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European forest carbon and biodiversity policies have a limited win-win potential

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Climate change mitigation and biodiversity conservation are key forest functions, but how to pursue them jointly in timber-managed forests is still unclear. We use a Europe-wide dataset of forest multi-taxon diversity and stand structure to (i) evaluate the importance of aboveground carbon stocks in determining species richness of six taxonomic groups; (ii) assess relationships between species richness and carbon stocks; (iii) discuss the potential to jointly enhance carbon and biodiversity and policy implications. Carbon-diversity relationships are positive for several groups, but mostly when deadwood pools are considered. Forest policies should consider the complex relationship between different carbon pools and taxonomic groups. Environmental policies emphasizing carbon sequestration in aboveground living biomass may conflict with biodiversity conservation by promoting homogeneous, fast-growing forests that fail to support species diversity of multiple groups. Sustainable forest management should acknowledge that deadwood carbon instead may translate into positive outcomes for both carbon storage and biodiversity conservation.

European forests are expected to mitigate climate change through carbon storage, since the carbon stock associated with living biomass keeps increasing, i.e., from 8 to almost 12 Mt from 1990 to 2020[1]. However, measures designed to increase forest carbon pools may conflict with timber production. As a matter of fact, while long-lasting wood products ensure that the sequestered carbon, i.e., about 40 $MtCO_2e$/year[2], remains out of the atmospheric cycle for extended periods[3], a significant portion of European forest wood is utilized for fuel or short-lived products, with approximately 24% of the EU's roundwood production in 2022 used as fuelwood. The remaining 76%

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was processed into industrial roundwood, including pulp and paper, which typically have short lifespans[4]. Regardless of the fate of woody biomass, removing carbon stocks from forest ecosystems hampers its support to forest biodiversity[5].

In Europe, about 30% of forest area is referred to as a habitat of conservation value. Accordingly, biodiversity conservation is among the priorities of the European forest strategy[6]. While forest area is increasing in Europe, about 80% of assessments of forest habitats report an unfavorable conservation status[7].

The need to improve the condition of forest biodiversity is intrinsically associated with sustainable forest management practices that are expected to simultaneously support biodiversity conservation, climate regulation[7], and timber production.

One approach to reconcile these objectives is to spatially balance productive and environmental functions. In this view, the triad framework was recently applied to forests to balance land sparing and land sharing approaches[8] by encompassing: areas devoted to high-yield plantations[9], areas managed extensively for multiple functions, and unmanaged areas accumulating old growth features[10]. The different levels of management intensity are unevenly represented across European forests[11], and result in an uneven representation of the three carbon pools here considered. High-yield plantations result in wide temporal fluctuations of standing live carbon depending on the harvesting regime. Unmanaged conservation areas face a slow yet constant increase in all carbon pools with a greater proportion of lying and standing deadwood. Extensively managed forests maximize the standing live carbon pools with a relative temporal stability.

These patterns in carbon pools, however, may have different outcomes in terms of biodiversity through direct and indirect mechanisms that are hard to disentangle. On the one hand, the amount of carbon stored in living trees may be associated with species and taxonomic groups related to long local ecological continuity and old-growth conditions[12,13], often dependent on woody substrates, i.e., epiphytic lichens and bryophytes. Not all species groups, however, benefit from high carbon stocks: trade-offs could emerge for those taxonomic groups whose species diversity is linked to light resources, e.g., vascular plants[14–16]. On the other hand, the amounts of lying and standing deadwood, along with the carbon it stores, play a crucial role in sustaining specialized species, including saproxylic beetles and wood-decaying fungi[1,17,18]. Overall, the impact of carbon stock on biodiversity varies greatly depending on the carbon pool and the taxonomic group[15,19,20].

Notwithstanding the relevance of both climate mitigation and biodiversity conservation in European forests, only few studies have explicitly tested the relationship between forest biodiversity and carbon stocks[20–22] or related functions[20]. In-depth knowledge of the trade-offs between biodiversity conservation and climate change mitigation in European forests is urgently needed since management and restoration strategies focused only on carbon sequestration could interfere with biodiversity conservation targets by promoting homogeneous and fast-growing stands of tree species with high carbon sequestration rates[23–25]. Understorey vegetation, epiphytic lichens and birds are less diverse in plantation forests, either dominated by native[25] or non-native tree species[26,27]. This is particularly relevant since one the main objectives of the 2030 EU forest strategy is to plant 3 billion trees by 2030[6]. Despite the recent awareness on the importance of forests for jointly addressing biodiversity conservation and climate change mitigation, current forest policies, i.e., 2015 Paris agreement and the REDD+ initiative only partially incorporate this link[28].

Here, we test the possibility of forests across Europe to simultaneously sequester high amounts of carbon and host high levels of biodiversity for multiple taxonomic groups to inform trade-offs between competing forest functions.

Our specific aims are to (i) assess the relative importance of different aboveground carbon stocks in determining species richness of six taxonomic groups in European forests; (ii) identify the relationship between the species richness of these groups and carbon stocks; (iii) discuss the potential to jointly enhance carbon stocks and biodiversity and the related policy implications.

We use the recently built European multi-taxonomic database from the “Bottoms-Up” platform[29] to derive the standardized species richness of six taxonomic groups, i.e., vascular plants; epiphytic and epixylic bryophytes and lichens, hereafter bryophytes and lichens; wood-inhabiting fungi, hereafter fungi; saproxylic beetles, hereafter beetles; and birds. We perform boosted regression trees (BRTs) to assess the response of their species richness to the carbon stocks in living aboveground biomass, standing and lying deadwood, also accounting for potential confounding effects.

We expect carbon stocks to be highly relevant in driving the species richness of multiple taxonomic groups. However, given the distinct roles that different carbon pools play in supporting various components of forest biodiversity[1,30], we expect taxon-specific responses that vary across carbon pools. Photosynthetic groups such as vascular plants, bryophytes, and lichens may decline with increasing aboveground carbon stocks[14–16]. However, this trend may be counterbalanced by an increase in substrate availability for epiphytic groups[12,13]. In contrast, saproxylic fungi and beetles may respond positively to deadwood carbon stocks[1,17,18]. More mobile taxa, such as birds, may show mixed responses, influenced by landscape-level factors rather than stand-level carbon stocks alone[31].

Results

Carbon stocks importance for variations in species richness

Carbon pools had a prominent role in explaining the variation in species richness, with differences across taxonomic groups (Fig. 1). The carbon stocks of lying deadwood showed the highest shares of explained deviances, ranging from 36% for fungi to 9% for birds. The carbon stocks of standing living trees were related to the species richness of birds and vascular plants (highest share of deviance, 22%, for birds, lowest, 5%, for lichens). Standing deadwood had the greatest effect (9%) on the species richness of beetles and the lowest (3%) on lichens.

A high share of deviance was explained by the models for lichens (84%), beetles (82%), bryophytes (80%), fungi (77%) and birds (77%), while the predictive value was lower for vascular plants (55%) (Table 1).

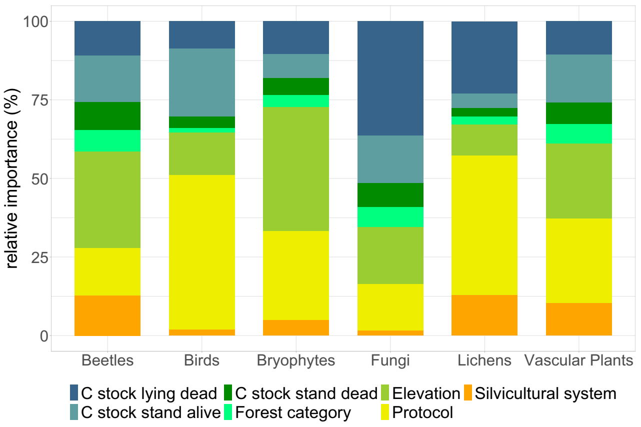

Fig. 1 | Relative importance of the predictor variables on scaled species richness across taxonomic groups. Relative importance values indicate the total reduction in model deviance attributable to each variable, averaged across all trees and scaled to sum to 100%, as derived from boosted regression tree (BRT) models fitted separately for six taxonomic groups (beetles, birds, bryophytes, fungi, lichens, and vascular plants). Each bar represents the proportion of explained deviance contributed by individual predictors. Source data are provided as a Source data file.

Table 1 | Statistics of the selected boosted regression trees (BRTs)

	Learning rate	Tree complexity	Bag fraction	Explained deviance	Cross-validated mean correlation coefficient	Self statistics
Beetles	0.005	5	0.75	0.82	0.78	0.91
Birds	0.005	5	0.75	0.77	0.81	0.88
Bryophytes	0.005	5	0.75	0.80	0.76	0.90
Fungi	0.005	5	0.75	0.77	0.77	0.88
Lichens	0.005	5	0.75	0.84	0.86	0.92
Vascular plants	0.005	5	0.75	0.55	0.61	0.75

Model parameters and validation metrics are reported to document the consistency and reliability of the BRTs across taxonomic groups.

It should be noted that the variable accounting for the effect of site and sampling protocol explained most of the variation in species richness, ranging from 49% to 14% of explained variance for birds and fungi respectively (Fig. 1). Elevation emerged as the second most influential factor, accounting for 39% of the explained deviance in bryophytes to 10% in lichens (Fig. 1). The silvicultural system showed the highest value of explained deviance (13%) for lichens and the lowest one (2%) for fungi. Forest category showed the lowest shares of explained deviances, ranging from 7% for beetles to 1% for lichens.

Taxon-specific effects of carbon stocks on species richness

Standing alive trees showed a positive effect mainly on fungi (Fig. 2), with an increase of the marginal effect on the logit of the scaled species richness of 0.2, starting at 1.5 (31.6 t C/ha); and a negative effect on vascular plants, with a decrease of 0.2, starting at 0 (1 t C/ha).

Lying deadwood showed the strongest positive relationships with fungi and lichens (Fig. 3), with an increase of the marginal effect on the logit of the scaled species richness of respectively 0.4 and 0.2. Interestingly, the scaled species richness of these two taxonomic groups showed a steep increase at different points in the gradient of carbon stocked in lying deadwood, i.e., while a value of −1 (0.1 t C/ha) was sufficient to point out an increase in lichen species richness, an increase in fungi species richness was evident at −1.5 (0.03 t C/ha). In contrast, vascular plants displayed a negative relationship with lying deadwood, with a decrease in the marginal effect on the logit of the scaled species richness by 0.3, starting at −3 (0.001 t C/ha).

Standing deadwood had a positive effect on saproxylic beetles and wood-inhabiting fungi (Fig. 4), with an increase in the marginal effect on the logit of the scaled species richness by 0.3 and 0.1, starting at −1 (0.1 t C/ha).

Discussion

Carbon stocks played a prominent role in explaining the variation in species richness. Deadwood is a fundamental component of the forest carbon pool (7% of growing stock in Europe) and has a key role in nutrient cycles[1]. It affects several taxonomic groups that are crucial in the detritus food web[32] and provides habitat to many saproxylic insects[33], lichens, fungi[34], and bryophytes[35]. Standing living trees also contributed to variation in species richness, with the largest relative importance observed for birds and vascular plants, though their influence was generally smaller than that of deadwood. By influencing forest structure[30], microclimate, and resource availability[36], living biomass remains an important carbon pool. Retaining trees in the forest, either as living biomass or deadwood, supports biodiversity across multiple taxonomic groups and enhances long-term carbon storage[37], underscoring the potential impacts of timber harvesting on forest ecosystem functions.

The relationship between aboveground living carbon stock and species richness across taxonomic groups was generally weakly positive[22], with some exceptions, most notably vascular plants, which declined above ~1 t C/ha. This decline likely reflects reduced light availability at the forest floor[14], where increases in shade-tolerant species only partially compensate for the decrease of species related to open areas[14]. In old-growth forests, both groups may coexist within fine-scale mosaics of successional phases[38], but such conditions are underrepresented in Europe and in our dataset. For most other taxonomic groups, the absence of strong positive responses suggests that the accumulation of carbon in living biomass and species richness are often driven by different ecological processes. Although increases in living biomass are typically linked with an increase in stand age[39] and may favor species linked to long ecological continuity and habitat structures associated with late-successional conditions[13]; a substantial share of forest biodiversity, including species adapted to disturbance or with high dispersal ability, relies on structural heterogeneity or periodic disturbance rather than continuous biomass accumulation[13]. These species can represent an important component of forest diversity, thereby weakening any simple positive link between aboveground living carbon and total species richness. Moreover, in the European context, high aboveground living carbon stocks are not necessarily linked to long ecological continuity, as anthropogenic disturbances strongly drive changes in forest carbon stocks[40]. Forests managed for timber production purposes can reach high carbon storage rates due to the silvicultural promotion of biomass accumulation processes (e.g., fast-growing species in even-aged forests). However, such stands often lack the structural complexity and ecological continuity required by many taxa[24,25]. This decoupling underscores that aboveground living carbon is a poor surrogate for forest biodiversity. High carbon stocks in living biomass do not necessarily coincide with high multi-taxon diversity.

We found significant associations between deadwood carbon stocks and species richness of several taxonomic groups[17,18]. Carbon in lying deadwood had strong positive links with fungi and lichens species richness in European forests. This can be explained by lying deadwood's role as both substrate and resource for these two taxonomic groups. Interestingly, their scaled species richness showed a steep increase at different values of lying deadwood carbon, with fungi responding at slightly smaller carbon stocks than epiphytic lichens. Fungal diversity is known to increase with lying deadwood carbon stock[41,42], with low amounts of lying deadwood potentially supporting a large number of species[43]. Lichen diversity, on the other hand, may respond only to greater carbon stocks due to the light conditions associated with the occurrence of large amounts of deadwood, i.e., large gap maker. On the other hand, we found a strong negative relationship between carbon in lying deadwood and vascular plant species richness, up to mid to high levels of carbon stocks. An increase in the carbon stock associated with lying deadwood is often linked to a higher stand age[44], with a potential reduced light availability at the forest floor[14,15]. However, at mid to high levels of carbon stocks this trend is not evident, likely counterbalanced by the occurrence of gap makers in forests with high amounts of deadwood[45]. Bryophytes did not show a positive response to increasing carbon stock in lying deadwood, even if previous works have highlighted decaying wood as a crucial substrate for the diversity of bryophytes in general within forest ecosystems[35,46]. Nevertheless, the relatively low number of

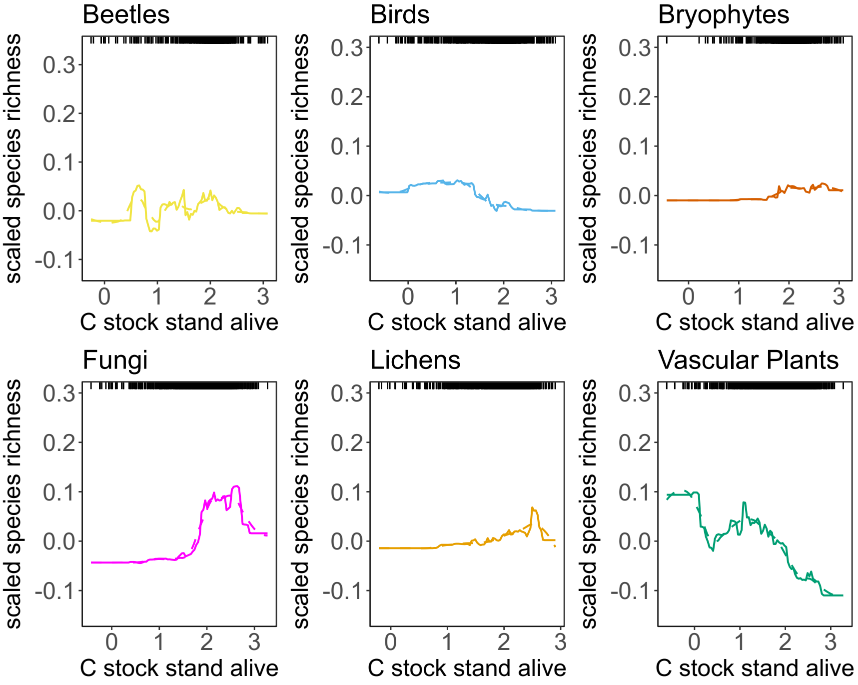

Fig. 2 | Partial dependence plots of the marginal effect of standing alive C stock on scaled species richness of studied taxonomic groups. Solid lines represent fitted functions from boosted regression-tree models, while dashed lines indicate smoothed trends summarizing overall patterns. Black stripes on the top of each graph represent the distribution of the data. Source data are provided as a Source data file.

bryophyte species in European forest ecosystems[47,48] may have hampered the detection of a consistent increasing trend in species richness across our database. Deadwood diversity, stand openness and large lying deadwood volume are largely recognized as the main drivers of saproxylic beetle species richness in temperate forests[49]. However, we were not able to detect a substantial positive response of this group to an increasing carbon stock in lying deadwood. This unexpected outcome may be associated with the fact that the vast majority of sampling units in the dataset showed a relatively low amount of lying deadwood volume, mostly composed of relatively fine deadwood fragments (see Supplementary Fig. 2), which may not be able to support the larvae of a high share of saproxylic beetle species. Interestingly, we found different results for standing deadwood, with a strong positive response of saproxylic beetles and a weak positive response for fungi, likely in relation to the generally larger sizes of standing deadwood, which, however, is less easily colonized by fungi[49]. Theoretically, an increasing amount of standing deadwood carbon is associated with an increasing amount of surface available for epixylic groups, i.e., bryophytes and lichens. For these groups, however, an increase of available surface does not necessarily mean an increase in species richness, which is rather influenced by tree species composition[50], stand-scale ecological continuity[51], local species dispersal capacity[52], microclimatic conditions[53] or seasonal rainfall distribution[54].

Increasing aboveground carbon stock in forests does not necessarily lead to a significant increase in species richness across different taxonomic groups. Species richness responses vary considerably depending on the carbon pool and taxonomic group. While aboveground living carbon stock showed weak or negative responses for most taxonomic groups, deadwood carbon stocks, including both lying and standing deadwood, demonstrated positive relationships with saproxylic, epiphytic, and epixylic groups. European and global policies focused on climate change mitigation may not jointly achieve the biodiversity conservation targets they emphasize[6] if they continue to prioritize carbon stocks in aboveground living biomass, following carbon accounting initiatives (e.g., REDD+)[28]. Although recent EU frameworks, such as the nature restoration law indicators[55], integrate other carbon pools (e.g., lying and standing deadwood, soil carbon), these components remain underrepresented in practical implementation and policy targets. Pursuing the target of carbon and biodiversity rich forests should account for the complex pathways that may link these two objectives, e.g., by promoting biodiversity-friendly measures in highly productive forest stands through integrated closer-to-nature forest management[56]. Similarly, measuring living biomass without accounting for successional pathways, human and natural disturbance regimes, landscape context and species composition, may not be used as a proxy of multi-taxon forest biodiversity, whereas it is commonly used as such[28,57]. This is particularly relevant in view of the current proposal for a European Union forest monitoring law and the LULUCF regulation[58], whose implementation continues to prioritize carbon stocks in living biomass[59].

On the other hand, our work highlights the importance of deadwood carbon pools for both climate change mitigation and biodiversity conservation targets. Over the past decades, the extraction of wood from European forests has been increasing, with growing pressures on logging residuals[60,61], as required by the need to achieve climate neutrality by substituting fossil-based materials[62]. Additionally, the limited assessment of deadwood forest carbon stock[63], constrained by the scarcity of broad-scale data[64] might have contributed to an underestimation of both the losses in deadwood carbon pools in European forests, and of the potential impacts of deadwood-dependent biodiversity[65]. It is crucial for policymakers to consider the multifaceted nature of these ecological interactions. Innovative approaches and case studies that address these dual objectives are required to inform and refine policy frameworks towards comprehensive and effective forest management strategies.

Opportunities and limitations

Local environmental conditions and sampling protocols influenced the variations in species richness for several taxonomic groups. The

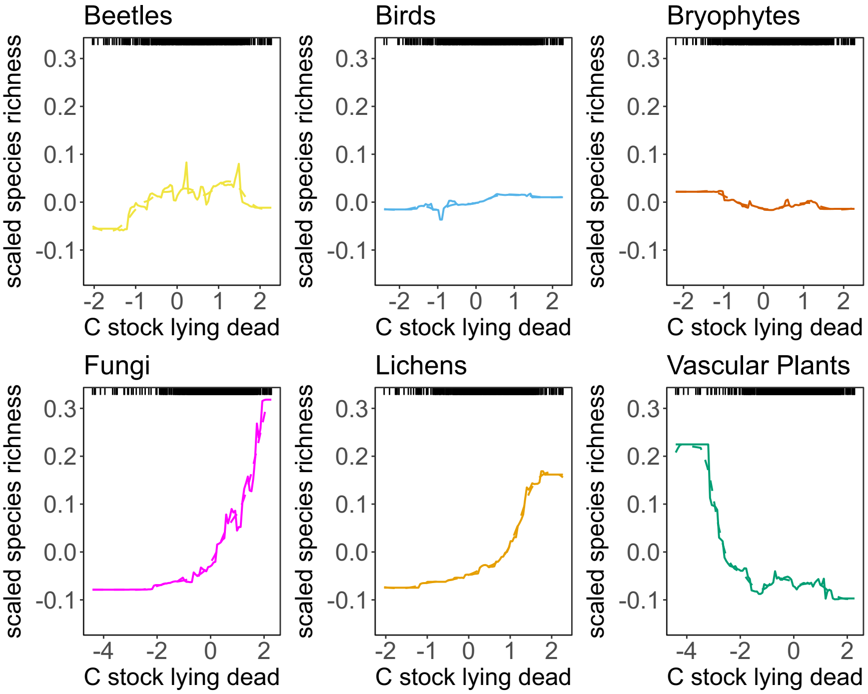

Fig. 3 | Partial dependence plots of the marginal effect of lying deadwood C stock on scaled species richness of studied taxonomic groups. Solid lines represent fitted functions from boosted regression-tree models, while dashed lines indicate smoothed trends summarizing overall patterns. Black stripes on the top of each graph represent the distribution of the data. Source data are provided as a Source data file.

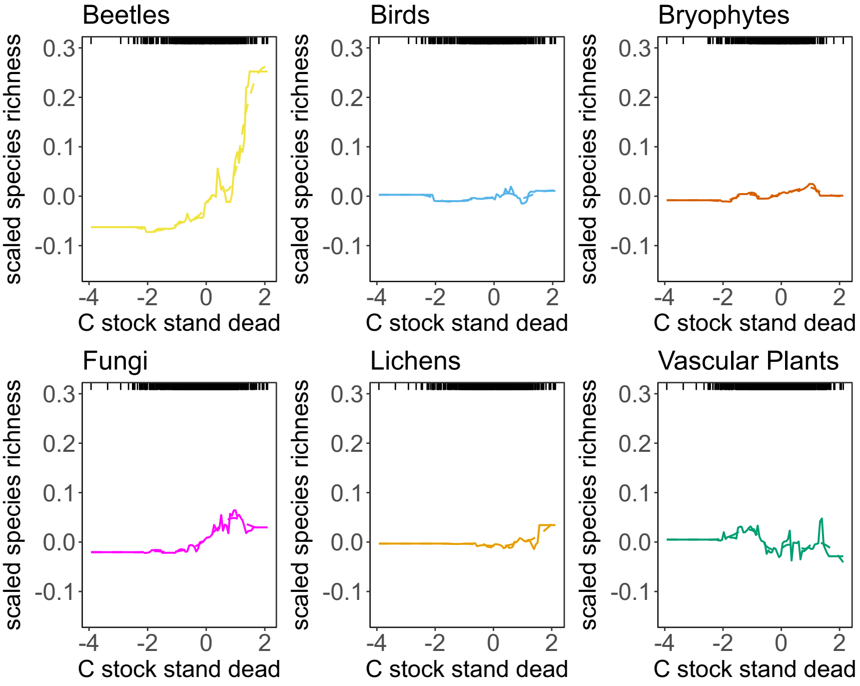

Fig. 4 | Partial dependence plots of the marginal effect of standing deadwood C stock on scaled species richness of studied taxonomic groups. Solid lines represent fitted functions from boosted regression-tree models, while dashed lines indicate smoothed trends summarizing overall patterns. Black stripes on the top of each graph represent the distribution of the data. Source data are provided as a Source data file.

discrepancies among sampling methods significantly affect biodiversity data, whose comparability across studies would greatly benefit from harmonization and standardization processes[66]. This need for protocol standardization is particularly urgent for the effectiveness of forest monitoring in Europe[59]. Beyond methodological issues, local environmental conditions play a crucial role in shaping species diversity across taxonomic groups. Context-related predictors explained a high share of the variation in species richness we observed, thus emphasizing the need to further investigate the effects of local conditions on the carbon-biodiversity relationship.

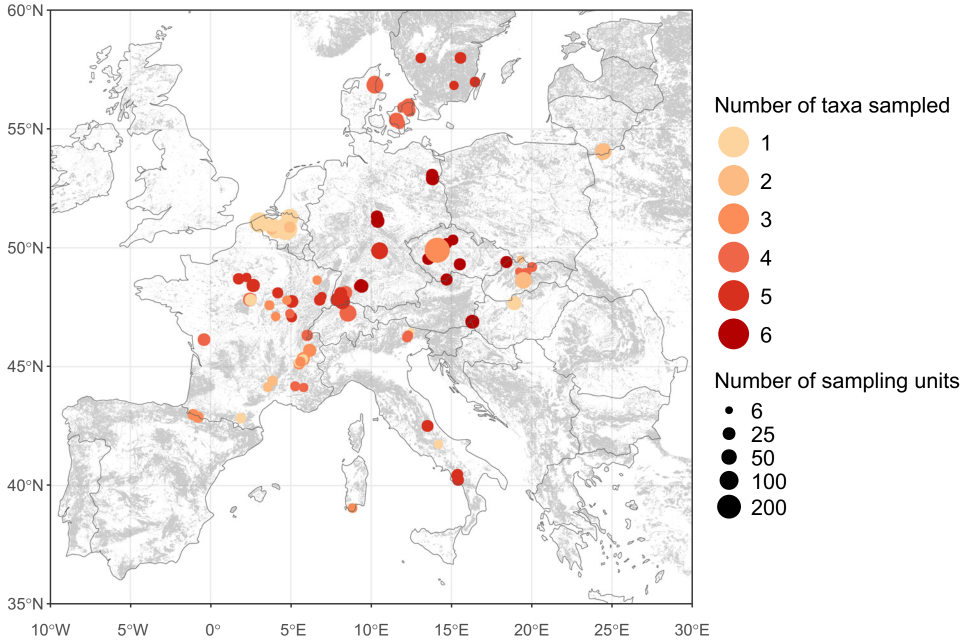

Fig. 5 | Distribution of the sampling sites in Europe. Gray areas are covered by forests with a tree cover greater than 40% according to the European Forest Institute Forest Map of Europe[88]. The number of taxonomic groups sampled at each site is represented by different shades of red, while the number of sampling units is indicated by the dot size. Source data are provided as a Source data file.

Since the dataset we used is largely focused on temperate forests, our analyses may be further improved after filling the gaps for boreal and southern Europe. Similarly, further information on stand age, forest size and connectivity could improve our ability to understand the links between forest carbon stocks and biodiversity temporal and spatial patterns.

Concluding remarks

Our work represents a step towards understanding the biodiversity-carbon stock relationships and dynamics in European forests, for which we did not find a univocal relation. Among the carbon pools, lying and standing deadwood were proven as much more relevant than living biomass in explaining the variation in European forest species richness. Aboveground living biomass carbon stock is highly relevant in global forest assessments in relation to the wide amount of available data; however, it cannot be a proper proxy for forest biodiversity. Regional and national forest inventories, as well as forest restoration initiatives (e.g., REDD+), should account for the deadwood carbon pool since it provides prominent support to several taxonomic groups. The achievement of biodiversity conservation targets may be jeopardized by climate change mitigation policies not accounting for the conservation of deadwood in forest ecosystems, as its extraction for fuel or wood products could compromise its support to species diversity.

Methods

Data

We used a recently built database encompassing 12 European countries and resulting from the harmonization of 32 datasets containing both field-sampled multi-taxon biodiversity information (i.e., at least three groups of organisms among animals and either plants or fungi), and tree-level stand structure data. Sampling units (i.e., concretely delimited forest areas of known geographical coordinates) were clustered in forest sites (i.e., an environmentally homogeneous geographical area)[29], where forest is defined as an area with a tree cover equal or greater than 40%. We analyzed a total of 140,146 observations of 3520 species in 7971 plots (see Supplementary Fig. 1). Most sampling units comprise two or more functional and taxonomic groups resulting in a total of 2615 spatially distinct multi-taxon plots across 99 sites (Fig. 5). We used data on six taxonomic and functional groups: saproxylic beetles, birds, epiphytic and epixylic bryophytes and lichens, wood-inhabiting fungi and vascular plants.

The sampling protocols used for each group used comparable approaches, with different efforts defined by the original researchers based on the site environmental and biological context[66]: vascular plants and wood-inhabiting fungi were sampled in areal plots or blocks of plots rising to an overall sampling area in the order of hundreds of square meters; epiphytic and epixylic lichens and bryophytes were sampled on all or part of the standing living trees and deadwood items in each plot; birds were sampled by point counts mostly during time frames from 5 to 20 minutes[67]; saproxylic beetles were sampled through window-flight interception traps (1–6 in each plot), in some cases also with emerging traps and Winkler extractors[68]. Species names and higher taxonomic information were checked automatically using the R-packages “taxize”[69] and, for vascular plants, “WorldFlora”[70] and either corroborated by experts or checked against the GBIF database (https://www.gbif.org/).

Data preparation

A complete assessment of plot-level species richness is almost impracticable due to the multiple constraints of sampling activities as opposed to the vastness and complexity of biological diversity[71]. A general rule is that, as the number of encountered individuals increases, species richness exhibits a nonlinear increase[72]. Until a coordinated forest biodiversity monitoring network using standardized protocols is put in place[48], the use of harmonized data from studies using different sampling efforts requires the standardization of richness data. Rarefaction operates by down-sampling data to achieve an equal sampling effort, i.e., the one of the smallest samples. A complementary approach is to extrapolate species richness to a larger sample size through an estimated asymptotic species richness[72,73]. We estimated the expected species richness for each site for each taxonomic group using the “estimateD” function within the R package

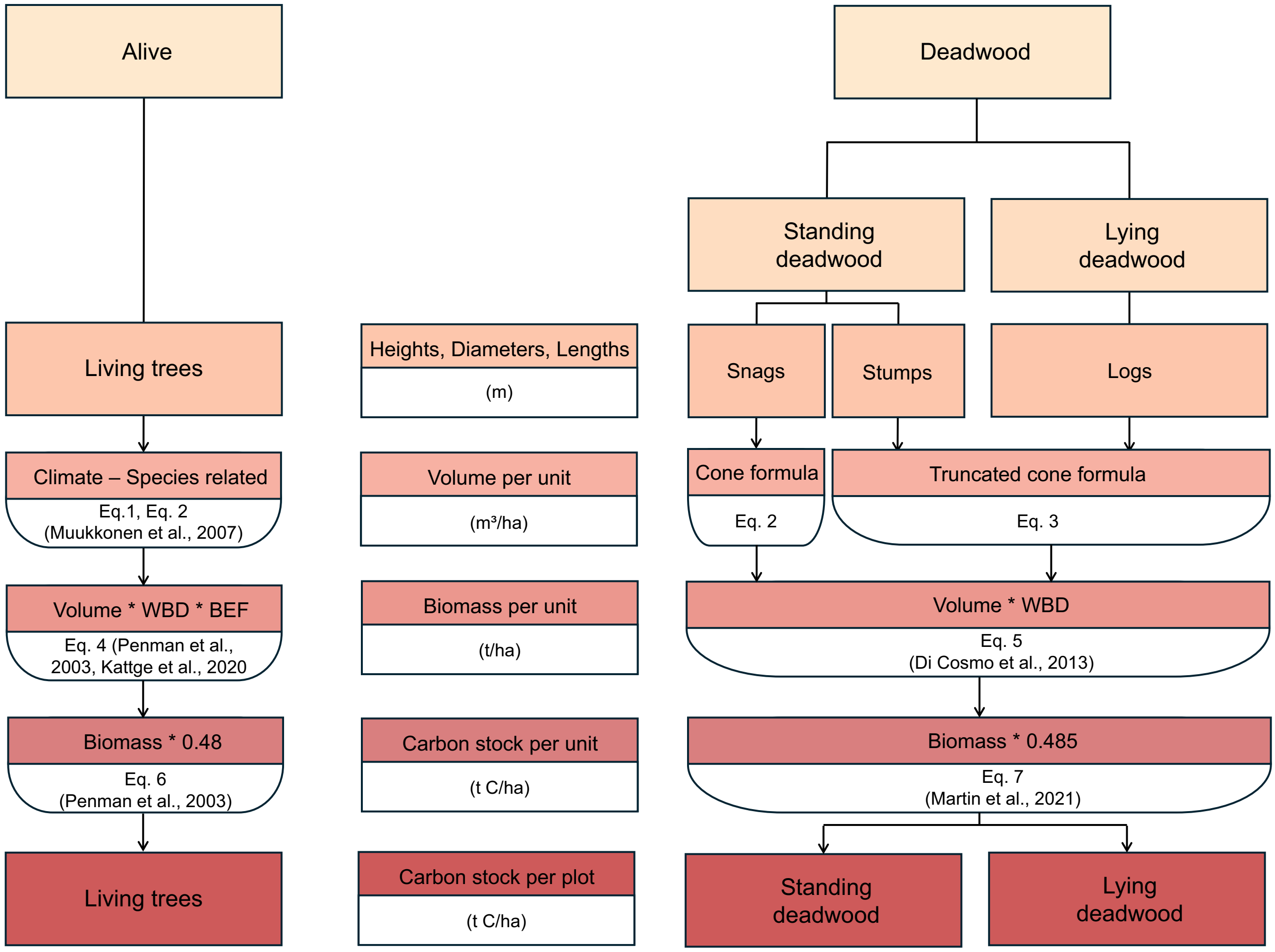

Fig. 6 | Workflow of the carbon stocks assessment for each sampling unit. Equation 1 is obtained from literature[76]; Eqs. 2 and 3 refer to the formula of the volume of the cone and truncated cone respectively; Eqs. 4 and 5[77] use wood basic density (WBD) derived from existing literature[77,79] or, when not available in the former paper, from TRY database[78] and different biomass expansion factors (BEF) based on the climatic conditions of the sampling unit (boreal or temperate) and the dominant species group (coniferous or broadleaf); Eq. 7[80] uses an improved carbon fraction of 0.485 for deadwood.

"iNEXT," set for sample-based incidence data[74]. Finally, a comparable measure of species richness (scaled species richness) was computed as the ratio between observed species richness for each taxonomic group (i.e., the quantity of sampled species) in each specific sampling unit (alpha diversity) and the expected species richness within each specific site (gamma diversity). Notwithstanding the importance of incorporating various measures of species diversity, we were not able to analyse species abundance due to the partial harmonization of this data within the database.

Stand structure data were thoroughly checked and corrected for possible errors (e.g., related to measurement units). Missing data for standing tree heights, diameters and lengths of lying deadwood were estimated based on other available measurements for the specific tree or fragment (e.g., unit length/height, unit diameter and unit ID). This process also took into account additional measurements of living and dead elements available for the sampling unit, site, and forest category. We used the predictive mean matching method of the mice function (R-package "mice"[75]) for these estimations. Overall, we modeled 25% of the standing trees' heights. Since some protocols included only one diameter measure for lying deadwood, 70 and 78% of the second (smaller) diameter of respectively, stumps and logs were imputed. Stump heights were derived for 11% of records, and log lengths for 25%. We used a set of equations to calculate tree/deadwood fragment's volume and thus biomass and carbon stocks in tonnes per hectare for each sampling unit for the three aboveground carbon pools (standing living trees, standing deadwood, and lying deadwood) (Fig. 6).

For the living trees volume estimation, we applied two different equations depending on the tree species. We used a generalized allometric volume equation developed for multiple tree species at the continental scale[76] (originally presented as Eq. 2 in the reference publication and hereafter referred to as Eq. 1). Species-specific β_0 and β_1, which are scaling coefficients, were extracted from Tab. 4 of the same publication for species where this information was available. The coefficients were selected based on the associated climatic zone of each sampling unit, covering 75% of the standing trees. For the remaining species (i.e., 25% of standing trees) the generic cone volume formula was used (Eq. 2). V_i refers to the volume of the stem of an individual tree (m^3), dbh refers to the diameter at breast height (cm in Eq. 1, as reported in the reference publication, and m in Eq. 2), h_i refers to the height of the individual tree (m).

$$V_i = \beta_0 \cdot dbh^{\beta_1} \tag{1}$$

$$V_i = \frac{\left(\frac{dbh}{2}\right)^2 \cdot \Pi \cdot h_i}{3} \tag{2}$$

The volume V_i (m^3) of deadwood fragments was calculated through the cone formula (Eq. 2) or truncated cone formula (Eq. 3) for

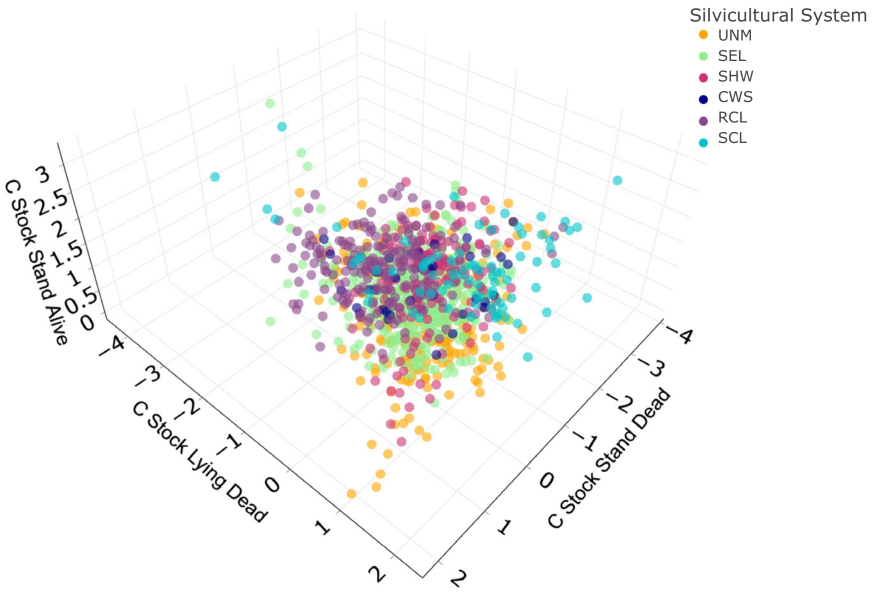

Fig. 7 | Three-dimensional scatter plot of the relationship between above-ground carbon stocks across different silvicultural systems. Each point represents a sampling unit, colored according to the silvicultural system: unmanaged (UNM), selection cutting (SEL), shelterwood (SHW), coppice with standards (CWS), retention clearcutting (RCL), simple clearcutting (SCL). Carbon stocks are logarithm base 10 transformed for better visualization and comparison with the partial dependence plots of the result section. An interactive version of the plot is available at https://zenodo.org/records/15096050. Source data are provided as a Source data file.

standing and lying deadwood, respectively. Dbh is the diameter at breast height (m), h_i refers to the height of the individual dead tree (m), r is the radius at the small end of the fragment (m), obtained from the minimum diameter reported in the database for the associated deadwood unit, and R is the radius at the large end of the fragment (m), obtained from the maximum diameter reported in the database for the associated deadwood unit.

$$V_i = \frac{(r_i^2 + R_i^2 + R_i \cdot r_i) \cdot \Pi \cdot h_i}{3} \tag{3}$$

We then calculated the volume per hectare (m^3/ha) of each unit by multiplying its volume (m^3) by 10,000 (m^2, the area of one hectare) and dividing it by the sampling unit size (m^2).

The biomass of each living tree B_i (t/ha) was estimated by multiplying its volume V_i (m^3/ha), by the corresponding wood basic density (WBD) and biomass expansion factor (BEF), following Eq. 4. This approach is derived from Eq. 3.2.3 of the IPCC good practice guidance for land use, land-use change, and forestry[77]. WBD values were obtained from IPCC standards[77], specifically Tab. 3 A.1.9–1, for available species. When species-specific values were unavailable, WBD was obtained from the TRY database[78], using genus or species-level estimates depending on data availability. BEF accounts for the additional biomass components not included in stem volume measurements, such as branches and foliage, allowing for a more accurate estimation of the total tree biomass. Different BEF values were applied to broadleaf and coniferous species, depending on the climatic zone of the sampling unit (boreal or temperate), as specified in Tab. 3 A.1.10 of the same guidelines[77].

$$B_i = V_i \cdot WBD \cdot BEF \tag{4}$$

The biomass of each deadwood unit B_i (t/ha) was estimated by multiplying its volume V_i (m^3/ha) by the corresponding wood basic density, WBD, following Eq. 5. This approach is derived from the same reference for living trees[77]. WBD values were obtained from Tab. 4 of the reference publication[79] which provides density values (t/m^3) based on decay stage, deadwood type (stump or log), and group (conifer or broadleaf).

$$B_i = V_i \cdot WBD \tag{5}$$

The carbon stock C_i (t C/ha) of each living tree was estimated by multiplying its biomass B_i (t/ha) by the carbon fraction of dry matter (0.48) as in Eq. 6, following IPCC standards[77].

$$C_i = B_i \cdot 0.48 \tag{6}$$

The carbon stock associated with each deadwood unit C_i (t C/ha) was obtained by multiplying the unit biomass B_i (t/ha) by an average carbon fraction of dry matter factor as in Eq. 7, following reference literature[80].

$$C_i = B_i \cdot 0.485 \tag{7}$$

Finally, the plot-level stock for each carbon pool (standing living trees, standing deadwood and lying deadwood) was obtained by summing the carbon of each tree/fragment (t C/ha) in each sampling unit (Eq. 8). In total, plot-level stock data were assessed for 2445 plots for standing living trees, 1458 plots for standing deadwood, and 1654 plots for lying deadwood.

$$C_{tot} = \sum\nolimits_i^n (C_i) \tag{8}$$

The three carbon pools did not show clear patterns of covariation. With the exception of unmanaged forests, mostly displaying high amounts of carbon across the three pools, a great variation of the three carbon stocks was evident for different forest categories and management regimes (Figs. 7 and 8).

Statistical analyses

The carbon stock for the standing living trees, standing deadwood and lying deadwood carbon pools in each plot were logarithm base 10 transformed to achieve a normal distribution. We ran six BRTs to assess the relationship between the scaled species richness of each taxonomic group as response variable and carbon stocks, along with other selected predictors at the plot level (Table 2).

The selection of predictors was based on their ecological relevance for the diversity of the selected taxonomic groups, as well as their availability and consistency across the entire dataset. The forest category[81] was included to account for: broad-scale climatic conditions, biogeographical patterns, and effects related to canopy features. Forest categories are defined by dominant tree species, which play a significant role in shaping community patterns by influencing structural attributes, light availability and soil characteristics[82], leading to a different spatial and temporal resource distribution for several taxonomic groups. The sampling units in our database encompassed a wide range of forest categories, including boreal forests (1), hemiboreal forests and nemoral coniferous and mixed broadleaved-coniferous forests (2), alpine coniferous forests (3), acidophilous oak and oak-birch forests (4), mesophytic deciduous forests (5), beech forests (6), mountainous beech forests (7), thermophilous deciduous forests (8), broadleaved evergreen forests (9), mire and swamp forest (11), non-riverine alder, birch, or aspen forests (13), and plantations and self-sown exotic forests (14)[81]. To better capture broad-scale climatic conditions, elevation (in meters) was included as a predictor variable in the model. Elevation is a key driver of temperature, precipitation, and soil properties, which shape species composition and biodiversity

Table 2 | Variables used in the boosted regression trees. Name, type, role in the model and source (BRTs)

Variable	Type	Selection	References
Scaled species richness	Continuous	Response	74
C stock standing alive	Continuous	Predictor	From raw data
C stock standing dead	Continuous	Predictor	From raw data
C stock lying dead	Continuous	Predictor	From raw data
Elevation	Continuous	Predictor	From raw data
Forest category	Categorical	Predictor	81
Silvicultural system	Categorical	Predictor	84
Protocol	Categorical	Predictor	66

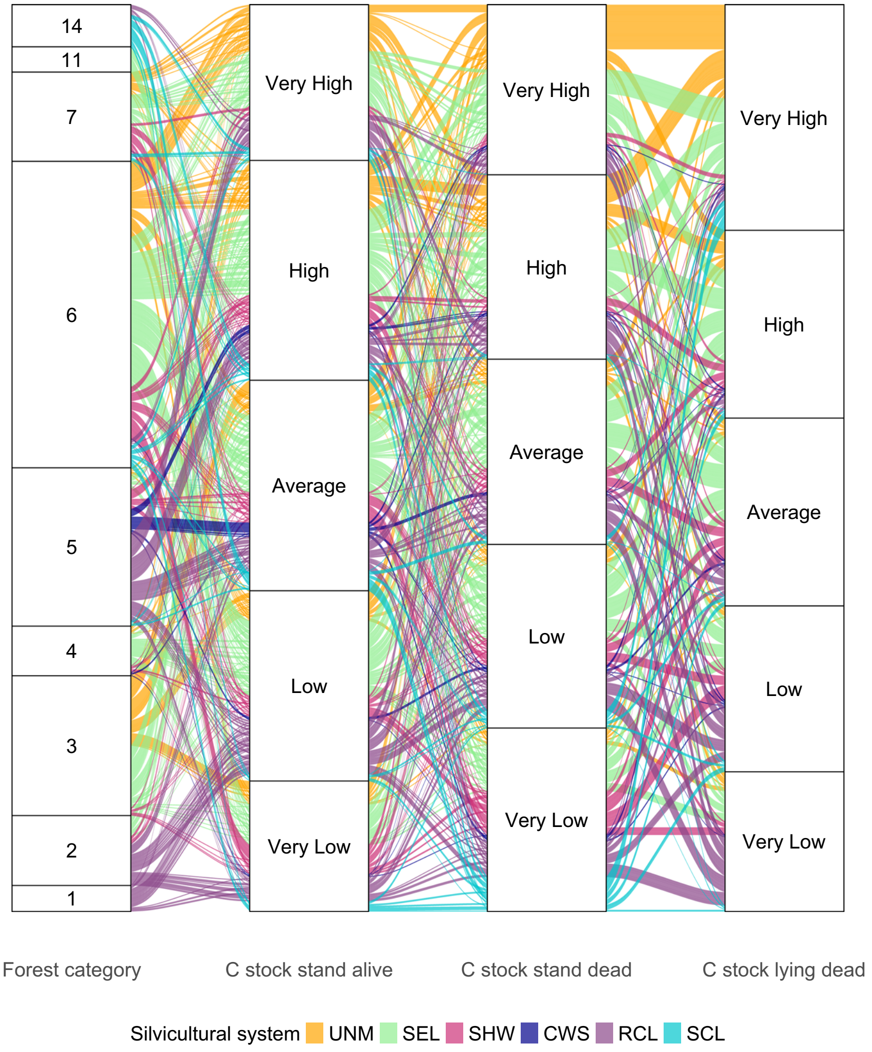

Fig. 8 | Alluvial plot of the distribution of sampling units across forest categories of aboveground carbon stocks. Each color represents a silvicultural system: CWS coppice with standards, RCL retention clearcutting, SEL selection cutting, SHW shelterwood, SCL simple clearcutting, and UNM unmanaged. Forest categories are numbered as follows: 1 = boreal forest, 2 = hemiboreal forest and nemoral coniferous and mixed broadleaved-coniferous forest, 3 = alpine coniferous forest, 4 = acidophilous oak and oak-birch forest, 5 = mesophytic deciduous forest; 6 = beech forest; 7 = mountainous beech forest, 11 = mire and swamp forest, and plantations and self-sown exotic forest (14). Carbon stocks were categorized into five levels (very low to very high) using quantile-based classification, where each category represents 20% of the data distribution. Sampling units with missing values for one or more carbon stocks were excluded from the graph to improve clarity. Source data are provided as a Source data file.

patterns[83]. The decision to include elevation rather than broad-scale climatic variables was based on exploratory analyses showing that, within our dataset, mean annual temperature (MAT) and mean annual precipitation (MAP) were definitely homogeneous within most forest categories (interquartile range for MAT and MAP was 2.11 °C and 292 mm, respectively). Only mountain forests, i.e., alpine coniferous forests (category 3) and mountainous beech forests (category 7), showed a substantially higher variability, up to 3.83 °C and 664 mm. Based on these patterns, we deemed elevation as an ecologically meaningful predictor able to capture residual climatic variation in the database that is not accounted for by forest categories. The silvicultural system for each sampling unit was included as a categorical predictor. This variable refers to the method by which trees in a forest are harvested and replaced through regeneration or planting, resulting in distinct forest stands for both structural and compositional characteristics. Different silvicultural practices have varying effects on forest structure, leading to different resource and habitat availability for several taxonomic groups[15,20,35,67]. The classification used in this study was based on a harmonization effort on the same database by Trentanovi et al. 2023[84]. We included the following terms referring to the "form of treatment" (Tab. 2), explicitly CWS = coppice with standards, RCL = retention clearcutting, SEL= selection cutting, SHW = shelterwood, SCL = simple clearcutting, and UNM = unmanaged. The sampling protocol was included as a categorical predictor to account for variations in data collection methodologies across different countries and forest types, as differences in sampling methods could influence diversity estimates, potentially introducing inconsistencies across the database. For a detailed overview of the different protocols, see Tab. 2 in Burrascano et al.[29]. The distribution of sampling units across forest categories, silvicultural systems and carbon stocks highlights the wide range of forest structures and management approaches represented in the database, with a certain influence of management strategies on carbon storage dynamics (Fig. 8).

BRTs effectively model complex non-linear relationships and enable reliable identification of relevant variables and interactions, with a strong predictive performance and robustness against overfitting, missing data, and collinearity[85]. The model setting involves finding the optimal combination of four main parameters ("number of trees", "learning rate", "tree complexity" and "bag fraction") to minimize predictive error: the number of trees refers to the total count of individual decision trees, influencing both predictive performance and model stability; the learning rate controls the contribution of each tree to the final model, providing a balance between accuracy and the risk of overfitting; tree complexity determines the maximum depth of each tree, affecting the model's ability to capture complex patterns in the data; and the bag fraction specifies the proportion of the training set randomly selected for each iteration[85]. We used the "gbm.step" function from the "dismo" package[86] to test various BRT settings by combining different learning rates (0.001, 0.0025, and 0.005), tree complexity values (2, 3, and 5), and bag fraction values (0.5, 0.75), and assess the relative importance of each explanatory variable, calculated as the total reduction in model deviance attributable to that variable, averaged across all trees and rescaled to a total of 100%[85]. We used the Gaussian error distribution.

We selected parameter combinations that resulted in models with over 1000 trees and evaluated their performance using three metrics, following the approach of Napoleone and colleagues[87]: (i) explained deviance (D^2), calculated as $D^2 = 1-(\text{residual deviance/total deviance})$. This metric ranges from zero to one, where a value of one indicates a perfect fit, and is considered a generalization of the traditional R^2 used in regression analysis[87]; (ii) the cross-validated mean correlation coefficient, which measures the average correlation between the training and test datasets; and (iii) self-statistics, which assesses the correlation between predicted and observed values. These correlation metrics are commonly used to evaluate the efficiency of BRTs[22,87].

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data used for this study are available upon request using the data explorer within the Cost Action website (https://www.bottoms-up.eu/en/results/data-explorer.html). Source data are provided with this paper.

Code availability

The code used in this study is available at Code Ocean: https://doi.org/10.24433/CO.9463772.v2.

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Author contributions

L.B. and S. Bu contributed to the data preparation, analysis and writing of the introduction, methods, results and the discussion of the manuscript. E. Hae, Y.P., and N.K. contributed greatly to the structuring of the paper.

F.N. and E.A. contributed to the methodological section. S. Bo and T.L. contributed to the discussion. F.C. worked on the harmonization of the database we used for this research. C.A., F.A., C.B., G.B., A.C., P.D.S., I.D., D.D., M.F., P.G., M.G., J.H.-C., E. Hol, J. Hof, J. Hos, I.G.M., P.J., K.J., S.K.R., D.K., T.K., J. Ma, A.M., M.M., J. Mu, B.N., P.O., Z.P., P.S., T.S., K.S., M.S., A.T., F.T., G.T., M.U., K.V., M.W., and W.W.W. contributed to the manuscript through fundamental feedback to the proposed draft. All authors have been involved in the collection of the data and building of the dataset.

Competing interests

The authors declare no competing interests.

Additional information

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