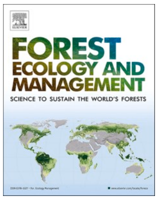
Forest Ecology and Management 592 (2025) 122827

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Soil secrets and tree tales: An in-depth comparison of carbon storage in mixed and pure stands of pine and birch

Nicolas Fanin [a,*], Laurent Augusto [a], Andreas Altinalmazis-Kondylis [a], Lucie Bon [b], Audrey Bourdin [a], Stephan Hättenschwiler [c], Soline Martin-Blangy [d], Tania L. Maxwell [e], Céline Meredieu [f], Xavier Morin [c], Nattan Plat [f], Maude Toïgo [f,g], Hervé Jactel [f], Mark R. Bakker [a,g]

[a] INRAE, Bordeaux Sciences Agro, ISPA, Villenave-d'Ornon 33140, France
[b] Université Clermont Auvergne, INRAE, VetAgro Sup, UMR Ecosystème Prairial, Clermont-Ferrand, France
[c] CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France
[d] Université de Lorraine, AgroParisTech, INRAE, UMR Silva, Nancy 54000, France
[e] Biodiversity, Ecology and Conservation Research Group, International Institute for Applied Systems Analysis (IIASA), Schloßplatz 1, Laxenburg 2361, Austria
[f] INRAE, Univ. Bordeaux, BIOGECO, Cestas, France
[g] Bordeaux Sciences Agro, Gradignan, France

ARTICLE INFO

Keywords:
Soil carbon sequestration
Tree diversity
Pine-birch mixtures
Pinus pinaster
Betula pendula
Water availability
Tree density
Carbon budget

ABSTRACT

With climate change intensifying droughts, pest outbreaks and fire risks, forest management practices are increasingly focused on stabilizing soil carbon (C) stocks, which are essential for long-term ecosystem productivity and climate change mitigation. Planting more species-rich forests has been proposed as a potential solution, but the impact of species selection and planting density on carbon stocks remains largely unknown, particularly in mixed-species plantations, where local water availability plays a key role. In this study, our objective was to examine the effects of tree diversity, water availability, and tree density on carbon stocks and fluxes. Using a 10-year-old tree diversity experiment, we investigated how pure monocultures of pine (*Pinus pinaster*) and birch (*Betula pendula*), as well as mixed pine-birch stands, influence carbon dynamics under contrasting water conditions and different tree densities. Our results indicated that tree species mixtures slightly increased total C stocks, primarily through enhanced soil C storage due to niche partitioning and greater root turnover. However, pine monocultures showed higher aboveground biomass productivity than birch monocultures and mixed stands, regardless of water availability. Overall, increased soil moisture enhanced both tree biomass and soil carbon stocks, especially in mixed stands, likely by alleviating drought stress for birch. In contrast, higher water availability accelerated litter decomposition, reducing C stocks in the litter layer. Tree density was a key driver of C storage, with denser stands of pine monocultures showing increased aboveground biomass but reduced understory C stocks. These findings highlight the context-dependent benefits of mixed stands: while species mixtures can enhance soil C storage and adaptability to drought, they may be inferior to pine monocultures in aboveground C storage, at least under the specific environmental conditions and temporal scale covered by our study. This study underscores the need for site-specific forest management strategies that balance productivity and C sequestration goals, offering guidance for climate change mitigation through alternative planting schemes adjusting tree density and species composition while maintaining ecosystem services.

1. Introduction

The *Landes de Gascogne* forest, covering nearly one million hectares in southwest France, is one of the largest and most intensively managed forests in Europe (Levers et al., 2014). This planted forest plays a crucial role in the region's bioeconomy and contributes to approximately 25 % of the national wood harvest (Agreste, 2019). Established in the 19th century on sandy, nutrient-poor, acidic, and seasonally waterlogged

---

* Corresponding author.
E-mail address: nicolas.fanin@inrae.fr (N. Fanin).

https://doi.org/10.1016/j.foreco.2025.122827
Received 12 February 2025; Received in revised form 17 May 2025; Accepted 19 May 2025

podzols (Jolivet et al., 2007; Achat et al., 2009), it consists almost entirely of monoculture of maritime pine (*Pinus pinaster* Ait.), a species well-adapted to stressful conditions like water drought and low phosphorus availability (Tóth et al., 2013). Native to the Mediterranean region, maritime pine was introduced worldwide for afforesting infertile soils (Farrington and Bartle, 1991; Bouffier et al., 2013; Etherington et al., 2022), and provides a steady supply for energy, green chemistry, fiber production, and wood products (Layton et al., 2021). However, pine monocultures are also exposed to substantial risks, such as frost damage, gales and fires, which may be intensified by climate change, along with emerging challenges like large-scale pest outbreaks and more frequent droughts (Cucchi et al., 2005; Loustau et al., 2005; Jactel et al., 2021; Battisti and Larsson, 2023). For instance, rising temperatures are linked to a higher development rate and number of generations for insects like bark beetles and processionary moths (Pineau et al., 2017; Jactel et al., 2019a), leading to significant pine damage during warm years (Vasconcelos and Duarte, 2018). Moreover, the highly flammable tissues of pine trees (Michalet et al., 2023), combined with exceptionally hot and dry climate conditions that increased ignition potential and enabled the fire to spread rapidly (Lanet et al., 2024), contributed to the devastating fire that scorched 30000 ha in the *Landes de Gascogne* forest during the summer of 2022 (Vallet et al., 2023). Given the predicted increase in extreme weather events (Cardell et al., 2020), developing alternative forest management practices becomes essential to maintaining productivity while reducing risks for planted forests and for human settlements.

One proposed solution to maintaining high productivity while mitigating the impact of future extreme events is planting more diversified forests (Messier et al., 2022; Depauw et al., 2024). In the *Landes de Gascogne* region, however, several studies based on arboreta showed that only a few tree species can cope with the infertile soil conditions (see Maris 2011 for a complete report). Among these tree species, silver birch (*Betula pendula* L.) may be particularly promising, notably because pine-birch associations are less prone to pest damage infestations (Castagneyrol et al., 2014; Jactel et al., 2019b; Poeydebat et al., 2021; Farinha et al., 2024), and silver birch exhibits higher resistance to wildfires compared to pine (Dubois et al., 2020). Furthermore, recent research demonstrated that pine-birch forests maintain a relatively similar level of productivity compared to pine monocultures (Morin et al., 2020; Toïgo et al., 2022). However, increasing birch presence in mixtures can also reduce understory plant diversity despite taller growth of individual plants (Corcket et al., 2020). This is likely due to the competitive advantage of only certain species, such as *Pteridium aquilinum* and *Molinia caerulea*, which are favoured by the improved light availability when birch is present, leading to the exclusion of less competitive species and a reduction in species richness in the understory vegetation layer. Additionally, mixing pine and birch may accelerate nutrient cycling by increasing soil enzyme activities in intermediate soil horizons (Maxwell et al., 2020), likely due to asymmetric competition between pine and birch roots along the soil profile (Altinalmazis-Kondylis et al., 2020). These changes in understory vegetation biomass, nutrient cycling or plant-soil interactions can also modify soil carbon (C) storage at the ecosystem level, as there are often trade-offs between C stored in aboveground biomass and in the soil (Bon et al., 2023). Therefore, it is important to gain a more detailed understanding of how tree species mixing affects total C budget beyond aboveground tree biomass, including C stocks and fluxes, to evaluate the impact and feasibility of converting monospecific stands to mixed forests.

The success of planting pine-birch forests depends on the environmental context because birch is more sensitive to drought than pine (Niinemets and Valladares, 2006; Andivia et al., 2020). This sensitivity may lead to increased tree mortality from inter-specific competition during summer droughts when water availability is limited (Morin et al., 2020). Therefore, access to water is crucial for maintaining both aboveground and belowground productivity (Altinalmazis-Kondylis et al., 2020; Toïgo et al., 2022), especially in ecosystems like in our study region, which experiences frequent summer droughts (Vidal et al., 2021; Taborski et al., 2022). Additionally, since water availability can vary significantly from wet to dry areas across the *Landes de Gascogne* region (Jolivet et al., 2007; Augusto et al., 2010), it is important to adapt local forest management practices to optimize tree biomass production under dry conditions, particularly by optimizing crown volume, which can in turn improve canopy packing and overall tree growth at the stand scale (Jucker et al., 2015; Martin-Blangy et al., 2023). One possible way to maintain high productivity in dry areas is to reduce the number of trees per unit area at the planting stage, with typical densities ranging from 1000 to 1400 trees per hectare for pine monocultures in the *Landes de Gascogne* (Mason and Meredieu, 2011). This strategy helps optimizing tree growth and water availability from the outset, distinguishing it from thinning, which is implemented later to reduce competition and further enhance resource availability for the remaining trees. Although it has been shown that reducing tree density can have contrasting effects on the forest carbon budget (Mayer et al., 2020), this approach remains advisable because reducing inter-specific competition may be the best compromise to increase tree survival while benefiting from the tree-mixing effect at the stand level (Sohn et al., 2016). In line with these results, Morin et al. (2020) demonstrated through simulations that mixing birch and pine trees had a greater positive effect on stand productivity at lower tree densities. This is likely because planting birches reduces intra-specific competition between pines, promoting their growth and resulting in greater complementarity at the stand level. However, it is not well understood how the interactive effects of stand density, composition, and water availability on the total carbon budget depend on site-specific conditions. Understanding these interactions will be crucial for determining how stand density and composition should be adjusted in response to water scarcity, as in the case of pine and birch in southwestern France.

In this study, our primary objective was to assess the impact of pine and birch mixtures on the forest C budget, and how it may vary with changing tree density and water availability. To do so, we estimated C stocks and fluxes in a plantation where tree diversity, tree density and water availability were experimentally manipulated. First, we tested the hypothesis (**H_1**) that total C stocks and fluxes would be higher in two-species mixtures than in the corresponding monocultures since mixing different tree species may lead to complementary resource use (Pretzsch and Schütze, 2016). Specifically, we hypothesized that the effect of mixing trees would improve both aboveground and belowground productivity, leading to higher tree C stocks (Zheng et al., 2024), with a positive feedback of higher tree biomass on soil C stocks and fluxes (Augusto and Boča, 2022; Fanin et al., 2022a). Secondly, we hypothesized (**H_2**) that an increase in water supply would have a positive effect on the overall C budget by alleviating the water constraint (Martin-Blangy et al., 2023). We anticipated that the effect of increasing water availability would be higher for birch trees in mixed plots, mainly because this tree species is more sensitive to drought than pines (Sullivan et al., 2021). Finally, we hypothesized (**H_3**) that the positive effect of mixing two tree species on soil C stocks and fluxes would be strongest at the low-density plots under low water supply, mainly because this would reduce inter-specific competition and tree mortality (Toïgo et al., 2022). However, we expected a greater effect of mixing trees at high density when water availability is relatively high, notably because increasing the number of trees per unit of ground area should increase aboveground biomass if mortality rates do not compensate for the higher density.

2. Materials and methods

2.1. *Study site and experimental design*

This study was carried out at the ORPHEE experimental plantation in southwestern France (44°44.35’ N, 00°47.9’ W), which is located 40 km southwest of Bordeaux and situated in the *Landes de Gascogne* forest. The climate during the period of our study, since the trees were planted (2008–2018), was characterized by a mean annual temperature of 13.1 °C and a mean annual precipitation of 940 mm. The dominant soil type is a podzol with coarse texture (95 % sand) and low fertility, particularly in phosphorus ($P_{Olsen} = 4.5$ mg kg^{-1} and 1.4 mg kg^{-1} in the 0–30 cm and 30–90 cm soil layers, respectively; Maxwell et al. 2020). This site was established in 2008 on a 12-ha clear-cut parcel of maritime pine land. Eight blocks were established with 32 plots in each block corresponding to the 31 possible combinations of five tree species (one coniferous species + four broadleaved species, including monocultures of each species), with an additional replicate of the combination of the five species (Castagneyrol et al., 2014). The plots were 20 m × 20 m large with a distance of 3 m from each other and species combinations were randomly assigned to the 32 plots within each block. Each plot comprised 10 rows of trees, with 10 trees in each row, planted at a 2-meter interval, totalling 100 trees per plot (total area of 400 m^2 per plot). The plots included pine [*Pinus pinaster* Ait.], birch [*Betula pendula* Roth] and three oak species [*Quercus pyrenaica* Willd., *Quercus robur* L., and *Quercus ilex* L.], either in monoculture or in combinations of two, three, four, or five species. The planting arrangement follows a substitutive pattern in an alternate design, i.e., trees of one species are interspersed with those of all other associated species (Castagneyrol et al., 2014).

In this study, our focus was on the density of pine trees and its interaction with birch trees, aiming to assess their effects on ecosystem carbon stocks and fluxes. The density of pine trees (presented in % of planted trees) varied from 0 % in the plots with pure silver birch to 50 % in mixtures, and up to 100 % in the plots with pure maritime pine. At a 50 % pine density, the plantation was characterized by an equal mix of pine and birch with the same number of trees per plot (referred to as 'high-density mixture'). However, we also considered pine-birch mixtures in plots where pedunculate oak [*Quercus robur* L.] was also planted in this mixture. This species, although planted at the same density as the other species, showed a very high mortality rate and the remaining individuals were as small as the dense understory vegetation after 7 years (pedunculate oak height ranged from 0.6 to 1.6 m). The contrast with the two other species was even larger at the time of sampling (10 years after planting in 2008). Due to their smaller size compared to other understory vegetation such as gorse and ferns, and the lack of resprouting, the few surviving pedunculate oaks (hereafter referred to as 'oak') were considered part of the understory vegetation layer. Consequently, considering the open spaces related to the absence of oak in the canopy layer of these plots at time of sampling, we considered only the pine and birch trees in these plots (referred to as 'low-density mixture'), similarly to what has been done in Castagneyrol et al. (2020), Toïgo et al. (2022) and Martin-Blangy et al. (2023). Thus, the density of pine trees ranged from 2500 stems ha^{-1} in pure pine plots, to 1250 pine stems ha^{-1} in mixed pine-birch plots considered as the high-density mixture, to 833 pine stems ha^{-1} in mixed oak-pine-birch plots considered as the low-density mixture, to 0 pine stem ha^{-1} in the pure birch plots, and *vice-versa* for the density of birch trees (Table 1).

In addition to manipulating pine and birch in monocultures or in mixtures at different densities, we also manipulated water availability. Overall, on average 19 % of the annual precipitation occurred in the summer during the period from 2008 to 2018 (INRAE station). In addition, the local sandy podzols have a very low water holding capacity, resulting in rapid soil drying and significant water stress for trees when summer precipitation is scarce, as observed in the ORPHEE experiment during our sampling period (Maxwell et al., 2020). To relieve this water limitation for the vegetation, we chose four out of eight blocks, where we installed an irrigation system. Accordingly, half of all blocks were irrigated seasonally from May to October to avoid drought occurrence, while the other half of all blocks experienced natural drought. Irrigation began in 2015 using water directly from the local water table, characterized by low nitrogen concentrations (average of 0.47 mg L^{-1}, corresponding to 0.22 g m^{-2} yr^{-1}) and negligible phosphorus concentrations according to data from the XyloSylve monitoring platform located near our study site (Trichet, pers. comm.). The water also contains moderate levels of other nutrient, such as calcium and magnesium, based on regional data (Jolivet et al., 2007). Each experimental plot assigned to the watering treatment is equipped with a 2 m tall sprinkler at the centre, spraying the equivalent of 3 mm of precipitation daily. Over the three summers before our samplings, control blocks received an average of 318 mm of water from early May to late September, while irrigated blocks received 777 mm during the same period (Maxwell et al., 2020). The different plots are illustrated in Supplementary Figure S1, which provides a graphical representation of the experimental design, highlighting the four composition-density treatments and associated irrigation blocks in a split-plot layout.

2.2. Quantification of carbon fluxes and stocks

To estimate carbon stocks (expressed as Mg C ha^{-1}), we studied seven different compartments: tree aboveground carbon stocks [Tree_AGC], understory aboveground carbon stocks [Us_AGC], forest floor carbon stocks [FFC], dead wood carbon stocks [DWC], tree belowground carbon stocks [Tree_BGC], understory belowground carbon stocks [Us_BGC] and soil organic carbon stocks [SOC] (Table 2). To estimate C fluxes (expressed in Mg C ha^{-1} yr^{-1}), we quantified three different components including foliar litterfall flux carbon [FLFC], wood litterfall flux carbon [WLFC] and total soil respiration [Rs] (Table 2). The corresponding carbon stocks were grouped in three categories including aboveground total carbon stocks [Tree_AGC + Us_AGC = Tot_AGC], ground total carbon stocks [FFC + DWC = Tot_GC], belowground total carbon stocks [Tree_BGC + Us_BGC + SOC = Tot_BGC]. Finally, these three categories were summed up to an estimate of the total ecosystem carbon stock [Tot_EC]. Details regarding

Table 1

Stand characteristics of tree species in different treatments. Tree survival, stem density (n ha^{-1}), basal area (m^2 ha^{-1}), and height (m) are reported as means ± standard deviation for each treatment. The treatments include birch monoculture, birch-pine low density, birch-pine high density, and pine monoculture under control and irrigated conditions.

Species	Birch		Birch-Pine low		Birch-Pine high		Pine	
	Control	Irrigated	Control	Irrigated	Control	Irrigated	Control	Irrigated
Birch								
Initial tree number (n ha^{-1})	2500		833		1250		-	
Basal area (m^2 ha^{-1})	5.56 ± 1.39	8.75 ± 1.53	2.01 ± 0.47	1.79 ± 0.42	2.78 ± 0.69	3.06 ± 1.13	-	-
Height (m)	6.5 ± 1.6	8.1 ± 1.4	6.7 ± 1.1	7.1 ± 1.9	6.9 ± 1.5	7.7 ± 1.8	-	-
Survival (%)	70 ± 24	98 ± 5	55 ± 19	100 ± 0	48 ± 35	100 ± 0	-	-
Pine								
Initial tree number (n ha^{-1})	-		833		1250		2500	
Basal area (m^2 ha^{-1})	-	-	16.53 ± 0.65	18.61 ± 1.18	21.25 ± 3.36	23.33 ± 0.99	32.57 ± 3.43	33.75 ± 2.47
Height (m)	-	-	8.7 ± 0.8	9.2 ± 0.7	8.8 ± 1.3	9.1 ± 0.9	8.6 ± 1.1	8.9 ± 1.1
Survival (%)	-	-	95 ± 6	100 ± 0	98 ± 5	100 ± 0	93 ± 10	70 ± 14

Table 2
Definitions of variables for carbon stocks and fluxes.

Category	Full name	Abbreviation	Definition
C stocks (Mg ha^{-1})	C_stock_tree_aboveground	(Tree_AGC)	Carbon stocks stored in the aboveground tree biomass (leaves, branches and trunks) estimated using specific allometric equations for both tree species (pine and birch)
	C_stock_understory_aboveground	(Us_AGC)	Carbon stocks stored in the aboveground understory biomass carbon estimated by phytovolume using allometric equations for each plant species (gorse, molinia, fern, ericaceous species…) present in the understory vegetation layer
	C_stock_forest_floor	(FFC)	Carbon stocks stored in the forest floor layer by collecting organic material at the soil surface
	C_stock_dead_wood	(DWC)	Carbon stocks stored in dead wood estimated after woody debris collection for twigs and branches an or by using allometric equations for dead trunks
	C_stock_tree_belowground	(Tree_BGC)	Carbon stocks stored in the belowground tree biomass estimated by allometric equations for coarse roots and collection of soil cores for fine roots
	C_stock_understory_belowground	(Us_BGC)	Carbon stocks stored in the belowground understory biomass estimated using root/shoot ratios for each plant species (gorse, molinia, fern, ericaceous species …) present in the understory vegetation layer
	C_stock_soil	(SOC)	Carbon stocks stored in the mineral soil estimated on soil cores of 1 m depth using the 'equivalent soil mass' approach with cubic spline interpolation for each soil layer
C fluxes (Mg ha^{-1} yr^{-1})	C_flux_foliar_litterfall	(FLFC)	Carbon flux in litterfall estimated through monthly collections of leaf litter in littertraps
	C_flux_wood_litterfall	(WLFC)	Carbon flux in wood fall estimated through monthly collections of twigs and small branches in littertraps
	C_flux_soil_respiration	(Rs)	Carbon flux from soil respiration estimated through monthly measurement of soil CO_2 fluxes in PVC collars coupled to soil probes temperature to calculate the daily CO_2 fluxes using an exponential equation
C budget (Mg ha^{-1})	C_stock_aboveground_total	(Tot_AGC)	Total carbon stocks in aboveground plant biomass [(Tree_AGC) + (Us_AGC)]
	C_stock_ground_total	(Tot_GC)	Total carbon stocks in ground layer and dead stumps [(FFC) + (DWC)]
	C_stock_belowground_total	(Tot_BGC)	Total carbon stocks in belowground plant biomass and soil [(Tree_BGC) + (Us_BGC) + (SOC)]
	C_stock_ecosystem_total	(Tot_EC)	Total carbon stocks in the ecosystem [(Tot_AGC) + (Tot_GC) + (Tot_BGC)]

the specific field and lab measurements employed for each component of carbon fluxes and stocks are presented in the following sections. However, it is important to note that due to technical challenges, we did not measure root necromass production and dissolved organic carbon losses through leaching, both of which are two SOC fluxes affecting SOC stocks.

2.3. *Tree aboveground carbon stocks [Tree_AGC]*

The dry aboveground biomass estimation for individual trees relied on allometric equations using diameter at breast height (DBH) for pine trees (Shaiek et al., 2011) or birch trees (Johansson, 1999). DBH and height measurements for all trees were recorded in 2018. The biomass calculation encompassed the dry mass of stems, branches, and leaves (Table 2). In cases where a tree had multiple stems, aboveground biomass values were estimated for each stem individually and then summed. It is worth noting, however, that while the pine allometric equations were developed locally and are well adapted to the site conditions, the birch equations were derived from a different region and may not fully capture the growth patterns of birch under our specific environmental conditions. Tree aboveground biomass was converted to tree aboveground C by using specific C concentrations for each tree species and each compartment (i.e., stem, branches, foliage and roots). In brief, fresh biomass was collected, oven-dried at 65°C for 48 hours and the C concentration was determined by dry combustion (NF [i.e., French standard] ISO [i.e., international standard] 10694 and 13878; AFNOR 1999) for tree leaves and roots using an Elemental Analyser (PE 2400 II CHN Elemental Analyser, Perkin-Elmer, Boston, MA, USA). For tree branches and stems, we used carbon concentration data from the literature (Bert and Danjon, 2006; Uri et al., 2012).

2.4. *Understory aboveground carbon stocks [Us_AGC]*

The quantification of aboveground biomass for the understory vegetation layer was conducted between May and July in 2018, which typically corresponds to the peak of vegetation in the studied region. The understory vegetation comprised approximately ten different herb, fern and woody species, most of which had dominant heights between 60 and 150 cm, with the tallest individuals reaching up to 300 cm. Bryophytes on the forest floor were ignored due to their very low abundance. Within each plot, we determined the understory height and vegetation cover by categorizing species into five functional groups, including ericaceous shrubs, other small woody plants, gorse, bracken, and herbs. We then assessed the 'phytovolume' (as the product of cover and height) in four 1 m^2 quadrats situated at the corners of the 10 × 10 m central subplot in case the understory was homogeneous, but used larger quadrats (up to 9 m^2) in case the understory was heterogeneous. The phytovolume method has been shown to be a reliable method to estimate vegetation biomass and was successfully validated in the *Landes de Gascogne* context (Porté et al., 2009). The calculations of biomass values were done using specific phytovolume-biomass models (Gonzalez et al., 2013; Vidal et al., 2021). For carbon concentration data of understory vegetation layer, we used unpublished data originating from the same geographical area (Gonzalez et al., 2013). Detailed results for each plant functional group can be found in Supplementary Table 2.

2.5. *Forest floor carbon stocks [FFC]*

We determined the pool of carbon in the forest floor layer, encompassing all dead, fresh, or dry and partially decomposed plant tissues above the topsoil surface (Fanin et al., 2022a). In brief, we sampled the forest floor in March 2018 at four different locations in each plot using a small quadrant (10 cm × 20 cm). Subsequently, these samples were dried at 65°C until a constant weight was achieved, pooled together, and the carbon concentration was analysed using the same elemental analyser as described previously.

2.6. *Dead wood carbon stocks [DWC]*

The deadwood C stock was inventoried across all plots in July 2018, encompassing fine woody debris (1 cm ≤ diameter ≤ 5 cm), coarse woody debris (diameter > 5 cm), stumps and dead trunks. In brief, we used the line intersect sampling method to inventory dead wood along transects, with smaller pieces (1–5 cm diameter) surveyed on four sub-transects of 5 m long within each plot (Stokland et al., 2004; Brin et al., 2008). The diameter of smaller pieces was categorized into classes A (1 – 2.4 cm) or B (2.5 – 4.9 cm) using a gauge, while quadratic mean diameters of 1.90 cm and 3.95 cm were utilized for volume calculations, respectively (Brin et al., 2008). Stumps were systematically inventoried along tree rows or in circular sub-plots, and snags were measured within circular sub-plots using allometric equations for each specific species. C concentration was analysed using the same elemental analyser as described previously. Detailed results for each class of dead wood residues can be found in Supplementary Table 4.

2.7. *Tree belowground carbon stocks [Tree_BGC]*

Tree root C was computed as the cumulative carbon content stored in tree coarse roots (diameter $\geq$ 2 mm) and tree fine roots (diameter $<$ 2 mm). The dry biomass of coarse roots for each tree was determined using allometric equations derived from previous studies for pine trees (Augusto et al., 2015) and birch trees (Bijak et al., 2013). For fine roots, we collected four sampling points per plot in March 2018 (Altinalmazis-Kondylis et al., 2020). In brief, the top 0–15 cm of soil was collected manually with a soil corer (8 cm diameter) and the bottom 15–90 cm of soil was collected with a mechanical drill, attached onto an auger (4 cm diameter). After sieving and cleaning, tree fine roots were oven-dried, weighed and pooled to estimate their biomass and C concentrations were analysed using the same elemental analyser as described previously.

2.8. *Understory belowground carbon stocks [Us_BGC]*

Understory root C was computed as the cumulative carbon content stored in coarse roots (diameter $\geq$ 2 mm) and fine roots (diameter $<$ 2 mm). We used root/shoot ratios based on observations on the same species (Bon et al., 2023) and compared them to allometric equations developed in the same geographical area (Gonzalez et al., 2013). Samples of roots were collected and analysed for C concentration using the same standardized procedure as described above.

2.9. *Soil organic carbon stocks [SOC]*

Soil C content was estimated using four soil cores per plot in March 2018. Briefly, the top 0–15 cm of soil was collected manually with a soil corer (8 cm width), while the bottom 15–90 cm was obtained using a mechanical drill with an attached auger (4 cm width), noting the presence of hardpan when applicable (Fanin et al., 2022a). Subsequently, each soil core was divided into five layers (0–5, 5–15, 15–30, 30–60, and 60–90 cm depth), and composite samples of the four core replicates were created for each soil layer per plot. These soil samples were promptly transported to the nearby laboratory and stored in a cool room at 4°C. Each soil sample was then sieved to 2 mm, homogenized, dried, and total C_{org} was analysed by dry combustion as described previously. Because there is no carbonate in these acidic soils (Augusto et al., 2010), all soil carbon was organic. Soil organic carbon stocks (SOC, Mg C ha^{-1}) were calculated separately for each soil layer using equivalent soil mass (ESM) and by employing cubic spline interpolation (Wendt and Hauser, 2013). The ESM approach uses cumulative mineral soil mass per unit area (Von Haden et al., 2020). This approach is less subjected to errors and variation in bulk density than the traditional 'fixed depth approach' (Ellert and Bettany, 1995). While both methods produced comparable results in our study, the ESM approach was retained for greater accuracy. The calculation was based on C concentration (g kg^{-1}), soil layer thickness (cm), and bulk density (g cm^{-3}) that was estimated using the pedotransfer function developed specifically for the local podzols (Augusto et al., 2010). One soil core was excluded due to poor fit with the ESM model, likely caused by the presence of undecomposed organic material. We considered the sum as the total soil carbon content per plot. Additionally, initial SOC stocks were measured using the loss-on-ignition method (Augusto et al., 2010) on soil samples collected in 2009 from the 0–15 cm horizon in the same plots, shortly after tree plantation. Our analysis showed no significant differences in SOC stocks among plots, indicating that initial carbon stocks were comparable across treatments (Table S1).

2.10. *Foliar litterfall flux [FLFC]*

Litterfall flux was assessed by collecting litter bi-monthly from 2018 to 2019, using two large traps, with 10 cm tall vertical plastic cylinder borders and a mesh covering the bottom (0.72 m^2 surface area), suspended from wooden stakes 50 cm above ground level. We acknowledge that only two litter traps per plot were used for this measurement, which is not optimal compared to the recommendation to use more traps for better representativeness of the plot (Ukonmaanaho et al., 2020), and this may have led to an overestimation of the actual litterfall flux. However, due to the large size of the traps compared to most studies, this approach was deemed acceptable for collecting both foliar litter and woody debris (see below). After collection, foliar samples were sorted, dried at 65°C to a constant mass, separated by species, and weighed. Samples of litter were analysed for C concentration using the same standardized procedure as described above.

2.11. *Wood litterfall flux [WLFC]*

The deadwood carbon flux of coarse woody debris was determined by quantifying the fallen fine woody debris (1 cm $\leq$ diameter $\leq$ 5 cm) and coarse woody debris (diameter $>$ 5 cm) in the above mentioned litter traps. Each piece of wood was dried at 65°C to a constant mass, separated by species, and weighed. Samples of ground pieces of woods were analysed for C concentration using the same standardized procedure as described previously.

2.12. *Total soil respiration [Rs]*

Soil respiration (Rs) was measured using three collars installed in all plots connected to a portable infrared gas analyser (PP systems, EGM-4, Hitchin, UK). PVC collars with a diameter of 15 cm and a height of 8 cm were evenly installed in each plot in 2019. The collars were inserted into the soil to a depth of 2 cm. Soil respiration measurements were carried out monthly from May 2019 to April 2020. Additionally, one probe in each plot recorded soil temperature every 15 min. Rs was calculated using the exponential equation provided by Lloyd and Taylor (1994). The total Rs was calculated as the cumulative value of the hourly mean Rs of the three replicated collars per plot.

2.13. *Statistical analyses*

Linear mixed models were used to assess the effect of tree species mixing (monocultures *versus* mixed pine-birch plots), water availability (control *versus* irrigation), the density of pine trees (ranging from 0 to 2500 trees ha^{-1}; see Fig. 1) and their interactions on various carbon fluxes and stocks (see Table 2 for more details about the studied variables). We used a split-plot design and implemented a superblock structure (Yang, 2010), grouping irrigated and control blocks based on their proximity within four superblocks (see Figure S1 for more details) (Maxwell et al., 2023). To account for spatial dependencies and ensure a more precise estimation of variability, blocks were considered as a random factor within superblocks to enable a comparison of stand composition and water availability treatment within each superblock separately in all the models using the package '*nlme*' (Pinheiro and Bates, 2000). The random effects were estimated using Restricted Maximum Likelihood (REML), which provides less biased estimates of variance components in the presence of small sample sizes. All models were checked for residuals to ensure model quality and to confirm that statistical assumptions were met. We then applied contrasts for each stand composition × water availability combination using Tukey's post-hoc tests indicated by the lowercase letters in Fig. 1, with the package '*multcomp*'. We also ran similar models and post-hoc tests to assess the overall effect of stand composition, independent of irrigation level, as indicated by the capital letters in the same Figure. We then applied hierarchical partitioning models to separate the amount of variation explained by the different explanatory variables when they were all considered together in a multiple regression model by using the package '*hier.part*' (Walsh and MacNally, 2013). Finally, we used principal component analysis (PCA) to visually evaluate how the carbon stocks and fluxes were interrelated using the package '*vegan*'. Total carbon stocks variables (which represent the sum of several stocks within each compartment) were then fitted as a supplementary variable to avoid affecting the relationships among the different variables. To visualize the differences among the different stand compositions × water availability, we calculated the barycentre and the projection area between plots of each treatment. All of the statistical analyses were performed using R software (version 4.3.1).

3. Results

Tree aboveground carbon (Tree_AGC) varied on average between 12.6 Mg C ha^{-1} in pure birch plots and 44 Mg C ha^{-1} in pure pine plots, with intermediate levels when the two species were mixed (Fig. 1). In line with these results, pine trees were overall taller and had a higher basal area compared to birch, particularly in the pure pine plots

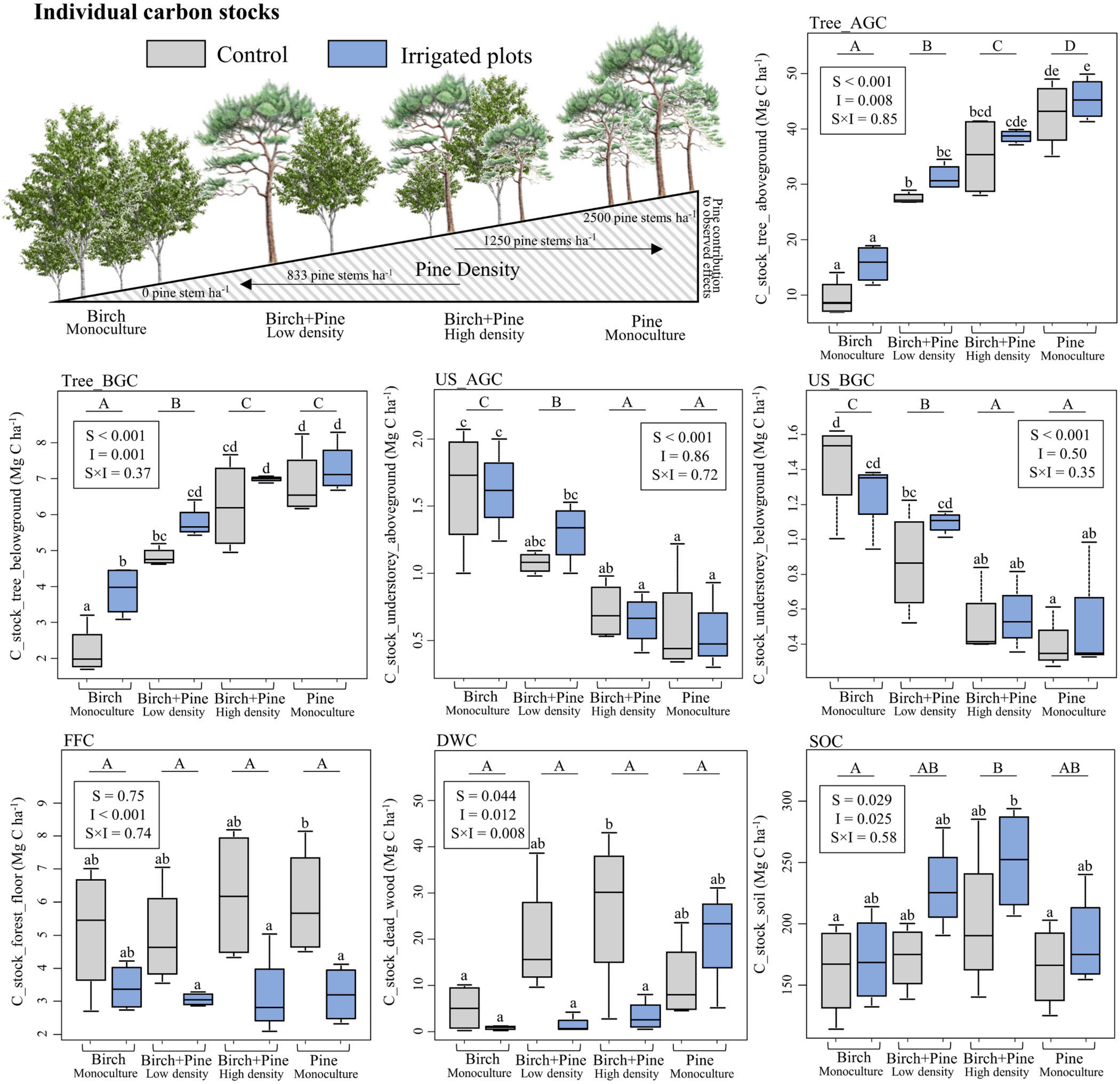


Fig. 1. Influence of tree diversity, irrigation and pine density on various individual stocks. For each level of pine density (from pure birch stand to pure pine stands) and tree diversity (mixtures of birch-pine are presented centrally at two levels of density), the panels depict the responses of individual ecosystem functions or fluxes and carbon budget (see Table 2 for a detailed description) at two different levels of water availability (natural conditions versus irrigated plots). The boxplots characterize the lower quartile, median, upper quartile and interquartile range (upper quartile – lower quartile), which covers the central 50 % of the data; the whiskers represent 95 % of the data. Different letters indicate significant differences between treatments ($P < 0.05$, Tukey-HSD tests); capital letters indicate differences among the different plots (four levels; birch, pine and pine-birch at two density levels), while lowercase letters indicating differences between plots at each level of water availability (eight levels; birch, pine and pine-birch at two density levels × water availability). In each panel, the statistical results (*p*-values) of stand (S), irrigation (I) and their interaction (S × I) are included to show the overall effect of these factors on various ecosystem functions and fluxes.

(Table 1). Variance partitioning indicated that pine tree density accounted for most of the variation in Tree_AGC (Fig. 2), with quite consistent effects for leaf, branch and trunk biomass C (Table S2), reflecting allometric constraints. Pine biomass C was also the dominant contributor to Tree_AGC in mixed pine-birch plots, accounting for more than 75 % of the total tree carbon in both low- and high- density stands, while birch contributed less than 25 % on average (Table S2). Irrigation also increased Tree_AGC and average basal area, but to a lower extent than stand composition (Table 1, Fig. 1). Tree belowground carbon (Tree_BGC) showed a similar pattern and varied from 3.0 Mg C ha^{-1} in birch plots to 6.6 and 7.1 Mg C ha^{-1} in high density mixtures of pine and birch and pure pine plots, with the low-density mixture showing an intermediate value of 5.5 Mg C ha^{-1} (Fig. 1). Coarse roots contributed to approximately 80 % of total Tree_BGC across all plots (Table S2). The pattern was opposite for understory aboveground carbon stocks (Us_AGC), with highest values of 1.6 Mg C ha^{-1} in pure birch plots compared to 0.7 and 0.6 Mg C ha^{-1} in high density mixtures of pine and birch and pure pine plots, respectively (Fig. 1). Variance partitioning showed again that the differences in Us_AGC were mainly associated with the density of pine trees across the different treatments (Fig. 2), with lower biomass with increasing pine density (Fig. 1). Understory belowground carbon stocks (Us_BGC) showed a similar pattern, with an almost fourfold lower amount of 2.3 Mg C ha^{-1} in pure pine plots compared to 8.3 Mg C ha-1 in pure birch plots (Fig. 1). Overall, the understory plant community was dominated by bracken (*Pteridium aquilinum*) followed by gorse (*Ulex europaeus*), herbs (*Molinia caerulea*), ericaceous shrubs (*Calluna vulgaris* and *Erica cinerea*) and finally other small woody species (Table S2).

There were no differences in forest floor carbon stocks (FFC) or dead wood carbon stocks (DWC) among the different stands, including the mixed pine-birch plots and their respective monocultures (Fig. 1). Instead, we found a strong irrigation effect (Fig. 2), with an overall decrease of 2.4 and 9.0 Mg C ha^{-1}for FFC and DWC in irrigated plots, respectively (Fig. 1). While the effects of irrigation were consistent for FFC (Fig. 1), we found that irrigation decreased DWC for birch in pure and mixed stands, but increased it in pure pine plots (Fig. 1). This is notable because the mortality of birch was lower in irrigated plots in mixed stands (Table 1). In contrast, the mortality of pine trees was higher in pure pine stands following irrigation (Table 1). In line with the results of FFC and DWC, we found a strong effect of irrigation on the annual cumulative total carbon loss through soil respiration (Rs; Fig. 3), with an overall decrease of 30 % of Rs values in irrigated plots (Fig. 3). However, when considering the C flux in foliar litterfall (FLFC) or wood litterfall (WLFC), we found a different pattern (Fig. 3), pine density explaining a greater portion of the variation for FLFC and tree species mixture explaining a greater portion of the variation for WLFC (Fig. 2). Overall, the FLFC increased by 2.5-fold from 1.1 Mg C ha^{-1} in pure birch plots to on average 2.8 Mg C ha^{-1} in all the other plots (Fig. 3), whereas WLFC increased by an average 34 % when trees are planted in mixtures (Fig. 3). Furthermore, we found that tree species mixture significantly explained soil carbon stocks (SOC; Fig. 2), with an overall increase of 25 % in mixed plots compared to the monocultures of both species (Fig. 1). This effect was primarily due to a large increase in SOC stocks at the intermediate horizon 15–30 cm, and particularly at high density (Supplementary Figure S2). We also found a significant effect of irrigation, which tended to increase soil SOC stocks by 34.4 Mg C ha^{-1} (Fig. 1). This effect was, however, mainly observed in the top layer 5–15 cm, notably when pine was present in the stands (Supplementary Figure S2). Finally, we found that tree mixture and irrigation had no significant effects on soil C:N ratio and soil pH, even though there was a significant decrease along the soil profile (Supplementary Table S3).

When studying the co-variation among the different variables, we identified two axes in the principal component analysis (PCA), with the first axis (PCA1) being related to pine density, whereas the second axis (PCA2) was related to water availability (Fig. 4). All the correlation coefficients among each pair of variables can be found in Supplementary Figure S3. Overall, we observed that carbon stocks in the tree aboveground and belowground parts (i.e., Tree_AGC and Tree_BGC), as well as foliar litterfall (FLFC), were positively correlated with each other, and negatively correlated with carbon stocks in the aboveground and belowground understory plant parts (i.e., Us_AGC and Us_BGC) along PCA1 (Fig. 4). Along PCA2, we found that soil carbon stocks (SOC) and the flux of wood litterfall (WLFC) were negatively correlated to soil respiration (R_s) and dead wood carbon (DWC) (Fig. 4). DWC strongly depended on tree mortality, whereas Tree_AGC, Tree_BGC and FLFC showed an opposite trend (Supplementary Figure S3). Overall, the increase in C stored in the dead wood was mainly related to an increase of dead trees and an increase in stumps and dead trunks (Supplementary Table S4). When considering the projection of plot values in the PCA, we found that C stored in understory plant parts was higher in pure birch plots, while the carbon stored in trees and litter increased with pine density in the plots (Fig. 4). On the other hand, we observed that soil carbon stocks and the flux of wood litterfall were higher when the plots were irrigated, whereas the quantity of dead wood and soil respiration were higher in non-irrigated plots.

When investigating the different ecosystem C stocks (Fig. 5), we found that total C stocks in the aboveground biomass (Tot_AGC) were mainly explained by pine density (Fig. 2). This is because Tot_AGC was primarily driven by the increase in Tree_AGC, even though Us_AGC decreases with increasing pine density (Fig. 4). Furthermore, this effect was accentuated by irrigation because it had a beneficial effect on pine biomass and, thus, on Tree_AGC (Figs. 4 and 5). Regarding carbon stocks in the ground layer (Tot_GC), we found that irrigation was the main factor explaining Tot_GC (Fig. 2), mainly because FFC and DWC decreased strongly with irrigation (Fig. 1). Additionally, we found a significant interaction between stand composition and irrigation, primarily driven by the increased mortality observed in irrigated pure pine plots (Table 1), whereas this was opposite in the other plots. We also found a positive effect of pine density on Tot_GC through its positive effect on DWC (Figs. 1 and 5). Regarding total carbon stocks in the belowground biomass (Tot_BGC), we found the same pattern as for Tot_AGC, i.e., Tree_BGC was positively explained by the density of pine trees and irrigation, whereas Us_BGC was negatively affected by pine density (Figs. 1 and 2). However, because SOC stocks increased in plots mixing birch and pine (Fig. 1), we also found that Tot_BGC was positively influenced by tree species mixture (Fig. 2). As such, Tot_BGC was influenced by all the studied factors in our experimental design, i.e., pine density, irrigation, and tree mixture (Fig. 4). In total, we found that the total carbon stocks in the ecosystem (Tot_EC) were positively influenced by pine density and tree mixture (Figs. 1 and 4). This is particularly notable because these factors exhibited positive or neutral effects on Tot_AGC, Tot_BGC and Tot_GC (Fig. 4). However, we did not observe a significant effect of irrigation on Tot_EC, primarily because the positive impact of irrigation on Tot_AGC and Tot_BGC was counteracted by its negative effect on Tot_GC (Fig. 1), although statistical analysis revealed a marginal overall positive effect (Fig. 5).

4. Discussion

Using a 10-year-old tree diversity experiment, we investigated the effects of tree species mixing, water availability, and tree density on carbon (C) stocks and fluxes. In line with our hypotheses, tree species mixing had an overall positive effect on the total C pool, but this effect was relatively small and depended on the ecosystem compartment considered (i.e., aboveground biomass or soil), the level of water availability and the pine tree density. These results highlight that the effects of forest management practices on ecosystem C stocks and fluxes depend on the environmental context and should be adapted to management objectives.

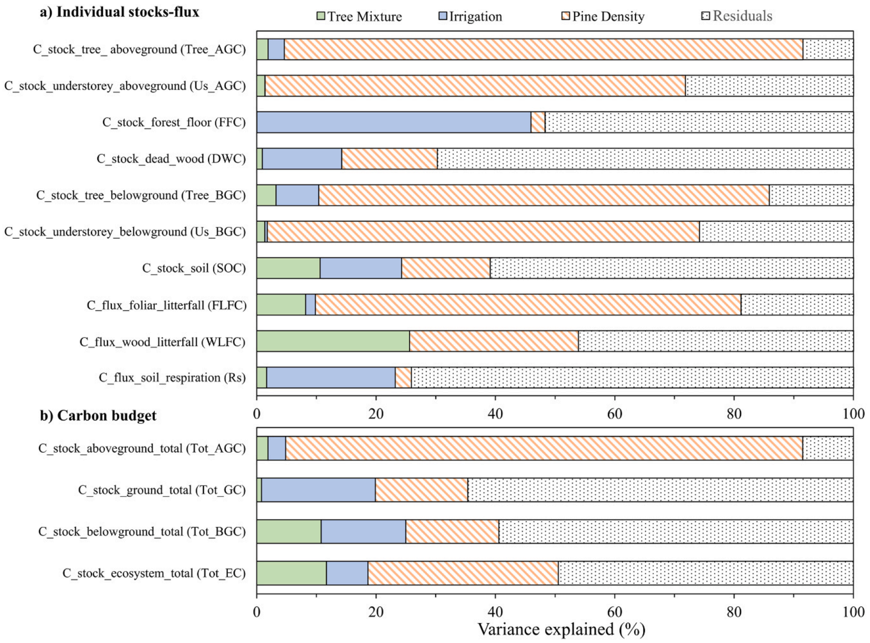


Fig. 2. Hierarchical partitioning of explained variance for (a) individual ecosystem functions or fluxes and (b) carbon budget. Each component of both carbon stocks and fluxes is explained by tree species mixture (monoculture *versus* mixed plots), irrigation (control *versus* irrigated plots), pine density (from 0 % to 100 % of pine trees). Residuals indicate the part of variance that remains unexplained by the three categorical factors tested in these models.

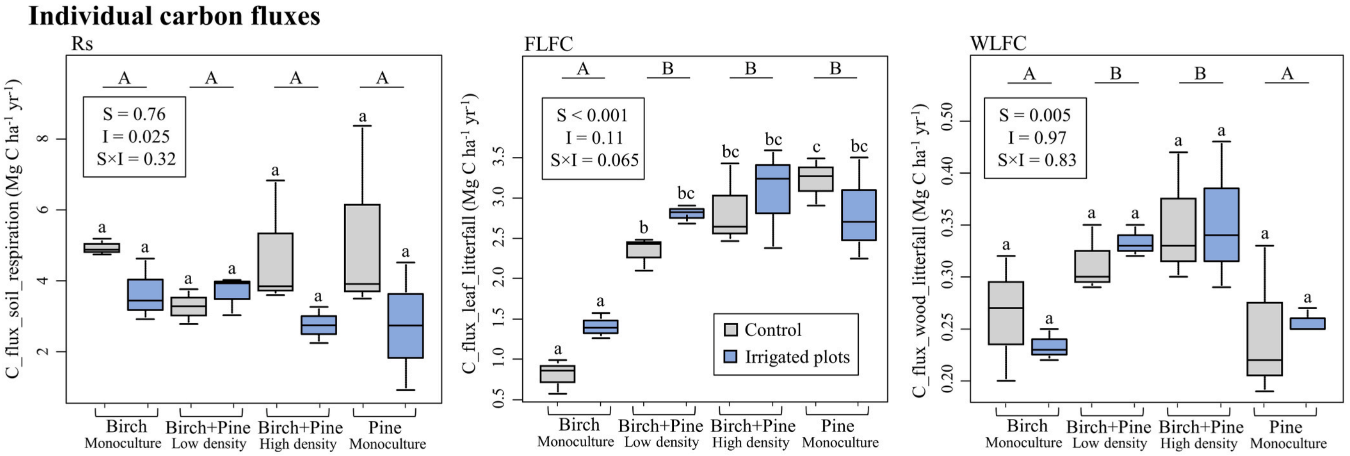


Fig. 3. Influence of tree diversity, irrigation and pine density on various individual carbon fluxes. For each level of pine density (from pure birch stand to pure pine stands) and tree diversity (mixtures of birch-pine are presented centrally at two levels of density), the panels depict the responses of individual ecosystem functions or fluxes and carbon budget (see Table 2 for a detailed description) at two different levels of water availability (natural conditions versus irrigated plots). The boxplots characterize the lower quartile, median, upper quartile and interquartile range (upper quartile – lower quartile), which covers the central 50 % of the data; the whiskers represent 95 % of the data. Different letters indicate significant differences between treatments ($P < 0.05$, Tukey-HSD tests); capital letters indicate differences among the different plots (four levels; birch, pine and pine-birch at two density levels), while lowercase letters indicating differences between plots at each level of water availability (eight levels; birch, pine and pine-birch at two density levels × water availability). In each panel, the statistical results of stand (S), irrigation (I) and their interaction (S × I) are included to show the overall effect of these factors on the different variables studied.

4.1. Tree species mixture effects on total C stocks and fluxes

In line with our first hypothesis (**H$_1$**), we found that total C stocks were, on average, higher in two-species mixtures than in the corresponding pure plots (green arrows in Fig. 6). However, it is important to note that this pattern holds only when considering the average of both monocultures, as pine monoculture alone showed no difference compared to the mixed plots, despite having overall lower values in total C stocks (Fig. 1). Higher total C stocks in mixtures compared to the respective monocultures resulted mainly from a 20 % increase in soil C stocks. This increase in soil C stocks can be attributed to asymmetric competition among tree roots through niche partitioning along the soil profile (Altinalmazis-Kondylis et al., 2020), which likely led to greater organic matter inputs through rhizodeposition and root turnover (Maxwell et al., 2020; Fanin et al., 2022a). The greater soil C stocks may also have resulted from increased litterfall inputs, as our study found that FLFC varied from 0.79 Mg C ha^{-1} in birch monoculture to an average of 2.57 Mg C ha^{-1} in mixed plots under ambient conditions. These values are relatively high compared to the values estimated from Çömez et al. (2019) ranging from 0.65 Mg C ha^{-1} in young Scots pine stands to 1.35 Mg C ha^{-1} in mature stands, but are within the range of other studies, varying from an average of 1.64 Mg C ha^{-1} (Roig et al., 2005) to 4.40 Mg C ha^{-1} in submature pine stands in central Spain (Santa Regina and Gallardo, 1995). In addition, higher soil C stocks could result

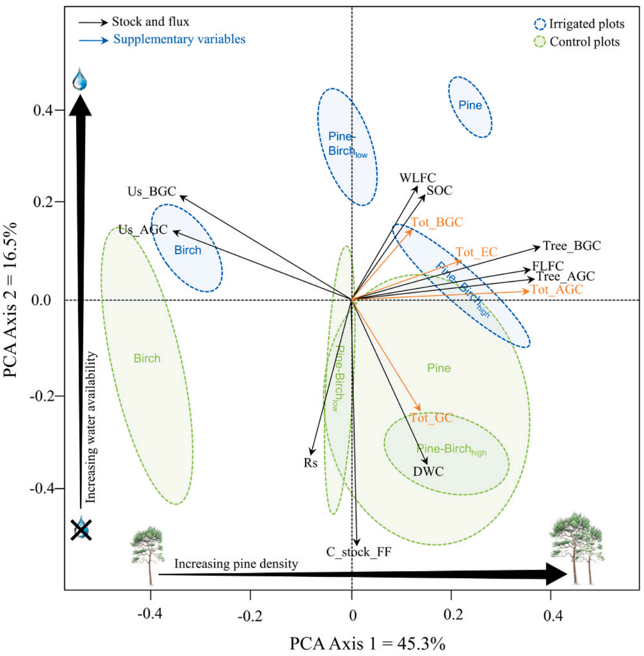


Fig. 4. A Principal component analysis with loading vectors related to stocks and fluxes (black arrows) across the experimental forest sites. Supplementary variables representing the total stocks and tree mortality were afterwards correlated with the PCA (orange arrows) to avoid any influence during the calculation of the PCA axes and eigenvectors. The convex hulls represent the distance of the experimental plots from the centroid for each treatment and according to each level of water availability.

from increased inputs of dead wood tissues on the forest floor (Augusto and Boča, 2022), for example, as a consequence of higher birch mortality when birch was mixed with pine (Table 1). In line with these results, Kaitaniemi and Lintunen (2010) demonstrated that birch experienced a more competitive environment when mixed with Scots pines compared to growing in monocultures. Pine competition may be mostly expressed through lower light availability for the birch trees, as the latter suffers from being overshadowed by the taller, larger pines surrounding them after eight years (Martin-Blangy et al., 2023). Additionally, birch trees may be more sensitive to water stress during extreme drought events (Sullivan et al., 2021). Although we cannot determine the exact mechanisms, these results suggest that mixing birch with pine trees may positively influence soil C stocks, a potentially beneficial effect aligned with the aim of sequestering more CO_2 from the atmosphere into the soil in the coming decades, as a way to counteract human-caused CO_2 emissions (Soussana et al., 2019).

In contrast to the results for total C stocks on the forest floor and in the soil, we found slightly lower total tree biomass in mixed stands, with an average of 36.8 Mg C ha^{-1} in mixed plots compared with 44.0 Mg C ha^{-1} in pure pine plots at equal density. This suggests that planting mixed pine-birch forests comes at the expense of maximising wood production with pine monocultures in the *Landes de Gascogne*. Monocultures of maritime pine may be more productive because this species is particularly well adapted to these sandy, phosphorus-poor soils (González-García et al., 2014), while birch seems to be outcompeted by pine, resulting in lower trunk volume and tree height after 10 years of plantation compared to birch trees growing in birch monocultures (Martin-Blangy et al., 2023). That said, the amount of wood biomass in mixed birch-pine forest stands appears to remain within an acceptable level of production on a regional scale (Mason and Meredieu, 2011). Interestingly, the understory vegetation layer showed an opposite pattern with on average a higher biomass C stock in birch monocultures followed by mixed stands and pine monocultures, most likely due to an increasing canopy openness with an increasing proportion of birch trees. In line with these results, Corcket et al. (2020) reported an increasing understory canopy height with higher birch proportions due to more light reaching the understory. This suggests that planting mixed forests leads to intermediate C storage in both tree and understory biomass, with pine and birch monocultures being dominant in terms of C stocks for trees and understory vegetation, respectively. Overall, this resulted in no significant tree mixture effect on the amount of C stored in total living biomass compared to the respective monocultures (Fig. 4). Although further research is needed to confirm these results across various pedo-climatic conditions, we conclude that there is a decoupling between aboveground and belowground compartments when considering the effects of tree diversity in our study area, and that the positive effects of planting mixed forests are primarily mediated by increased soil C stocks rather than C stored in plant biomass. Furthermore, changes in tree canopies and their overlap, as well as the dynamic nature of C storage over time, are important factors to consider, as they may influence the long-term carbon sequestration potential of mixed forests.

4.2. Water availability effects on total C stocks and fluxes

In partial agreement with our second hypothesis (**H_2**), we observed a positive trend of increasing water availability on various C stocks at the

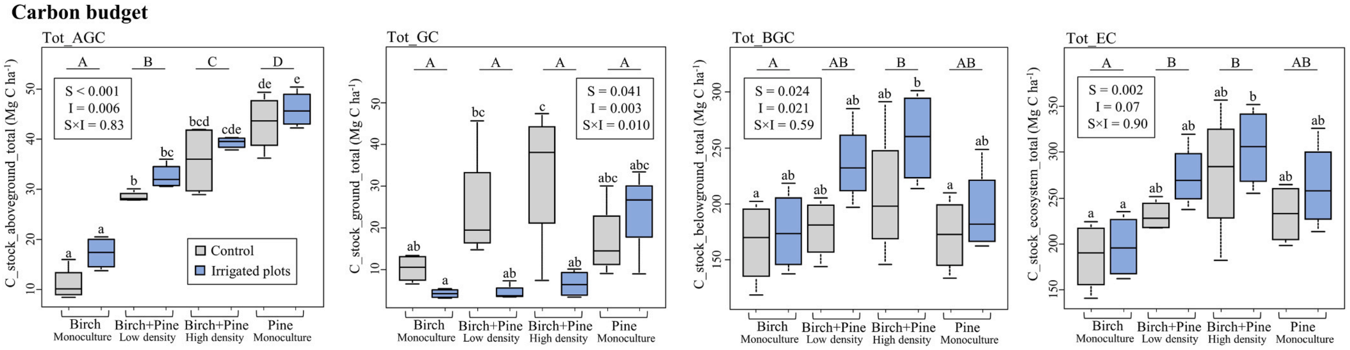


Fig. 5. Influence of tree diversity, irrigation and pine density on total carbon budget. For each level of pine density (from pure birch stand to pure pine stands) and tree diversity (mixtures of birch-pine are presented centrally at two levels of density), the panels depict the responses of individual ecosystem functions or fluxes and carbon budget (see Table 2 for a detailed description) at two different levels of water availability (natural conditions versus irrigated plots). The boxplots characterize the lower quartile, median, upper quartile and interquartile range (upper quartile – lower quartile), which covers the central 50 % of the data; the whiskers represent 95 % of the data. Different letters indicate significant differences between treatments ($P < 0.05$, Tukey-HSD tests); capital letters indicate differences among the different plots (four levels; birch, pine and pine-birch at two density levels), while lowercase letters indicating differences between plots at each level of water availability (eight levels; birch, pine and pine-birch at two density levels × water availability). In each panel, the statistical results of stand (S), irrigation (I) and their interaction (S × I) are included to assess the overall effect of these factors on the different variables studied.

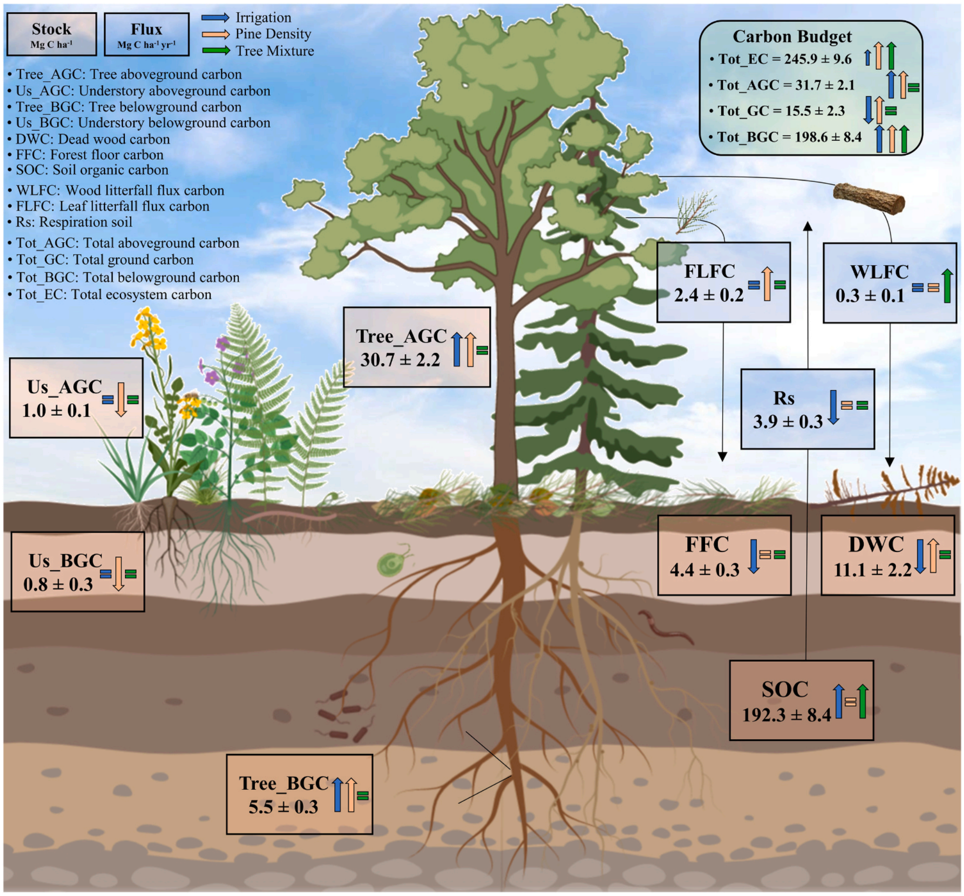


Fig. 6. Benchmarking map of individual ecosystem functions or fluxes and carbon budget. Carbon fluxes (light blue boxes), carbon stocks (light brown boxes) and average carbon budget (light green box) across all forest stands. Numbers represent means ± standard errors (Mg C ha^{-1} yr^{-1} for fluxes and Mg C ha^{-1} for stocks and carbon budget). Different colours of arrows indicate the effects of tree species mixture (green), irrigation (blue) and pine density (orange). Directions of arrows show positive (upward) and negative (downward) effects of mixture, irrigation and pine density with respect to carbon fluxes or stocks. The sign '= ' is shown when no effect was significant. For Tot_EC, the effect of irrigation was marginally positively significant at 0.07, suggesting a positive trend (which was indicated by a smaller arrow), even though this effect was not statistically significant. This figure was created using BIORENDER and MS POWERPOINT.

stand scale, but this effect was only marginally significant for total C stocks, primarily due to two contrasting effects on the C pool in the ground layer, living biomass, and soil (blue arrows in Fig. 6). Overall, we found a considerable decrease in litter and dead wood C stocks stored with irrigation. This result can be attributed to two complementary mechanisms. First, increasing soil water content may accelerate decomposition rates (Bengtson et al., 2005), particularly during summer droughts when water availability typically limits soil microbial activity while temperature is favourable (Maxwell et al., 2020). In line with this potential stimulating irrigation effect on decomposition, we found that C stocks in the forest floor, particularly in the organic layer, decreased by more than 70 % when plots were irrigated compared to control conditions, suggesting rapid organic matter recycling when water is not limiting (Fanin et al., 2022a). Second, increased water availability may reduce tree mortality, especially that of birch trees in mixed stands. Higher tree survival and healthy biomass may, in turn, reduce the amount of dead wood production in the plots, ultimately lowering C stocks on the ground. One exception is that increased water availability led to more dead wood in pure pine plots, likely because alleviating water stress intensified intra-specific competition and tree mortality in these stands (Table 1). At this stage pine tree growth has led to overcrowding and natural mortality, a phenomenon known as self-thinning (Pretzsch, 2006; Charru et al., 2012).

In contrast to the C stored in dead trunks and on the forest floor, we found that increasing water availability increased C stored in both the living tree biomass and in the soil. First, we found that irrigation increased tree above- and below-ground C stocks by 13 % and 16 %, respectively, and in particular for birch trees in monoculture and mixed stands (Fig. 1). These results confirm that birch is particularly sensitive to summer drought (Niinemets and Valladares, 2006; Andivia et al., 2020), and may be less competitive than pines when water availability becomes limiting (Morin et al., 2020). Second, the effects of irrigation on soil C stocks were particularly important in mixtures, highlighting that the effects of tree species mixing are stronger when the conditions are more favourable on these sandy soils (Maxwell et al., 2020; Fanin et al., 2022a). A reasonable explanation for this effect is greater organic matter inputs in mixtures, as described before, while such inputs tend to be larger when water resources are non-limiting (Martin-Blangy et al., 2023). An alternative, but not mutually exclusive explanation may be that these findings are driven by greater competition between mycorrhizae and saprotrophs for organic nitrogen (Fanin et al., 2022b). This competition may slow down litter decomposition rates through a 'Gadgil effect' (Fernandez and Kennedy, 2016), which may in turn reduce soil respiration while limiting saprotroph activity in the upper soil layers. Although we cannot test this hypothesis with our data, this would also contribute to explaining the higher decomposition rates in the litter layer while decreasing soil respiration from the soil (Fig. 1).

4.3. *Tree density effects on total C stocks and fluxes*

Overall, increasing pine density in the plots was one of the most important factors influencing the majority of the measured variables

(Fig. 2). We found that increasing pine density had a positive effect on the C stored in tree biomass, but a negative effect on the C stored in the understory vegetation (orange arrows in Fig. 6). These results are in line with those of Mason and Meredieu (2011), showing that increasing the number of stems is the most important factor for producing more wood in the *Landes de Gascogne*. However, in contrast to our third hypothesis (**H_3**), we found that the positive effect of mixing pine and birch on soil C stocks was weaker at high density with irrigation. Similarly, we did not find a greater effect of mixing tree species when water was becoming limiting during summer drought, even though birch mortality was lower in mixtures than in birch monocultures (Table 1). Instead, we found that the differences in C stocks and fluxes between the low and the high density in mixed plots were marginal (Fig. 1), which suggests limited effects of higher tree density in species mixtures on total C. Instead, our results indicate that the beneficial effects of mixing trees on tree biomass or soil C stocks may occur even at lower tree density, but that these effects will depend on water availability during summer. Finally, it is important to note that even if the C stored in the aboveground biomass was higher when plots were dominated 100 % by pine, this was not the case when considering the total C pool, notably because increasing pine density in plots was not the main factor controlling C stocks in the forest floor or in the soil.

4.4. Implications for forest management

The results of our long-term experiment contributed to a better understanding of the mechanisms of tree-soil interactions during the first phase of tree growth in plantations in the *Landes de Gascogne* forest (Fig. 6). In addition to previously identified mechanisms revealing that planting more diversified forests increased resistance to climate change and pest outbreaks (Vasconcelos and Duarte, 2018; Vallet et al., 2023), our results indicated that certain tree species mixtures, such as pine-birch stands, can promote soil C stocks. However, these effects depend on the density of pine and the environmental context, which should both be considered during plantation. First, because the density of pine trees remains the primary factor influencing total wood production and total C stocks in general, and because this species is particularly competitive in nutrient-poor and dry environments (Richardson et al., 1990; Maris, 2011), its presence may increase birch mortality in mixtures, particularly during drought events and at high pine density. One possible solution would be to cut birch between 5 and 10 years after plantation, as this can provide an additional source of dead wood, or to use the total stand density to accelerate the self-thinning of birches and the smallest pines, which would favour the growth of the remaining pine trees during stand maturation (Toïgo et al., 2022). While economic constraints must be considered, proposing such management strategies can contribute to discussions with stakeholders on optimizing stand development and addressing ecological and silvicultural objectives. Second, we found that the beneficial effect of mixing tree species on total C stocks was higher when water availability allowed sustained growth during dry summers. This reinforces the idea of harvesting birch at earlier stages of stand development in drier areas, whereas longer transition periods can be achieved when the water table is high enough to sustain tree growth rates of both species simultaneously (Vincke and Thiry, 2008). Finally, we found that mixed pine-birch stands also increased the C stocks in the understory vegetation layer compared to pure pine plots. Although the quantity of C stored is far lower than in trees, understory vegetation also has an important share of total plant biomass and contributes to ecosystem C storage (Wardle et al., 2012). This is particularly true for slow-growing ericaceous shrubs and their associated ericoid mycorrhizal fungi (Clemmensen et al., 2013), which may reduce decomposition rates by competing for nitrogen with other fungal guilds, increase nutrient limitation, and lead to a progressive accumulation of organic matter, thereby positively influencing soil C stocks (Fanin et al., 2022b). However, the presence of understory vegetation may also increase fire risk, especially during drought events, which suggests that understory management may be necessary compared to pure pine plots if aiming at preventing fire to the detriment of C storage in the ecosystem. Collectively, our data suggest that mixing maritime pine and silver birch has overall positive effects on ecosystem C storage, but that these effects vary depending on water availability and tree density.

CRediT authorship contribution statement

Stephan Hättenschwiler: Writing – review & editing. **Soline Martin-Blangy:** Writing – review & editing. **Lucie Bon:** Writing – review & editing, Investigation. **Audrey Bourdin:** Writing – review & editing. **Laurent Augusto:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Andreas Altinalmazis-Kondylis:** Writing – review & editing, Investigation. **Nicolas Fanin:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Bakker Mark:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Toïgo Maud:** Writing – review & editing. **Hervé Jactel:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Xavier Morin:** Writing – review & editing. **Nattan Plat:** Writing – review & editing, Investigation. **Tania Maxwell:** Writing – review & editing, Investigation. **Céline Meredieu:** Writing – review & editing.

Fundings

This work was supported by the GesDivAr project by the Region Nouvelle Aquitaine (AAPR2020A-2019–8472310), the DiPTiCC project funded by the Agence nationale de la recherche (ANR16-CE32–0003), and the ECODIV department at the ‘Institut national de la recherche en agriculture, alimentation, et environnement’ (INRAE).

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.

Acknowledgements

We thank Sylvie Milin and Catherine Lambrot for their assistance in the field and the lab, Nicolas Devert and Alexandre Bosc for their help with the soil respiration measurements, and Inge Van Halder for her support with the woody debris measurements. We also extend our thanks to all the colleagues from the Dipticc consortium, particularly Charlotte Poeydebat, Bastien Castagneyrol, Marie Charru and Damien Bonal, who contributed scientifically through engaging discussions, advice and insights during the course of this project. Finally, we would like to thank the Forest Experimental Facility, especially Bernard Issenhuth, for maintaining the ORPHEE experiment. We thank the editor and the anonymous reviewers for their valuable feedback, which significantly improved our manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122827.

Data availability

Data will be made available on request.

References

Achat, D.L., Bakker, M.R., Augusto, L., Saur, E., Dousseron, L., Morel, C., 2009. Evaluation of the phosphorus status of P-deficient podzols in temperate pine stands: combining isotopic dilution and extraction methods. Biogeochemistry 92 (3), 183–200.

Agreste, 2019. Memento de la statistique agricole - La filière forêt-bois. 1-23.

Altinalmazis-Kondylis, A., Muessig, K., Meredieu, C., Jactel, H., Augusto, L., Fanin, N., Bakker, M.R., 2020. Effect of tree mixtures and water availability on belowground complementarity of fine roots of birch and pine planted on sandy podzol. Plant Soil 457, 437–455.

Andivia, E., Ruiz-Benito, P., Díaz-Martínez, P., Carro-Martínez, N., Zavala, M.A., Madrigal-González, J., 2020. Inter-specific tolerance to recurrent droughts of pine species revealed in saplings rather than adult trees. For. Ecol. Manag. 459, 117848.

Augusto, L., Achat, D.L., Bakker, M.R., Bernier, F., Bert, D., Danjon, F., Trichet, P., 2015. Biomass and nutrients in tree root systems–sustainable harvesting of an intensively managed Pinus pinaster (Ait.) planted forest. Gcb Bioenergy 7 (2), 231–243.

Augusto, L., Bakker, M.R., Morel, C., Meredieu, C., Trichet, P., Badeau, V., Arrouays, D., Plassard, C., Achat, D., Gallet-Budynek, A., 2010. Is 'grey literature'a reliable source of data to characterize soils at the scale of a region? A case study in a maritime pine forest in southwestern France. Eur. J. Soil Sci. 61 (6), 807–822.

Augusto, L., Boča, A., 2022. Tree functional traits, forest biomass, and tree species diversity interact with site properties to drive forest soil carbon. Nat. Commun. 13 (1), 1097.

Battisti, A., Larsson, S., 2023. Climate Change and Forest Insect Pests. Forest Entomology and Pathology: Volume 1: Entomology. Springer International Publishing, Cham, pp. 773–787.

Bengtson, P., Falkengren-Grerup, U., Bengtsson, G., 2005. Relieving substrate limitation-soil moisture and temperature determine gross N transformation rates. Oikos 111 (1), 81–90.

Bert, D., Danjon, F., 2006. Carbon concentration variations in the roots, stem and crown of mature Pinus pinaster (Ait.). For. Ecol. Manag. 222 (1-3), 279–295.

Bijak, S., Zasada, M., Bronisz, A., Bronisz, K., Czajkowski, M., Ludwisiak, Ł., Tomusiak, R., Wojtan, R., 2013. Estimating coarse roots biomass in young silver birch stands on post-agricultural lands in central Poland. Silva Fenn. 47 (2).

Bon, L., Augusto, L., Gaudry, J., Bakker, M.R., Lambrot, C., Milin, S., Trichet, P., Fanin, N., 2023. Effects of fertilisation and understory removal on aboveground and belowground carbon stocks in wet and dry moorlands in south-western France. Eur. J. For. Res. 142 (4), 723–737.

Bouffier, L., Raffin, A., Alía, R., 2013. Maritime pine–Pinus pinaster Ait. Best practice for tree breeding in. Europe 65–76.

Brin, A., Meredieu, C., Piou, D., Brustel, H., Jactel, H., 2008. Changes in quantitative patterns of dead wood in maritime pine plantations over time. For. Ecol. Manag. 256 (5), 913–921.

Cardell, M.F., Amengual, A., Romero, R., Ramis, C., 2020. Future extremes of temperature and precipitation in Europe derived from a combination of dynamical and statistical approaches. Int. J. Climatol. 40 (11), 4800–4827.

Castagneyrol, B., Kozlov, M.V., Poeydebat, C., Toïgo, M., Jactel, H., 2020. Associational resistance to a pest insect fades with time. J. Pest Sci. 93 (1), 427–437.

Castagneyrol, B., Régolini, M., Jactel, H., 2014. Tree species composition rather than diversity triggers associational resistance to the pine processionary moth. Basic Appl. Ecol. 15 (6), 516–523.

Charru, M., Seynave, I., Morneau, F., Rivoire, M., Bontemps, J.-D., 2012. Significant differences and curvilinearity in the self-thinning relationships of 11 temperate tree species assessed from forest inventory data. Ann. For. Sci. 69, 195–205.

Clemmensen, K., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R., Wardle, D., Lindahl, B., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339 (6127), 1615–1618.

Çömez, A., Tolunay, D., Güner, Ş.T., 2019. Litterfall and the effects of thinning and seed cutting on carbon input into the soil in Scots pine stands in Turkey. Eur. J. For. Res. 138 (1), 1–14.

Corcket, E., Alard, D., Van Halder, I., Jactel, H., Garrido Diaz, B., Reuzeau, E., Castagneyrol, B., 2020. Canopy composition and drought shape understorey plant assemblages in a young tree diversity experiment. J. Veg. Sci. 31 (5), 803–816.

Cucchi, V., Meredieu, C., Stokes, A., de Coligny, F., Suarez, J., Gardiner, B.A., 2005. Modelling the windthrow risk for simulated forest stands of Maritime pine (Pinus pinaster Ait.). For. Ecol. Manag. 213 (1-3), 184–196.

Depauw, L., De Lombaerde, E., Dhiedt, E., Blondeel, H., Abdala-Roberts, L., Auge, H., Barsoum, N., Bauhus, J., Chu, C., Damtew, A., 2024. Enhancing tree performance through species mixing: Review of a quarter-century of TreeDivNet experiments reveals research gaps and practical insights. Curr. For. Rep. 10 (1), 1–20.

Dubois, H., Verkasalo, E., Claessens, H., 2020. Potential of birch (Betula pendula Roth and B. pubescens Ehrh.) for forestry and forest-based industry sector within the changing climatic and socio-economic context of Western Europe. Forests 11 (3), 336.

Ellert, B.H., Bettany, J., 1995. Calculation of organic matter and nutrients stored in soils under contrasting management regimes. Can. J. Soil Sci. 75 (4), 529–538.

Etherington, T.R., Peltzer, D.A., Wyse, S.V., 2022. Future climates are predicted to alter the potential distributions of non-native conifer species in New Zealand. N. Z. J. Ecol. 46 (1), 1–14.

Fanin, N., Clemmensen, K.E., Lindahl, B.D., Farrell, M., Nilsson, M.C., Gundale, M.J., Kardol, P., Wardle, D.A., 2022b. Ericoid shrubs shape fungal communities and suppress organic matter decomposition in boreal forests. N. Phytol. 236 (2), 684–697.

Fanin, N., Maxwell, T.L., Altinalmazis-Kondylis, A., Bon, L., Meredieu, C., Jactel, H., Bakker, M.R., Augusto, L., 2022a. Effects of mixing tree species and water availability on soil organic carbon stocks are depth dependent in a temperate podzol. Eur. J. Soil Sci. 73 (1), e13133.

Farinha, A., Castagneyrol, B., van Halder, I., Branco, M., Meredieu, C., Jactel, H., 2024. Reduction of damage by the exotic invasive conifer seed bug Leptoglossus occidentalis in mixed pine-birch plantations: a case of biotic resistance. For. Ecol. Manag. 569, 122193.

Farrington, P., Bartle, G., 1991. Recharge beneath a Banksia woodland and a Pinus pinaster plantation on coastal deep sands in south Western Australia. For. Ecol. Manag. 40 (1-2), 101–118.

Fernandez, C.W., Kennedy, P.G., 2016. Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? N. Phytol. 209 (4), 1382–1394.

Gonzalez, M., Augusto, L., Gallet-Budynek, A., Xue, J., Yauschew-Raguenes, N., Guyon, D., Trichet, P., Delerue, F., Niollet, S., Andreasson, F., 2013. Contribution of understory species to total ecosystem aboveground and belowground biomass in temperate Pinus pinaster Ait. forests. For. Ecol. Manag. 289, 38–47.

González-García, S., Bonnesoeur, V., Pizzi, A., Feijoo, G., Moreira, M., 2014. Comparing environmental impacts of different forest management scenarios for maritime pine biomass production in France. J. Clean. Prod. 64, 356–367.

Jactel, H., Koricheva, J., Castagneyrol, B., 2019a. Responses of forest insect pests to climate change: not so simple. Curr. Opin. Insect Sci. 35, 103–108.

Jactel, H., Moreira, X., Castagneyrol, B., 2021. Tree diversity and forest resistance to insect pests: patterns, mechanisms, and prospects. Annu. Rev. Entomol. 66 (1), 277–296.

Jactel, H., Poeydebat, C., Van Halder, I., Castagneyrol, B., 2019b. Interactive effects of tree mixing and drought on a primary forest pest. Front. For. Glob. Change 2, 77.

Johansson, T., 1999. Biomass equations for determining fractions of pendula and pubescent birches growing on abandoned farmland and some practical implications. Biomass-.-. bioenergy 16 (3), 223–238.

Jolivet, C., Augusto, L., Trichet, P., Arrouays, D., 2007. Les sols du massif forestier des Landes de Gascogne: formation, histoire, propriétés et variabilité spatiale. Rev. For. ère française 59 (1), 7–30.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. 29 (8), 1078–1086.

Kaitaniemi, P., Lintunen, A., 2010. Neighbor identity and competition influence tree growth in Scots pine, Siberian larch, and silver birch. Ann. For. Sci. 67, 604. -604.

Lanet, M., Li, L., Ehret, A., Turquety, S., Le Treut, H., 2024. Attribution of summer 2022 extreme wildfire season in Southwest France to anthropogenic climate change. npj Clim. Atmos. Sci. 7 (1), 267.

Layton, R.J., Horta Arduin, R., Yazdeen, H., Pommier, R., Sonnemann, G., 2021. Material flow analysis to evaluate supply chain evolution and management: an example focused on maritime pine in the Landes de Gascogne forest, France. Sustainability 13 (8), 4378.

Levers, C., Verkerk, P.J., Müller, D., Verburg, P.H., Butsic, V., Leitão, P.J., Lindner, M., Kuemmerle, T., 2014. Drivers of forest harvesting intensity patterns in Europe. For. Ecol. Manag. 315, 160–172.

Lloyd, J., Taylor, J., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 315–323.

Loustau, D., Bosc, A., Colin, A., Ogée, J., Davi, H., François, C., Dufrêne, E., Déqué, M., Cloppet, E., Arrouays, D., 2005. Modeling climate change effects on the potential production of French plains forests at the sub-regional level. Tree Physiol. 25 (7), 813–823.

Maris, C., 2011. Changements climatiques et gestion forestière en Aquitaine-Interrogations et recherches de réponses concrètes via le programme d'expérimentation Climaq. èt M. éditerranéenne 32 (2), 197–204.

Martin-Blangy, S., Meredieu, C., Jactel, H., Bonal, D., Charru, M., 2023. Species-mixing effects on crown dimensions and canopy packing in a young pine–birch plantation are modulated by stand density and irrigation. Eur. J. For. Res. 142 (1), 197–216.

Mason, W.L., Meredieu, C., 2011. Silvicultural Strategies, Sustainability, and Adaptation to Climate Change in Forests of the Atlantic Region of Europe (< Special Issue> Multipurpose Forest Management). J. For. Plan. 16 (Special_), 67–77.

Maxwell, T.L., Augusto, L., Bon, L., Courbineau, A., Altinalmazis-Kondylis, A., Milin, S., Bakker, M.R., Jactel, H., Fanin, N., 2020. Effect of a tree mixture and water availability on soil nutrients and extracellular enzyme activities along the soil profile in an experimental forest. Soil Biol. Biochem. 148, 107864.

Maxwell, T.L., Augusto, L., Tian, Y., Wanek, W., Fanin, N., 2023. Water availability is a stronger driver of soil microbial processing of organic nitrogen than tree species composition. Eur. J. Soil Sci. 74 (1), e13350.

Mayer, M., Prescott, C.E., Abaker, W.E., Augusto, L., Cécillon, L., Ferreira, G.W., James, J., Jandl, R., Katzensteiner, K., Laclau, J.-P., 2020. Tamm Review: Influence of forest management activities on soil organic carbon stocks: A knowledge synthesis. For. Ecol. Manag. 466, 118127.

Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., Bruelheide, H., Caldwell, B., Cavender-Bares, J., Dhiedt, E., 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! Conserv. Lett. 15 (1), e12829.

Michalet, R., Carcaillet, C., Delerue, F., Domec, J.C., Lenoir, J., 2023. Assisted migration in a warmer and drier climate: less climate buffering capacity, less facilitation and more fires at temperate latitudes? Oikos, e10248.

Morin, X., Damestoy, T., Toigo, M., Castagneyrol, B., Jactel, H., de Coligny, F., Meredieu, C., 2020. Using forest gap models and experimental data to explore long-term effects of tree diversity on the productivity of mixed planted forests. Ann. For. Sci. 77, 1–19.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76 (4), 521–547.

Pineau, X., David, G., Peter, Z., Sallé, A., Baude, M., Lieutier, F., Jactel, H., 2017. Effect of temperature on the reproductive success, developmental rate and brood characteristics of I ps sexdentatus (B oern.). Agric. For. Entomol. 19 (1), 23–33.

Pinheiro, J., Bates, D., 2000. Mixed-effects models in S and S-PLUS. Springer science & business media.

Poeydebat, C., Castagneyrol, B., Van Halder, I., Jactel, H., 2021. Changes in host basal area explain associational resistance of mixed forests to primary pests. For. Ecol. Manag. 495, 119374.

Porté, A.J., Samalens, J.-C., Dulhoste, R., Du Cros, R.T., Bosc, A., Meredieu, C., 2009. Using cover measurements to estimate aboveground understorey biomass in Maritime pine stands. Ann. For. Sci. 66 (3), 1–11.

Pretzsch, H., 2006. Species-specific allometric scaling under self-thinning: evidence from long-term plots in forest stands. Oecologia 146 (4), 572–583.

Pretzsch, H., Schütze, G., 2016. Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur. J. For. Res. 135, 1–22.

Richardson, D., Cowling, R., Le Maitre, D., 1990. Assessing the risk of invasive success in Pinus and Banksia in South African mountain fynbos. J. Veg. Sci. 1 (5), 629–642.

Roig, S., del Río, M., Cañellas, I., Montero, G., 2005. Litter fall in Mediterranean Pinus pinaster Ait. stands under different thinning regimes. For. Ecol. Manag. 206 (1-3), 179–190.

Santa Regina, I., Gallardo, J., 1995. Biogeochemical cycles in forests of the" Sierra de Béjar" mountains (province of Salamanca, Spain): decomposition index of the leaf litter. Annales des sciences forestières. EDP Sciences, pp. 393–399.

Shaiek, O., Loustau, D., Trichet, P., Meredieu, C., Bachtobji, B., Garchi, S., El Aouni, M. H., 2011. Generalized biomass equations for the main aboveground biomass components of maritime pine across contrasting environments. Ann. For. Sci. 68, 443–452.

Sohn, J.A., Saha, S., Bauhus, J., 2016. Potential of forest thinning to mitigate drought stress: a meta-analysis. For. Ecol. Manag. 380, 261–273.

Soussana, J.-F., Lutfalla, S., Ehrhardt, F., Rosenstock, T., Lamanna, C., Havlík, P., Richards, M., Chotte, J.-L., Torquebiau, E., Ciais, P., 2019. Matching policy and science: rationale for the '4 per 1000-soils for food security and climate'initiative. Soil Tillage Res. 188, 3–15.

Stokland, J., Tomter, S., Söderberg, U., 2004. Development of dead wood indicators for biodiversity monitoring: experiences from Scandinavia. Monitoring and indicators of forest biodiversity in. Eur. — ideas Oper. 51, 207–226.

Sullivan, P.F., Brownlee, A.H., Ellison, S.B., Cahoon, S.M., 2021. Comparative drought sensitivity of co-occurring white spruce and paper birch in interior Alaska. J. Ecol. 109 (6), 2448–2460.

Taborski, T., Domec, J.-C., Chipeaux, C., Devert, N., Lafont, S., Wingate, L., Loustau, D., 2022. Quantifying canopy conductance in a pine forest during drought from combined sap flow and canopy surface temperature measurements. Agric. For. Meteorol. 323, 108997.

Toïgo, M., Castagneyrol, B., Jactel, H., Morin, X., Meredieu, C., 2022. Effects of tree mixture on forest productivity: tree species addition versus substitution. Eur. J. For. Res. 1–11.

Tóth, G., Gardi, C., Bódis, K., Ivits, É ., Aksoy, E., Jones, A., Jeffrey, S., Petursdottir, T., Montanarella, L., 2013. Continental-scale assessment of provisioning soil functions in Europe. Ecol. Process. 2, 1–18.

Ukonmaanaho, L., Pitman, R., Bastrup-Birk, A., Bréda, N., Rautio, P., 2020. Part XIII: Sampling and analysis of litterfall. Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests, 19 p.

Uri, V., Varik, M., Aosaar, J., Kanal, A., Kukumägi, M., Lõhmus, K., 2012. Biomass production and carbon sequestration in a fertile silver birch (Betula pendula Roth) forest chronosequence. For. Ecol. Manag. 267, 117–126.

Vallet, L., Schwartz, M., Ciais, P., Van Wees, D., De Truchis, A., Mouillot, F., 2023. High-resolution data reveal a surge of biomass loss from temperate and Atlantic pine forests, contextualizing the 2022 fire season distinctiveness in France. Biogeosciences 20 (18), 3803–3825.

Vasconcelos, T.M., Duarte, I.M., 2018. How can global change affect insect population dynamics in Mediterranean ecosystems? A case study with pine shoot beetle and pine processionary moth. Theory Pract. Clim. Adapt. 479–490.

Vidal, D.F., Augusto, L., Bakker, M.R., Trichet, P., Puzos, L., Domec, J.-C., 2021. Understorey-overstorey biotic and nutrient interactions are key factors for Pinus pinaster growth and development under oligotrophic conditions. Scand. J. For. Res. 36 (7-8), 563–574.

Vincke, C., Thiry, Y., 2008. Water table is a relevant source for water uptake by a Scots pine (Pinus sylvestris L.) stand: evidences from continuous evapotranspiration and water table monitoring. Agric. For. Meteorol. 148 (10), 1419–1432.

Von Haden, A.C., Yang, W.H., DeLucia, E.H., 2020. Soils' dirty little secret: depth-based comparisons can be inadequate for quantifying changes in soil organic carbon and other mineral soil properties. Glob. Change Biol. 26 (7), 3759–3770.

Walsh, C., MacNally, R., 2013. Hiert. part: hierarchical partitioning. R Package v1. 0-4. In.

Wardle, D.A., Jonsson, M., Bansal, S., Bardgett, R.D., Gundale, M.J., Metcalfe, D.B., 2012. Linking vegetation change, carbon sequestration and biodiversity: insights from island ecosystems in a long-term natural experiment. J. Ecol. 100 (1), 16–30.

Wendt, J., Hauser, S., 2013. An equivalent soil mass procedure for monitoring soil organic carbon in multiple soil layers. Eur. J. Soil Sci. 64 (1), 58–65.

Yang, R.-C., 2010. Towards understanding and use of mixed-model analysis of agricultural experiments. Can. J. Plant Sci. 90 (5), 605–627.

Zheng, L., Barry, K.E., Guerrero-Ramírez, N.R., Craven, D., Reich, P.B., Verheyen, K., Scherer-Lorenzen, M., Eisenhauer, N., Barsoum, N., Bauhus, J., 2024. Effects of plant diversity on productivity strengthen over time due to trait-dependent shifts in species overyielding. Nat. Commun. 15 (1), 2078.