

# Optimizing stand density for climate-smart forestry : A way forward towards resilient forests with enhanced carbon storage under extreme climate events

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## Optimizing stand density for climate-smart forestry: A way forward towards resilient forests with enhanced carbon storage under extreme climate events

Frank (F) Sterck <sup>a,\*</sup>, Marleen (A.E.) Vos <sup>a</sup>, S. Emilia (S.E.) Hannula <sup>b</sup>, Steven (S.P.C.) de Goede <sup>b</sup>, Wim (W) de Vries <sup>c</sup>, Jan (J) den Ouden <sup>a</sup>, Gert-Jan (G.J.) Nabuurs <sup>a</sup>, Wim (W. H) van der Putten <sup>b,d</sup>, Ciska (G.F.) Veen <sup>b</sup>

<sup>a</sup> Forest Ecology and Forest Management Group, Wageningen University and Research, PO Box 47, 6700 AA, Wageningen, the Netherlands

<sup>b</sup> Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands

<sup>c</sup> Environmental Systems Analysis Group, Wageningen University and Research, PO Box 102, 6700 AC, Wageningen, the Netherlands

<sup>d</sup> Department of Nematology, Wageningen University and Research, Wageningen, the Netherlands

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#### ABSTRACT

As a response to the increased pressure of global climate change on most ecosystems, national and international agreements aim at creating forests that are productive, resilient to climate change, and that store carbon to mitigate global warming. However, these aims are being challenged by increased tree mortality rates and decreased tree growth rates in response to increased incidence of extreme drought events. These phenomena make us aware of a lack of crucial insights into the effects of forest management on the growth and survival of trees, and on carbon storage in both trees and forest soils under increased incidence of drought. Here we compile current knowledge on how forest management and drought impact on tree growth and survival, and above- and belowground carbon storage in forest ecosystems. Based on this, we propose that climate-smart forestry may benefit from controlling stand density at intermediate levels (>60%, e.g.~80%) by applying low levels of tree harvest intensity on a regular base. Furthermore, we propose that the actual optimal density will depend on the tree species, site conditions and management history. As a next step, studies are needed that take an above- and belowground approach and combine forest experiments with mechanistic models on water, carbon and nutrient flows in trees and soils within forests in order to transform current results, which focus on either soil or trees and are often highly-context dependent, to a more generic forest framework. Such a generic framework would be needed to enhance understanding across forest ecosystems on how forest management may promote forest resilience, productivity and carbon storage with increasing drought.

#### 1. Introduction

Global climate change is threatening forest ecosystems worldwide. The increase in the frequency of severe droughts and high temperature events resulting from climate change (Dai, 2013; IPCC, 2013; Trenberth et al., 2014) has a detrimental effect on the growth and mortality of trees worldwide (Bennett et al., 2015; DeSoto et al., 2020), putting the ecological, societal and cultural services provided by forests at stake (Costanza et al., 1997). Yet, forests also have the potential to mitigate climate change: the Paris Agreement (2015) identified forest management as a means to mitigate increasing CO<sub>2</sub> levels and warming (Bastin et al., 2019) by storing carbon in forests, both in trees and soils (Pan et al., 2011). These aims could however be jeopardized by a lower crown vitality (Carnicer et al., 2011; De Vries et al., 2014), increased tree mortality rates (Anderegg et al., 2012; Neumann et al., 2017; Senf et al., 2018) and decreased tree growth rates (Bennett et al., 2015; Socha et al., 2021; Weemstra et al., 2013) in response to droughts, but the implications of this for carbon cycling and storage in soils remain largely

\* Corresponding author.

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*E-mail addresses*: frank.sterck@wur.nl (F.(F. Sterck), marleen.vos@wur.nl (M.(A.E.) Vos), e.hannula@nioo.knaw.nl (S.E.(S.E.) Hannula), stevendegoede@gmail. com (S.(S.P.C.) de Goede), wim.devries@wur.nl (W.(W. de Vries), jan.denouden@wur.nl (J.(J. den Ouden), gert-jan.nabuurs@wur.nl (G.-J.(G.J.) Nabuurs), w. vanderputten@nioo.knaw.nl (W.(W.H) van der Putten), c.veen@nioo.knaw.nl (C.(G.F.) Veen).

#### unknown.

Tree mortality rates take dramatic forms with over 100 million m<sup>3</sup> of dead trees in Europe after the summer drought in 2018 (Nabuurs et al., 2019), which may translate into an economic loss of approximately 3.5 billion euros (Toppinen et al., 2005). More recently, wood losses in response to the sequence of three dry years from 2018 to 2020 were estimated at 12.7 billion euros for Germany alone and additional costs related to other ecosystem functions were not even included (Mohring et al., 2021). Although losses are most severe for Norway spruce and limited for species like common beech, oak and Scots pine (Mohring et al., 2021), these figures nevertheless demonstrate that many European forests are at stake with increasing drought. Hence, a new way to manage forests that sustains or increases productivity, resilience and carbon storage of forests, both above- and belowground, is urgently needed to meet the Paris Agreement ambitions. Such new management practices have been coined as climate-smart forestry (CSF) (Nabuurs et al., 2018b), but CSF is not yet operational (Bowditch et al., 2020).

Currently, more than 95% of the 162 million hectares of forests in Europe is under some form of active multifunctional management (Forest Europe, 2020). Often, raw wood material is used for producing logs, fibers or fuelwood, but provision as energy source for the biobased economy occurs as well (Forest Europe, 2020; Mayer et al., 2020). For vast forest areas, there are basically two tree harvest approaches: successive partial harvests when only a proportion of trees is harvested to promote the growth of residual trees, or final harvests when all trees are harvested by clear-cutting. In traditional forestry practice these operations are often combined: partial harvest operations during a rotation followed by a clear-cut harvest at the end of the rotation. With so-called selective logging forestry practices, however, partial harvests can be applied without time limits because young trees benefit from relatively open conditions and, with time, gradually take over the dominant positions of larger, older harvested trees (Pommerening and Murphy, 2004). The consequences of partial harvests for stand density will not only impact tree growth and tree resilience to drought (Sohn et al., 2016), but can also have important implications for carbon, water and nutrient cycling and carbon storage in soils as the rate and magnitude of soil processes are tightly linked to tree performance (Achat et al., 2015). Generally, tree and soil responses to forest management are considered separately, but to make climate-smart forestry operational it will be essential to use a combined approach, particularly because there may be trade-offs between carbon storage above- and belowground (Terrer et al., 2021).

In this perspectives paper, we explore the potential for CSF by managing forests at an intermediate stand density to maximize the longterm storage of carbon in both the trees and the soil within the forest under a changing climate. This long-term focus implies a dynamic equilibrium, where the larger harvested trees are gradually replaced by smaller developing trees. In this sense, maintaining forests at intermediate density turns forests, also the originally even-aged ones, to unevenaged forests. We specifically focus on effects of drought, i.e. the effects of persistent periods of low rainfall and/or increased transpiration demands during heat periods, because droughts have severe impacts on forests and ecosystem functioning (Bennett et al., 2015; DeSoto et al., 2020) and are known to increase strongly in frequency and intensity with global change (Dai, 2013; IPCC, 2013). We show evidence from research in temperate forests that are known to harbor around 60% of their total carbon in soils (Pan et al., 2011), but many of the principles also apply to tropical and boreal forest. Maximizing carbon pools in forests - thus contributing to climate change mitigation - is only one of the key components of the CSF aims, but will be linked to other CSF aims such as sustainable productivity and forest resilience (Nabuurs et al., 2018b). With our perspective, we integrate evidence of climate and management effects on above- and belowground carbon storage within temperate forests, which allows us to provide a holistic view on patterns and mechanisms that underlie long-term carbon storage, productivity and resilience of forests. In addition, we specify the major research

caveats that should be tackled to make CSF of forests operational.

#### 2. Approach

We start with the description of a forest system framework characterized by the major carbon pools and fluxes - and linked to this water and nutrient pools and fluxes - for trees and soils in forests (Fig. 1). This forest system framework provides the context for our discussion on observed drought and stand density effects on the growth and survival of trees, as well as for biological processes related to carbon storage in forest soils. We use the framework to visualize relative differences in carbon, nutrient and water fluxes in and out of trees and soil for virtual forests differing in stand density (closed, intermediate, vs. open forests) and climate (normal versus drought-affected climate, Fig. 2). We focus on effects of droughts and do not account for changes in other global change factors, for example ozone pollution or nitrogen deposition, but we acknowledge that these have additive implications for carbon storage by trees and soils within forests (De Vries et al., 2014, 2017). As a last step, we use the framework of Fig. 2 to predict the long term implications for carbon storage in forests from the underlying tree and soil responses (Fig. 3). In this last step, we present the hypothesis that long term carbon storage in forests with increasing drought will be maximized by maintaining forests at intermediate stand density, and we show how this hypothesis emerges by scaling empirical-support-based responses and more speculative responses of trees and soils to an entire forest. Although an essential aspect of CSF, we do not explicitly consider the roles of species choice or tree species composition or tree diversity for creating climate change adapted forests, see discussion by others for this (Baeten et al, 2013, 2019; Bowditch et al., 2020). The hypothesis and predictions of our framework are only qualitative since quantitative responses presented in published case studies depend on soil, tree species (or mixtures of species), forest stocks, climate and management history, and since results for different processes in soils and trees are presented separately and not yet integrated in the literature.

#### 3. The forest and soil system

The forest carbon cycle system includes trees, soils and their mutual interactions, as well as their interactions with atmosphere and society (Fig. 1). Trees grow and accumulate carbon by fixing carbon in their leaves via photosynthesis, which is then allocated to maintain living plant parts (leaves, fine roots, living wood and bark parts), and construct new leaves, roots and stem parts and fruits (Fig. 1). Dead and lost leaves, twigs, stem bark and fine roots create carbon and nutrient inputs for the soil (Fig. 1), whereas the dead wood usually accumulates within the stem. These carbon fluxes are intimately linked with nutrient and water fluxes. On the one hand, the uptake of nutrients allows trees to metabolize and thus fix carbon via photosynthesis, lose carbon via respiration and store carbon via growth (e.g., Cannell and Dewar, 1994). On the other hand, nutrients are lost by natural litter from dropped leaves, twigs and/or bark parts, but also as components of root exudates (Preece et al., 2018) and fine-root turnover (Brunner et al., 2013). In this context, replenishment of nutrients by atmospheric deposition is also crucial, certainly for forests on coarse-grained poor soils with low nutrient input by soil weathering (De Vries et al., 2021). Water uptake is closely linked to carbon fixation (via photosynthesis) in the leaves since  $CO_2$  uptake from and water loss (transpiration) to the atmosphere is regulated via the same pores in the leaves, i.e. the stomata (Brodribb et al., 2020; Zweifel et al., 2007). In addition, tree crowns reduce water infiltration into the soil by intercepting rain water which evaporates directly (Link et al., 2004). They also limit direct sunlight penetration buffering diel fluctuations in temperature, soil respiration (Zhang et al., 2018), and transpiration from understory vegetation and evaporation from the forest floor (Simonin et al., 2007). Trees thus influence the major fluxes of water, nutrients and carbon in and out of the soil, as well as the soil microclimate.



Fig. 1. Visualization of the forest system including trees and soils and their interactions with the society and the atmospheric conditions. Major fluxes are given for carbon, water and nutrients, the abbreviations between parentheses represent the same fluxes in Fig. 2. TREES: all living trees, including their crown, stem and roots. Tree carbon fluxes include photosynthesis (mainly by leaves); tree respiration associated with the maintenance and growth of leaves, stem and roots; the natural losses of leaves, twigs, bark and (fine) roots (L); the release of root exudates (E) to symbionts (sugars) and soil (E, also including carbon compounds); and possible losses by harvest of stems and/or crown for, for example, construction material and biofuel. These carbon fluxes are linked with the fluxes for nutrients (nutrient uptake by trees, nutrient losses via natural losses (litter) and losses by harvest, and indirectly, deposition, weathering, and leaching) and water (water uptake and transpiration, and more indirectly, rain, infiltration, and evaporation from soil or water intercepted by crowns). Important,

but not shown, is that trees limit direct sunlight penetration to the soil, and thus buffer diurnal temperature fluctuations and limit the rise of soil temperature during sunny days (see Fig. 2). <u>SOIL</u>, layer where tree-derived organic inputs, such as root and shoot litter (L) and root exudates (E) are processed by the soil food web. Saprotrophs and detritivores convert organic residues into (in)organic nutrients that can be taken up by trees and soil organisms, CO<sub>2</sub> that is respired to the air (soil respiration) and organic carbon compounds that can be stored in the soil. Symbionts, such as ectomycorrhizal fungi (ECM), deliver nutrients to trees in exchange for carbon compounds, which directly influences tree performance and also plays a key role in driving soil organic carbon storage. Nutrients in soil are further replenished by weathering and deposition. In addition to decomposers (saprotrophs and detritivores) and symbionts, other soil organisms such as pathogens, herbivores and predators (indirectly) consume substantial amount of tree-derived carbon as well, but these organisms are not depicted for simplicity. <u>SOCIETY</u> is beyond the scope of this perspective, but added here because a harvested stem (and possibly crown) removes carbon and nutrients from the forest, but carbon may be stored when stems end up in persistent products.

Tree carbon fluxes vary largely across forests, as suggested by the variation in carbon allocation fractions for leaf maintenance respiration (10-23%), leaf production (4-13%), stem maintenance respiration (4-26%), stem production (8-31%) and roots (25-63%; including maintenance, production and exudation) observed across >50 temperate forests (Litton et al., 2007). The large variation in the root-allocated carbon is partially attributed to plastic root responses to soil fertility: for example, conform optimal allocation theory (Bloom et al., 1985; Brouwer, 1963), beech and spruce trees produced more than double or triple root amounts on poor soil compared to rich soils (Weemstra et al., 2017). Root exudates have also been recognized as important carbon fluxes between roots and soil (Hobbie et al., 2006; Jones et al. 2006). These exudates provide, with the above- and belowground litter, the tree-derived inputs into the soil and, with the deposited and weathered nutrient inputs, they are the main energy and nutrient source for the soil food web (Cline and Zak, 2015; Wardle et al., 2004, Fig. 1). The soil food web in turn drives the soil carbon and nutrient cycling thereby providing nutrients to trees, regulating the respiration of CO<sub>2</sub> into the atmosphere and the storage of organic carbon belowground (Fig. 1) (Averill et al., 2014; Crowther et al., 2019; Jackson et al., 2017; Smith et al., 2015; Villarino et al., 2021). In forests, saprotrophic fungi - together with detritivores - play a key role in degrading inputs of above- and belowground litter and root exudates, while ectomycorrhizal fungi acquire carbon compounds from trees in exchange for soil nutrients (Clemmensen et al., 2013; López-Mondéjar et al., 2018; van der Wal et al., 2013). Therefore, understanding whether and how forests lose or store carbon in soils appears critically dependent on understanding the role of the soil fungal community in carbon cycling (López-Mondéjar et al., 2018).

Saprotrophic fungi are dominant in the forest litter layer and, together with litter fragmenting animals, directly responsible for breaking down plant organic inputs into organic and inorganic nutrients and carbon compounds (Swift et al., 1979; van der Wal et al., 2013). Their activity and community composition are regulated by litter quality and quantity and environmental conditions (Bergmann et al., 2020; Cornelissen, 1996; Hannula et al., 2017; Steidinger et al., 2019; Veen et al., 2021). When saprotrophic fungi and other microbes have a high efficiency of converting organic inputs into fungal biomass relative to losses via respiration, this will increase the amount of carbon in soils that can potentially be stored (Kallenbach et al., 2019). Soil carbon losses via respiration by saprotrophs are accelerated when fresh organic inputs such as leaf litter boost the activity of saprotrophic microbes, referred to as priming (Kuzyakov, 2010; Sayer et al., 2011). In addition, soil respiration may be stimulated by enhanced microbial biomass/activity at low N inputs (Allen and Schlesinger, 2004) and reduced by enhanced formation of high-lignin recalcitrant compounds at high N inputs (Fog, 1988; Janssens et al., 2010).

Ectomycorrhizal fungi are dominant symbionts in temperate and boreal forest ecosystems and constitute up to one-third of the microbial biomass in soils (Clemmensen et al., 2013; Högberg and Högberg, 2002; Read, 1991; Steidinger et al., 2019). They form intimate relationships with tree roots and receive root exudates in exchange for soil nutrients (Read, 1991, Fig. 1), which not only favors tree performance, but also plays a pivotal role in soil organic carbon storage (Averill et al., 2014; Clemmensen et al., 2013; Ekblad et al., 2013). First, ectomycorrhizal fungi transport tree-derived carbon to deeper soil layers and the fungal hyphae are protected from degradation in these soil layers (Ekblad et al., 2013). However, when decomposers can access and recycle dead mycelium, carbon will be lost quickly again via respiration (Brabcová et al., 2016; López-Mondéjar et al., 2018). Second, ectomycorrhiza are strong competitors for soil nutrients by mining nitrogen from organic matter, which directly reduces the activity of free-living decomposers (e. g. Saprotrophic fungi) and further degradation of soil organic matter (Averill et al., 2014; Averill and Hawkes, 2016), especially in early



Fig. 2. A conceptualization of impacts of tree density (closed forest, intermediate open forest, open forest) and drought (no drought versus drought) on water, carbon and nutrient fluxes at the entire forest level. Since maximum stand density (close to the idea of a carrying capacity in ecology, or full stock in forestry) largely varies across forests, we do not express the stand density by any metric of stand density (e.g. basal area, stem volume, of tree biomass), but consider it from a reference point referred to as closed forest (considered close to a maximum density) to an intermediate open forest (with c. 80% biomass or basal area left, within the "moderate thinning category (>60% left) of Sohn et al., 2016), to relatively open forest (e.g. c 50% left, within the heavy thinning category (<60%) of Sohn et al., 2016), the latter two maintained by partial tree harvests of different intensity (see also X-axis in Fig. 3). The images of Figs. 2 and 3 can be interpreted as long-term implications of a forest in a dynamic equilibrium, where larger harvested trees are gradually replaced by smaller developing trees. In this sense, maintaining forests at intermediate density turns forests, also the originally even-aged ones, to uneven-aged forests. Such intermediate forests may depend on natural regeneration and turn to mono-specific forests in mixed-species forests, or vice versa, but those species-implications are not discussed here. Arrow colours represents the type of flux: grey for carbon fluxes, blue for water fluxes and yellow for nutrient fluxes. Three arrow widths were used to show relative differences in fluxes across the 6 virtual forests represented in the six figure panels (a-f). In some cases, no arrow was presented to emphasize the low level of that flux in that particular situation (e.g. "inf" and "leaching": in 2d-f). The following fluxes are included: rain = precipitation; inf = infiltration; T = transpiration; Et = evaporation of intercepted water from tree crown; Es evaporated water from soil surface; P = tree photosynthesis; Rt = tree respiration; Rs = soil respiration; leaching = leaching and run-off; L = litter; E = root exudates; dep = deposition; Nut = nutrient uptake by trees; SOC = soil organic carbon; rad = radiation on forest floor; ECM : SAPR is the relative importance/activity of ectomycorrhizal fungi relative to saprotrophic fungi. The red crowns in some of the scenario's indicate relatively high risks for tree mortality. The presence of arrows and arrow sizes are based on the literature discussed in section 4 and 5. When evidence is weak or conflicting arrows are presented, but should be interpreted with caution. Knowledge gaps are identified in section 3, 4 and 6 and summarized in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

stages of decomposition and in top-soil (Sterkenburg et al., 2018). How ectomycorrhiza affect soil carbon storage is mediated by the quality of root exudates, as well as mycorrhizal community composition (Fernandez et al., 2020; Soudzilovskaia et al., 2015; Steidinger et al., 2019). When the mycorrhizal community shifts towards a higher abundance of ericoid mycorrhiza, for example in late-successional boreal forests, carbon storage will be enhanced even further (Clemmensen et al, 2015, 2021).

Forest management, tree performance and environmental conditions can shift the balance between saprotrophic and ectomycorrhizal fungi (Zhou et al., 2020). Therefore, to enhance carbon pools in forests, it is essential to understand how interactions between management, tree inputs and fungal community composition drive soil carbon and nutrient cycling. In addition, it is important to note that other soil organisms, such as other microbial decomposers, pathogens, herbivores and carnivores, can also consume substantial amounts of carbon and nutrients from trees and each other, thereby affecting carbon and nutrient fluxes in soils (Gan and Wickings, 2020; not in Fig. 1). Moreover, it will be essential to not only increase the amount of carbon stored in soils, but also the persistence, as this will result in long-term carbon storage and can help to mitigate climate warming (Bossio et al., 2020; Lehmann and Kleber, 2015; Paustian et al., 2016). On the one hand, the type of organic input and microclimate are key factors regulating carbon stabilization in soils (Lehmann and Kleber, 2015; López-Mondéjar et al., 2018; Sokol

and Bradford, 2019, Fig. 1). On the other hand, we know from grasslands and agricultural systems that the interplay between soil organisms and soil physical and chemical conditions is pivotal (Lehmann and Kleber, 2015; Liang et al., 2017), because the majority of carbon stabilized in soils originates from microbial products and remains (necro-mass) that easily bind to soil minerals and become occluded in soil aggregates (Cotrufo et al., 2013; Kallenbach et al., 2016; Lehmann and Kleber, 2015; Liang et al., 2019). Whether such processes are also important in forest soils and how they are affected by forest management and soil physio-chemical conditions is much less well understood (Villarino et al., 2021). Therefore, understanding how interactions between soil communities and forest management affect the amount and persistence of soil carbon in forests is at the forefront of our knowledge (López-Mondéjar et al., 2018; Sayer et al., 2019; Sokol and Bradford, 2019) and is needed to link above- and belowground carbon storage in forest ecosystems.

#### 4. Stand density and drought effects on trees

We use the presented forest system framework of Fig. 1 to compare the relative differences in carbon, nutrient and water fluxes in and out of trees (this section) and soils (section 5) between forests differing in density and in a "normal"-climate versus a "drought-affected" climate (Fig. 2). For trees, we here focus on growth and mortality since they F.(F. Sterck et al.



**Fig. 3.** Visualization of the optimal stand density hypothesis with respect to the long term carbon storage in the forest, based on a number of key responses of trees and soils to stand density. We distinguish between patterns based on relatively robust empirical evidence from multiple studies (green lines), more anecdotical or ambiguous evidence from few studies only (yellow lines), and hypothesized emergent long term patterns for carbon storage (red lines). Given our holistic approach, we on purpose did not quantify the stand density on the X-axis nor the long-term forest response on the Y-axis, because both depend much on the species, climate, soil and forest history. Response variables on Y-axis are thus independent from one another. For a more extensive explanation of the stand density (X-axis), see also the caption of Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

determine the long term potential for carbon storage in trees. First we discuss tree responses to stand density in a "normal"-climate (Fig. 2a–c) and then in a "drought-affected" climate (Fig. 2d–f). We focus this discussion on the responses of the larger trees of the forest, and not the regeneration. Yet, the regeneration is likely to be more successful in intermediate open forest and open forest where they may gradually replace harvested trees, and thus contribute to maintaining a long term dynamics equilibrium in forest structure.

The effect of reducing stand density by partial harvests on promoting stem growth of remaining trees (Lu et al., 2016) is well known and used by foresters. Such positive effects may however level off with greater reductions in stand density resulting in open stands (Sohn et al., 2016). In more open stands, trees intercept more light per individual tree crown and benefit from their access to more soil water because of higher water infiltration into the soil (see "inf"-flux arrows in Fig. 2a-c, Molina and del Campo, 2012) and lower competition for soil water amongst trees (Bréda et al., 1995). Directly after tree harvest, trees have better access to soil nutrients in the short term since litter on the forest floor often increases after harvests (this short term effect is not shown in Fig. 2) and high exposure of forest soils to direct sunlight accelerates decomposition owing to high midday temperatures (Hobbie et al., 2006; Zhang et al., 2018). Inversely, however, the external input of nutrients from the atmosphere is lower in open stands due to more limited interception of nutrients by tree crowns (De Schrijver et al., 2007; De Vries et al., 2007; Wuyts et al., 2008), but the highest interception may occur in intermediate open forests where higher air turbulence increases interception relative to homogeneous closed forests (compared "dep" arrows between Fig. 2a-c, (Erisman and Draaijers, 2003). Particularly on coarse-textured low-fertility soils, such an increase in nutrient availability may allow for better growth (Page-Dumroese et al., 2010). Over the years, more open stands will also face lower litterfall (compare "L" arrows between Fig. 2a-c, (Zhang et al., 2018), although remaining trees gradually develop bigger and denser crowns contributing to growth (Giuggiola et al., 2013), which partially mitigates lower litterfall. The reduced inputs of nutrients and organic matter in forests soils (Vesterdal et al., 1995) nevertheless partially limit the uptake of nutrients in low-fertility forests (Rio et al., 2017) and thus constrain the mentioned positive effects of higher resource levels on tree growth. In addition, heavy thinning which causes open forests creates high risks for windthrow (Lohmander and Helles, 1987) (see "red crowns" indicating high mortality risks, in Fig. 2c), since trees become suddenly exposed to high wind forces while they are not yet acclimated by increasing stem diameters and/or root systems, or adjusting crown features (Scott and Mitchell, 2005). In taller stands, trees are generally more vulnerable for windthrow than in shorter stands (Lohmander and Helles, 1987), but interestingly such vulnerability can be mitigated by starting low intensity thinning from early stand age stimulating trees to develop more stable features in stems and roots, which contributes to more stable trees at later age (Cameron, 2002). Overall, these results imply that individual trees will benefit from higher resource levels with increasing stand openness, but that high windthrow risks should be considered after heavy thinning of older and taller stands. Trees in intermediate open forest benefit - compared to closed forest trees - from better access to water and nutrients and light, such that forest growth in closed and intermediate open forest may converge (see similar carbon uptake "P", respiration "Rt" and nutrient uptake "Nut" in Fig. 1a and b), and compared to open forests - they face lower mortality risks by windthrow (compare green versus red crowns, Fig. 2b and c).

In a climate affected by persistent dry periods (Fig. 2d-f), we expect stronger reductions in growth of trees in closed forests compared to those in intermediate open forest and open forests as a result of strong competition for soil water (Bottero et al., 2017; compare transpiration "T" between Fig. 2d-f). Moreover, a stronger interception of water reduces the availability of water in closed forests (compare lack of water infiltration "inf" in Fig. 2d with arrows Fig. 2e and f). With increasing drought, trees avoid hydraulic failure (e.g. by massive cavitation events) by closing stomata and thus reduce water loss (resulting in lower forest transpiration ("T" arrow) in Fig. 2d-f compared to Fig. 2a-c, respectively) and limit dehydration, but this stomatal response impairs carbon uptake and photosynthesis (resulting in low forest photosynthesis ("P" arrow) in Fig. 2d and e compared to Fig. 2a-c, respectively) and may deplete carbon sources and limit growth (Brodribb et al., 2020; Sterck and Schieving, 2011). In addition, trees in closed stands reduce water loss via transpiration by dropping leaves, whereas trees in more open stands (intermediate open or open) maintain leaves longer (not shown in Fig. 2, but see (Sohn et al., 2016)). Another reason for reduced growth during drought is that trees stop growing when the turgor in the stem cambium drops below a critical threshold (Hsiao et al., 1976), which hinders cell diversion and expansion (Steppe et al., 2015) and ultimately limits annual stem growth during dry years (Peters et al., 2021). In the extreme drought case, such mechanisms would stop photosynthesis, nutrient uptake, transpiration and growth earlier in closed forests than in intermediate and open forest potentially causing lower forest transpiration ("T"-arrows), forest photosynthesis ("P"-arrows), and forest nutrient uptake ("Nut"-arrows) in closed forest compared to intermediate forest (Fig. 2d and e). However, such forest level fluxes are probably lost because of the low number of trees in open stand (Fig. 2f)). Years after a thinning operation, such differences become smaller when trees from intermediate or open forests would establish an enlarged crown and roots (Giuggiola et al., 2013) resulting in higher transpiration and rapid water depletion at tree level (Sohn et al., 2016). A meta-analysis showed that broad-leaf trees from intermediate or open stands showed indeed weaker growth reductions during dry years than trees from closed forests, whereas conifers more rapidly recover to pre-drought growth rates in intermediate or more open forests (Sohn et al., 2016). Interestingly, the same study showed that broad-leaf tree species showed weaker growth reductions to drought than conifers, and attributed this to the deep rooting of the studied broad-leaf tree species. Alternatively, such differences may be a general phenomenon (DeSoto et al., 2020) driven by larger amounts of parenchyma (Zhang et al., 2020) and carbon reserves (Martínez-Vilalta et al., 2016) in broad-leaf trees allowing them to better maintain stem turgor and growth during drought compared to conifers, but the relative roles of such alternative mechanisms remain uncertain (e.g. Brodribb et al., 2020). In general, both broad-leaf and conifer tree species usually recover to their pre-drought growth rates within 1-2 years (DeSoto et al., 2020), with

intermediate and open stand trees again experiencing faster growth rates than closed stand trees (Rio et al., 2017; Sohn et al., 2016). These results suggest that trees in intermediate and open forest are more growth resilient to drought than closed-forest trees, but our relative predictions for growth responses and associated water and nutrient fluxes for forests differing in density (Fig. 2) remain qualitative, since the actual effects are modified by species, level of forest openness, and management history of the forest.

Persistent dry conditions also cause higher mortality risks for trees in more closed forests (Goulden and Bales, 2019; Young et al., 2017; higher mortality risks "red crowns" in Fig. 2d than 2e, "red crowns" in Fig. 2f result from higher wind throw risks). These closed forest trees face lowest soil water levels because low rainfall may come with relatively lower water throughfall and water infiltration in the soil (smaller "inf" arrow in Fig. 2d compared to Fig. 2e and f), and with strong competition between trees for the low amount of available water left (Bréda et al., 1995, Fig. 2d). In such water-limiting conditions, trees may not avoid hydraulic failure anymore and/or gradually deplete carbon, which can lead to a higher vulnerability to pathogens, and ultimately cause mortality (McDowell et al., 2008). Current studies suggest that hydraulic failure indeed often precedes tree mortality and that sometimes, particularly for conifers, carbon depletion precedes mortality too (Adams et al., 2017). Across Europe, the massive mortality of Norway Spruce following the 2018 drought (Mohring et al., 2021) is an example of severe carbon limitation reduced defense against the mortal attack by bark beetle (Pretzsch et al., 2014). Such a more important role of carbon depletion in tree mortality for conifers is in line with their larger hydraulic safety margins compared to broad-leaf trees (Choat et al., 2012; Martínez-Vilalta and Garcia-Forner, 2017) and their small fraction of parenchyma tissue (Morris et al., 2016; Zhang et al., 2020) constraining their carbon storage in stems (Martínez-Vilalta et al., 2016). In addition, within these two taxonomic groups, species largely differ in their cavitation vulnerability (Maherali et al., 2004) as well as stomatal response to reducing (drier) water potentials (Adams et al., 2017). Interestingly, it was recently shown that species in a tropical forest community with stronger resistance against cavitation faced lower mortality than species with weaker resistance (Powers et al., 2020), and such mechanisms may also operate in temperate forests (Brodribb et al., 2020). Overall, the increase in frequency and severity of droughts in combination with high temperature events - as predicted for this century (Dai, 2013; IPCC, 2013) - may thus challenge the successful recovery and ultimately the survival following drought (DeSoto et al., 2020), particularly in closed forests (Young et al., 2017).

# 5. Stand density and drought effects on soil processes and soil carbon storage

Partial tree harvesting generally limits soil carbon losses compared to clear-cut harvesting (James and Harrison, 2016; Lull et al., 2020; Nave et al., 2010; Riutta et al., 2021), and can even lead to an increase in the amount of soil organic carbon compared to a non-logging situation (Gong et al., 2021; Mayer et al., 2020; Zhang et al., 2018). Positive effects of partial tree harvesting on soil carbon storage are often mediated by reduced soil disturbances or a higher amount of tree residues left on site (Jandl et al., 2007). In addition, harvesting regimes alter the quality and quantity of carbon inputs that enter the soil ("L" and "E" arrows in Fig. 2), and thereby drive shifts in soil food web composition and functioning (Bååth, 1980; Canarini et al., 2017; Chen et al., 2021). Ectomycorrhizal fungi, which are dependent on root exudates provided by living trees, are generally reduced by tree harvesting (see relative role of "ECM" compared to "SAPR" in Fig. 2) (Amaranthus, 1998; Parladé et al., 2019, Fig. 2a-c). Although this impact was found to be comparable across harvesting intensities (Parladé et al., 2019), new tree saplings are colonized more rapidly by ectomycorrhiza when mature trees are still nearby (Cline et al., 2005). As a result, we expect that ectomycorrhiza will become increasingly important for soil carbon cycling and compete with saprotrophic fungi (Sterkenburg et al., 2019) and enhance carbon storage with higher stand densities ("ECM" > "SAPR" in Fig. 2a), and thus weaker with lower harvesting intensities (Fig. 2a-c; Fig. 3). In contrast, clearcutting will favor saprotrophic relative to ectomycorrhizal fungi ("ECM" < "SAPR" in Fig. 2c) (Parladé et al., 2019). Up to 30% of the total tree mass may remain on-site after clear-cut harvesting providing a large input of dead organic material (brown crowns in Fig. 2b and c) (Aherne et al., 2012). This boosts the activity of saprotrophs, resulting in enhanced decomposition and respiration and potential losses of soil carbon upon harvest, which may be further accelerated by priming effects (Sayer et al., 2011). Clear-cut harvesting will at least temporarily lead to lower inputs of litter and root exudates which limits microbial activity and the buildup of soil carbon ("Rs" and circular arrow and "SOC" box in Fig. 2). Although thinning is found to have impacts on soil carbon cycling that are similar to impacts of clear-cut harvesting (Zhang et al., 2018), our hypothesis is that the magnitude of effects decrease with lower harvesting intensities (Fig. 2 a-c; Fig. 3). Furthermore, there will be changes in soil abiotic conditions due to forest management which will have direct effects on the soil fungal community composition (Tedersoo et al., 2020) and hence the soil carbon cycling.

We expect that impacts of tree harvesting regimes on soil communities and soil carbon cycling will become more pronounced under extreme weather conditions, such as drought (Fig. 2d-f). Drought reduces the activity of soil organisms directly (De Vries et al., 2020; Zhou et al., 2020), which can limit both carbon losses via respiration (Gao et al., 2021; Zhou et al., 2020) and the buildup of new carbon from microbial products ("Rs" and circular arrows in Fig. 2d-f). However, this may be compensated or even counteracted upon rewetting (Canarini et al., 2017). We expect immediate effects of drought to be strongest in closed forests where trees compete with soil organisms for available soil moisture and in open forest where low tree cover results in high water losses from soils via evaporation ("Es" arrow in Fig. 2f). Moreover, in closed forests, the abundance of soil pathogens may be higher, further reducing resistance and resilience of trees to drought (Ávila et al., 2021). Drought also influences the activity and species composition in soil communities by altering tree performance and resource allocation and thereby the quality and quantity of resources that enter the soil food web ("L" and "E" arrows in Fig. 2d-f) (Gao et al., 2021; Poorter et al., 2012). Although effects depend on the intensity and duration of the drought, in general the amount of labile carbon inputs into the soil is reduced under drought ("L" and "E" arrows Fig. 2a-c compared with 2d-f) (Gao et al., 2021; Gargallo-Garriga et al., 2018; Preece and Peñuelas, 2016). Moreover, drought can drive plants to shift towards traits associated with resource conservation strategies, further reducing root exudation rates and litter quality (De Vries et al., 2016). Finally, drought-induced tree mortality will cause a sudden pulse of root and leaf litter (read crowns Fig. 2d), but reduce litterfall and root exudation on the longer term as the number of trees is reduced ("L" and "E" arrows Fig. 2). Taken together, we expect that these impacts of drought on tree-derived soil carbon inputs will strongly reduce the ectomycorrhizal fungal network of trees (Hagedorn et al., 2016), particularly in closed forests where competition for water between trees severely limits tree performance and thus carbon fluxes to ectomycorrhiza ("ECM < SAPR" in Fig. 2d). We summarized changes in carbon and nutrient fluxes and the activity of soil organisms in a qualitative way to predict the magnitude of carbon accumulating in SOC pools (Fig. 2; grey boxes with "SOC"). However, it will be important to quantify implications of drought and forest management for soil carbon accumulation and storage in future studies.

# 6. Scaling from trees to entire forests: a hypothesis for an optimal stand density

An important question is how tree and soil responses to stand density and drought - as visualized in Fig. 2d-f - translate into the carbon storage in forests in the long-term. We have summarized our qualitative

predictions for this in Fig. 3. For trees, we predict that carbon storage peaks when forests are maintained at an intermediate stand density (Fig. 3). The reasons are that these trees in intermediate dense forests largely benefit from increased resource levels (Fig. 2e), including access to water, build larger crowns and root systems, and grow more rapidly while they face lower mortality risks compared to trees in closed forest (Fig. 2d-f, and Fig. 3). Towards lower stand densities (Fig. 2e and f, and Fig. 3, from intermediate to open forest), the increase in the growth of trees gradually levels off (Fig. 3), as trees cannot capture the water and nutrients from the entire large open space around them. This individual tree effect in combination with the reduced number of trees and lower crown cover will result in water loss via larger evaporation from the soil (Simonin et al., 2007), boosted by direct sunlight arriving on the forest floor (see Fig. 2f), such that the overall forest productivity - and linked to that carbon accumulation - will go down (Rever et al., 2017). The long term carbon storage in trees will further reduce because trees in such open stands - known to be more wind prone - face higher windthrow-driven mortality risks (Fig. 2f). Overall, these trends suggest that long-term aboveground carbon storage will peak at intermediate density. Yet, this prediction remains uncertain because the individual tree (growth and mortality) responses can – to an unknown extend – be compensated by a higher number of trees in closed forests, and such compensation is expected to be largely dependent on tree species, site conditions, and the severity and frequency of encountered droughts.

For soil carbon cycling and storage, much of our current understanding is based on plot-level measurements, and not on responses of soil organisms and soil processes to performance of individual trees. Based on this current understanding, we predict that the combination of direct and indirect impacts of droughts will have negative consequences for soil carbon storage, but that the magnitude of effects is lowest at intermediate stand density (optimum "soil carbon storage" in Fig. 3). On the one hand, at intermediate stand density soil disturbance by harvesting and direct water losses from the soil are limited compared to open stands. On the other hand, trees can maintain performing relatively well because competition between trees is lower than in closed stands. Taken together, at intermediate stand densities root exudate inputs into the soil may be maintained resulting in the support of an ectomycorrhizal network, even under drought (Fig. 2d-f; "ECM vs SAPR" line in Fig. 3). This will optimize carbon storage relative to open and closed stands, where the relative importance of ectomycorrhiza will decline due to reduced tree inputs, increased inputs of litter or overall lower activity of soil organisms due to water limitations. To test our predictions (Fig. 3) on how soil communities and functioning respond to a range of tree densities under drought will require linking the performance of individual trees to processes in the soil directly.

When combining tree and soil community responses to drought and forest density management (Figs. 2 and 3), we hypothesize that longterm carbon storage in forests would be optimized at intermediate stand density (Fig. 3 "Forest carbon storage" line). This is because at these stand densities forests sequester and store carbon relatively well under ambient conditions, but will outperform high- and low-density forests under dry conditions, both with regard to above- and belowground carbon storage (Figs. 2 and 3). Therefore, we propose that light partials harvests without time limits provides a potentially, important operational tool when implementing CSF. We emphasize that our predictions are largely of qualitative nature, and that the actual quantitative responses will vary across forests composed of different tree species, in different climates, on different soils, and with a different management history. The implications of our hypothesis for carbon storage in whole forests play out over longer periods of time (decades towards centuries) and can be interpreted as a long term dynamic, equilibrium of tree and soil responses to stand density and droughts. In this dynamic equilibrium, larger harvested trees are gradually replaced by smaller trees, resulting in uneven-aged stands in forests managed for intermediate density. This may not only be optimal for carbon storage, but is also and closely linked to long-term productivity and resilience of forests, and

may have strong implications for biodiversity too (Cosyns et al., 2020).

#### 7. Outlook for a way toward climate-smart forestry

Here, we proposed a generic hypothesis for the effects of stand density management on long-term carbon storage in forests, integrating both above- and belowground processes, which is rarely done but important for setting a new step towards climate-smart forestry. We show that combining current above- and belowground evidence suggests that maintaining forests at intermediate stand densities may optimize carbon storage in trees and soils under future climate scenarios (Figs. 2 and 3). Our predictions on how controlling stand density and drought affect forest carbon storage both above- and belowground are still qualitative. Based on this, we identify the main future challenges for making such predictions operational for climate-smart forestry:

- Since studies on the capacity of forests to store carbon either focused on carbon sequestration or storage in trees aboveground (Aun et al., 2021; DeSoto et al., 2020) or on the amount of organic carbon in the soil (Achat et al., 2015) (James and Harrison, 2016), we make a plea for studies that quantify and integrate above- and belowground processes for the same forests with experimental stand density treatments to better understand how and where forests store carbon in response to forest management and climate change. Linking above- and belowground carbon storage empirically is critical in order to identify when and where trade-offs and synergies occur between carbon storage in trees and soils (Terrer et al., 2021).
- A key question for climate-smart forestry that remains is what exact intermediate stand density will ultimately optimize long-term the productivity and carbon accumulation of forests. Related to this, it will be essential to untangle how optimal densities differ between tree species and site conditions, as well how species and site conditions should be combined to create more diverse, mixed forests, which is another important aspect of CSF.
- We propose to use tree density gradients to monitor the performance of individual trees and the soil processes underneath them and use this information to feed models that predict optimal forest management strategies. It will be essential to perform factorial, long-term experiments in the field (Clarke et al., 2015; Mayer et al., 2020), where both management and climate conditions are manipulated. Such experiments replicating management treatments within different plots increase the statistical power for showing generic patterns in forest dynamics, which preferentially include coupled nutrient, water and carbon dynamics in soil and trees (as visualized in Fig. 2). These experiments should focus on the most promising forest management tools allowing for CSF, of which controlling stand density is only one. Other important candidates are choice of species or species mixtures (with variable functional traits), whole tree harvest versus stem only harvest, and soil treatments (Mayer et al., 2020).
- These experiments should benefit from recent developments in methodology to monitor carbon, nutrients and water fluxes on seasonal and multiple-annual scale in trees (Steppe et al., 2015), to trace carbon to follow the fate of carbon and estimate potential storage and losses within soils using stable isotope probing (Hungate et al., 2015), and couple those tree and soil observations to carbon, water and nutrient fluxes between soil, trees and atmosphere by measuring respiration fluxes from soils and trees, litter input and exudation fluxes from trees to soils, and deposited nutrient inputs and weathered nutrient inputs.
- Upscaling of experimental results to regional scale requires experimental plot networks at regional scale. There are several promising developments in this respect. Continental experimental networks are under development (e.g. the European Holisoil project, replicating stand density treatments in forests across Europe) with the objective to couple the key below ground processes to the current state of art

forest models (Luyssaert et al., 2018; Nabuurs et al., 2018a), which still have a major focus on aboveground processes. Soil models are developed to include the role of microbial processes in soil carbon sequestration and storage (Filser et al., 2016; Shi et al., 2018). Moreover, there are mechanistic tree models that integrate carbon acquisition in the crown with nutrient and water acquisition by roots explicitly (Buckley and Roberts, 2006; Weemstra et al., 2020). Better integration of above- and belowground processes (Fig. 2) in such models will be required to integrate local, context-dependent, experimental data on above- and belowground processes to the carbon dynamics of trees and surrounding soils and ultimately entire forests (Bossio et al., 2020; Mayer et al., 2020) and allow for validation across forests differing in species, soil, climate and history context.

• We suggest to include soil ecologists, soil chemists, tree ecologists, and forest users to match forest management treatments with realistic forest operations, and allow for direct application by forest managers.

#### Declaration of competing interest

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

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