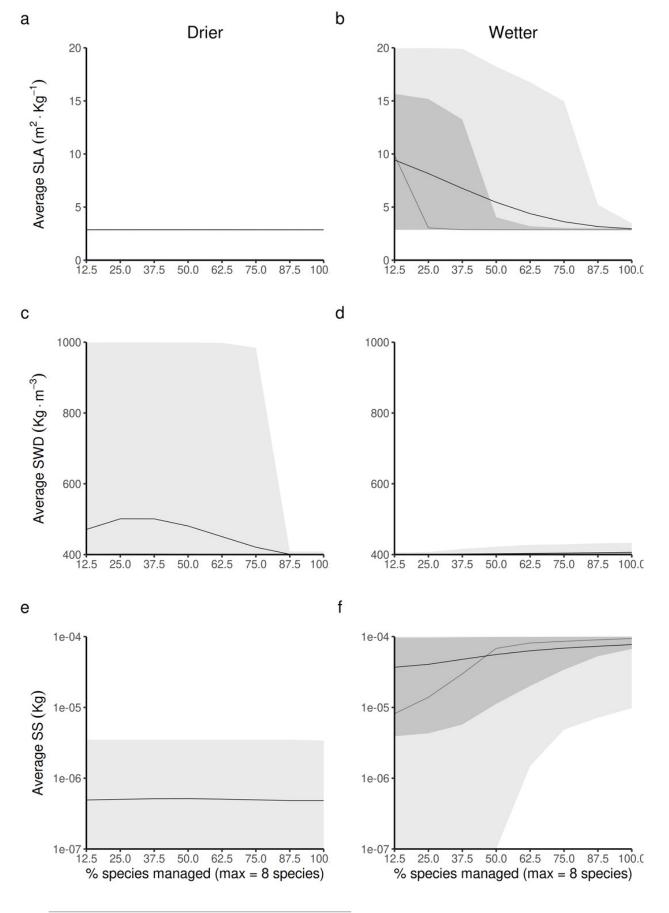




Figure 6: Expected relationship between three average forest-level indexes of life history traits

Expected relationship between three average forest-level indexes of life history traits, in both drier (a, c, e) and in wetter (b, d, f) forest commons: (a, b) the Specific Leaf Area (SLA) index, (c, d) the specific wood density index (SWD), and (e, f) the seed size index (SS).



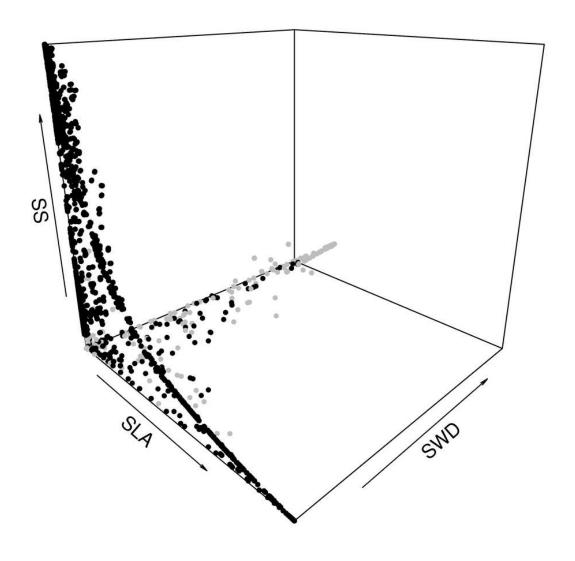




Figure 7: Expected relationship between the Shannon index of biological diversity and three average forest-level indexes of life history traits

Expected relationship between the Shannon index of biological diversity and three average forest-level indexes of life history traits, in both drier (a, c, e) and in wetter (b, d, f) forest commons: (a, b) the Specific Leaf Area (SLA) index, (c, d) the specific wood density index (SWD), and (e, f) the seed size index (SS).



