Forest Ecology and Management 605 (2026) 123527

Contents lists available at ScienceDirect

Forest Ecology and Management

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

As forests reclaim the land: Latitudinal variations in carbon-biodiversity trade-offs under natural forest expansion in Italy

Lorenzo Orzan [a,b,*], Antonio Tomao [a], Gabriele Antoniella [c], Gianmaria Bonari [d,e], Valentino Casolo [a,e], Tommaso Chiti [c], Paolo Cingano [a,b], Alessandro Foscari [a], Guido Incerti [a,e], Speranza Claudia Panico [a,e], Natalie Piazza [a], Giacomo Trotta [a,f], Giorgio Alberti [a,d]

[a] *Department of Agri-food, Environmental and Animal Sciences, University of Udine, via delle Scienze 206, Udine 33100, Italy*
[b] *Department of Life Sciences, University of Trieste, via Weiss 2, Trieste 34128, Italy*
[c] *Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, via San C. De Lellis s.n.c, Viterbo 01100, Italy*
[d] *Department of Life Sciences, University of Siena, Italy*
[e] *National Biodiversity Future Center, Piazza Marina, 61, Palermo 90133, Italy*
[f] *Biodiversity Research Institute (IMIB), University of Oviedo – CSIC - Principality of Asturias, Mieres, Asturias, Spain*

ARTICLE INFO

Keywords:
Carbon stock
Climate change
Chronosequence
Land abandonment
Natural reforestation
Plant diversity

ABSTRACT

Spontaneous forest expansion following land abandonment can play a key role in achieving European targets for climate-change mitigation and biodiversity conservation. Understanding how biodiversity relates to carbon (C) stocks across successional stages can inform management strategies that simultaneously promote species diversity and C sequestration, thereby optimizing land use for ecosystem multifunctionality. We analysed 16 chronosequences spanning five successional stages, from meadows and pastures to mature forests (up to ~75 years since abandonment), organized into four clusters along a latitudinal gradient in Italy, encompassing the Alpine, Continental, and Mediterranean biogeographical regions. We quantified vegetation, deadwood, and soil C pools and calculated diversity indices for herbaceous plant species. Linear and generalized linear mixed models were used to assess successional stage and site effects on C stocks and diversity indices. Total ecosystem C increased along succession, driven primarily by tree biomass, reaching 195–289 Mg C ha^{-1} in late-successional forests. Soil C showed no clear successional trend, with weak or site-specific patterns. Herbaceous species richness and diversity peaked in managed meadows/pastures and early encroachment stages but declined towards closed-canopy forests in three sites. By contrast, a U-shaped pattern emerged in the southernmost site. Consequently, the C–diversity relationship was predominantly negative, except for the non-linear response observed in the Mediterranean site. Overall, spontaneous reforestation promotes C storage but often reduce herbaceous plant diversity, revealing potential trade-offs between climate mitigation and plant diversity. However, under favourable environmental conditions, partial recovery of plant diversity in late-successional forests may occur, suggesting for win-win management policies.

1. Introduction

Forest ecosystems play a pivotal global role in addressing two of the most pressing environmental challenges of our time: biodiversity loss and climate change (Grassi et al., 2017; Kikstra et al., 2022; Shin et al., 2022). They support most terrestrial biodiversity (FAO and UNEP, 2020) and provide essential ecosystem services for human well-being (Mori et al., 2017; Thompson et al., 2011), including carbon (C) sequestration and storage in both above- and below-ground pools (Friedlingstein et al., 2020; Pan et al., 2024).

While forest cover continues to decline in many parts of the world, particularly in tropical and sub-tropical regions, due to ongoing deforestation and land-use change (FAO and UNEP, 2020), Europe has experienced a steady increase in forest area over recent decades, mainly driven by natural succession after land abandonment (FAO and UNEP, 2020; Palmero-Iniesta et al., 2021). This spontaneous forest expansion is

---

* Corresponding author at: Department of Agri-food, Environment and Animal Sciences, University of Udine, via delle Scienze 206, Udine 33100, Italy.
E-mail address: lorenzo.orzan@phd.units.it (L. Orzan).

https://doi.org/10.1016/j.foreco.2026.123527
Received 28 November 2025; Received in revised form 8 January 2026; Accepted 9 January 2026

particularly relevant for achieving European targets related to global warming mitigation and biodiversity conservation (Pugh et al., 2019; Fayet and Verburg, 2023). Natural reforestation now affects tens of thousands of square kilometres (Frei et al., 2024) and is expected to continue, as rural depopulation and agricultural abandonment persists—some projections suggests that up to 15 % of cultivated land present in 2000 will be abandoned by 2030 (Verburg and Overmars, 2009; Castillo et al., 2018). These naturally expanding forests are increasingly recognised as potential nature-based solutions (NBSs) (Seddon et al., 2020), offering opportunities to enhance C sequestration and provide habitat for a wide range of plants, animals, and fungi, but can also generate trade-offs, such as the increase in fire risk (Oliveira et al., 2017), landscape homogenization (Jongman, 2002; Cimini et al., 2013), and reduced water availability (López-Moreno et al., 2011). Moreover, the ecological responses to land abandonment are highly context-dependent and remain debated (Nadal-Romero et al., 2023).

To fully characterize total ecosystem C stocks, it is essential to account for all major pools: living biomass, dead organic matter, and soil (Penman et al., 2003). Living biomass, litter and woody debris generally increases along successional gradients (Alberti et al., 2008; Pellis et al., 2019). Soil organic C (SOC) dynamics are more variable, depending on local climate and previous land use (Alberti et al., 2008; Jackson et al., 2002; Pellis et al., 2019). SOC generally increases when succession follows croplands (Guo and Gifford, 2002; Yang et al., 2016; Bell et al., 2021), whereas patterns from pastures or meadows are variable. In fact, previous studies show pastures-to-forest transition often reduces SOC (Guo and Gifford, 2002; Alberti et al., 2008; Fino et al., 2020), especially under high precipitation (Jackson et al., 2002). Some evidence also indicates that soil C tends to remain stable especially in early abandonment stages (Nezhad et al., submitted).

While natural forest expansion's role in climate mitigation is established, effects on plant diversity are context-dependent (Frei et al., 2024). In temperate regions, plant diversity often follows a U-shaped trajectory during succession, namely lower in mid-successional dense stands and higher in early and late stages (Hilmers et al., 2018). In arid/semi-arid regions, diversity may peak at mid-succession (Qianwen et al., 2022). Tropical forests often increase in richness in later stages (Salete Capellesso et al., 2021; van der Sande et al., 2024), whereas Mediterranean and Alpine sites may lose species (Amici et al., 2013; Höchtl et al., 2005). Grassland degradation and reforestation can thus negatively impact biodiversity and ecosystem multifunctionality (Prangel et al., 2023).

Understanding how biodiversity relates to C pools across successional stages can help balance diversity conservation and C sequestration strategies (Van de Perre et al., 2018). Evidence for positive plant diversity–C relationships derives mainly from tropical forests, and primarily focuses on tree species (Cavanaugh et al., 2014; Poorter et al., 2015; Sullivan et al., 2017). Relationships vary across taxa, with positive associations often limited to trees (Van de Perre et al., 2018), and is weak or variable in temperate forests (Sabatini et al., 2019; Potter and Woodall, 2014; Wu et al., 2015). Thus, previous findings highlight the complexity of the biodiversity–C relationship and underscore the need for context-specific analyses. Secondary successions provide natural laboratories to investigate these relationships over time.

Successional dynamics are commonly investigated using two main approaches: (i) permanent or semi-permanent plots with long-term observation and (ii) chronosequences, based on a space-for-time substitution approach (Pickett, 1989; Řehounková et al., 2024). Here, we adopted a space-for-time substitution approach to investigate trends in herbaceous plant diversity and C stocks along secondary successional gradients following the abandonment of meadows and pastures. We established 16 chronosequences, each composed of five successional stages, organized into four clusters representing distinct sites along a latitudinal gradient in Italy (Friuli Venezia Giulia, Tuscany, Abruzzo, and Basilicata administrative regions), thus encompassing the Alpine, Continental, and Mediterranean biogeographical regions. In total, 80 plots were sampled, covering approximately 75 years of natural succession. We hypothesised that (i) total ecosystem C stock would increase along the successional gradient, with living tree biomass progressively replacing soil as the dominant C pool; (ii) plant diversity would decline from open habitats to closed-canopy forests, primarily due to the loss of light-demanding species, and (iii) trade-offs would emerge between C accumulation and plant diversity, with potential management implications for balancing climate change mitigation with the preservation of species-rich open habitats.

2. Materials and methods

2.1. *Study sites*

The study was conducted along a latitudinal gradient of about 700 km in Italy (Fig. 1). Four study sites were selected in different Italian administrative regions for investigation: Friuli Venezia Giulia, Tuscany, Abruzzo, and Basilicata. The main climatic characteristics of each study site, including mean annual temperature and total precipitation, are presented in Table 1.

The northernmost site, located in Friuli Venezia Giulia region, has the highest mean annual temperature and precipitation. Forest vegetation is dominated by European ash (*Fraxinus excelsior* L.) and sycamore maple (*Acer pseudoplatanus* L.), with additional presence of hop hornbeam (*Ostrya carpinifolia* Scop.), chestnut (*Castanea sativa* Mill.), and hazel (*Corylus avellana* L.). In the Tuscany site, the dominant species are Turkey oak (*Quercus cerris* L.) and European beech (*Fagus sylvatica* L.), with less frequent occurrences of hop hornbeam, sycamore maple, and wych elm (*Ulmus glabra* Huds.). The site in Abruzzo, which is the highest in elevation and the coldest, is dominated by European beech and Turkey oak. The same tree species also dominate the forests of the southernmost site, located in the Basilicata region.

The four sites are located in areas belonging to the beech forest vegetation series (Blasi and Rosati, 2010) and share a common history of significant depopulation beginning in the 1950s, which led to the widespread abandonment of grasslands, meadows, pastures and cultivated land (Malandra et al., 2018; Agnoletti et al., 2022).

2.2. *2.2 Sampling design and data collection*

For each site, four chronosequences were identified using historical georeferenced orthophotos following the approach proposed by Panico et al., (2025). Through photointerpretation, we identified landscape patches where land use transitioned from meadow/pasture to forest over the past 70 years. A time series of orthophotos dated 1954, 1978, 2000, and 2020 was analysed to detect these changes. The age of each successional stage was assigned as the midpoint between the dates of the two images used to documenting the transition. This procedure allowed us to reconstruct five stages (Fig. 1): (i) patches still managed as meadows or pastures in 2024 (stage 0); (ii) newly established forests that expanded between 2000 and 2020 (stage I; about 14 years since abandonment); (iii) intermediate forests that developed between 1978 and 2000 (stage II; about 35 years since abandonment); (iv) late-successional forests established between 1954 and 1978 (stage III; about 58 years since abandonment); and (v) old forests present since at least 1954 (stage IV; about 75 years since abandonment).

A total of 80 plots were sampled in the field (4 sites × 4 chronosequences × 5 succession stages), with all forest stages restricted to undisturbed stands showing no signs of recent management. In each successional stage, a circular plot with a 13 m-radius was established for dendrometric data collection following the protocol of the Italian National Forest Inventory (Gasparini et al., 2022). Within each plot, all trees with a diameter at breast height (DBH) greater than 9.5 cm were measured, while those with a DBH between 4.5 cm and 9.5 cm were surveyed within a 4-m radius concentric subplot. For each tree, species identity and vitality (living, unbroken snag, broken snag, stump) were

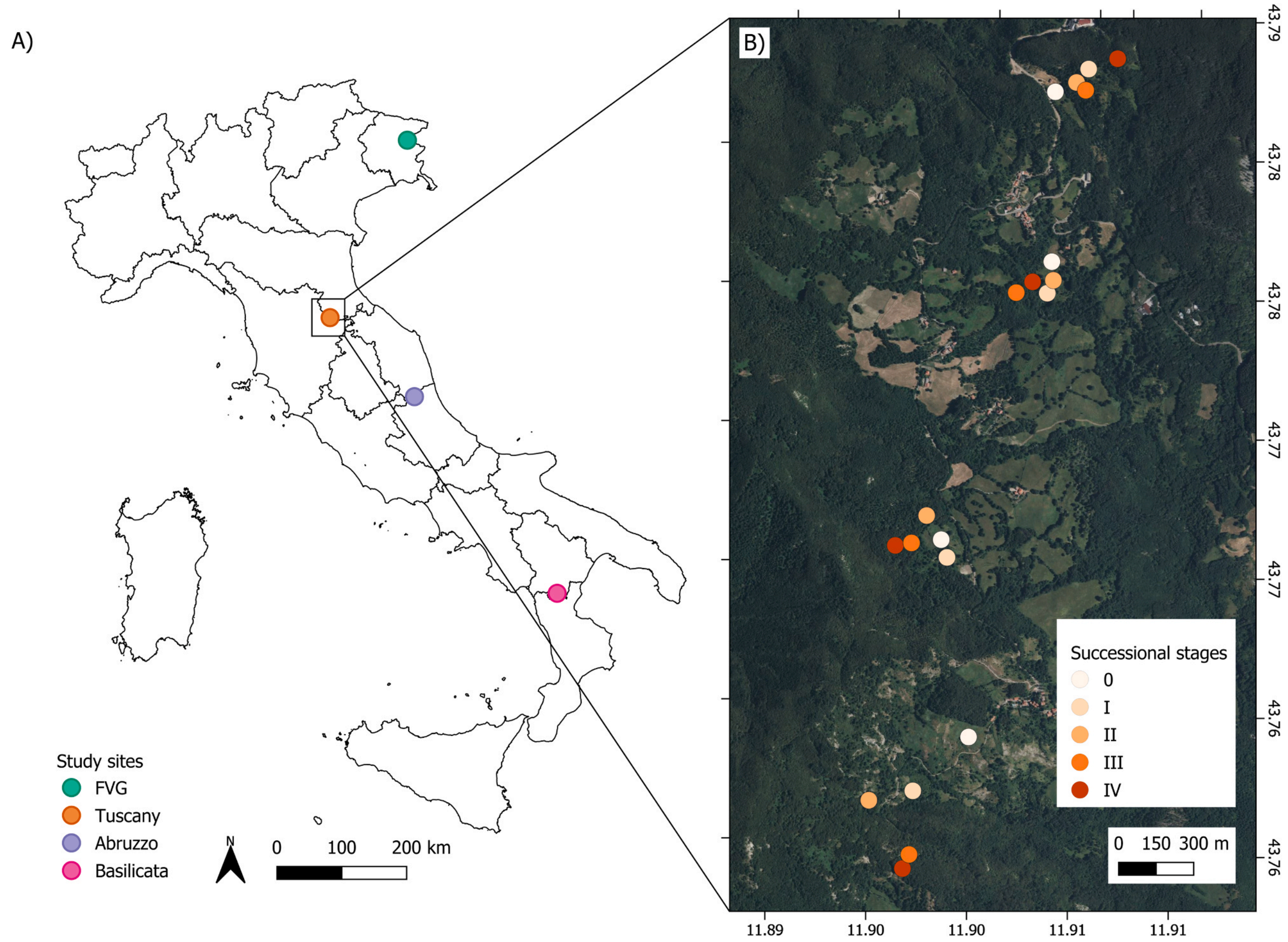

Fig. 1. Panel A shows the location of the four study sites distributed in Italy. Coloured dots indicate the centroid of each site: Friuli Venezia Giulia (FVG; green), Tuscany (orange), Abruzzo (blue), and Basilicata (purple). Panel B illustrates the sampling design using Tuscany as an example, in which plots area clustered into four chronosequences and shades of orange colour represent different successional stages (0, I, II, III, IV, V). Each site follows the same chronosequence structure. Coordinates are reported in EPSG:4326 (WGS84).

Table 1

Characteristics of the four study sites. For each site, mean elevation, mean annual temperature, mean annual precipitation, and biogeographical region (EEA, 2024) are reported. Coordinates correspond to the centroids of the chronosequences (EPSG: 4326; WGS84). Climatic values are long-term means (WorldClim v2; Fick and Hijmans, 2017).

Site	Coordinates (WGS84)	Mean elevation (m a.s.l)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Biogeographical region
Friuli Venezia Giulia	46°26’N, 13°31’ E	580	11	2660	Alpine
Tuscany	43°77’N, 11°90’ E	900	10	1460	Continental
Abruzzo	42°70’N, 13°54’ E	1180	9	890	Continental
Basilicata	39°97’N, 16°18’ E	1060	10	890	Mediterranean

recorded; total height was measured for all stumps and snags only and for a subset of living trees distributed in different diameter classes. For each piece of lying deadwood with a minimum diameter of 10 cm, the total length and the diameters at the upper and lower ends were measured, and decay status was classified into five classes (Di Cosmo et al., 2013). Woody debris with diameters between 2.5 cm and 10 cm was surveyed using the line-intersect method proposed by Harmon and Sexton (1996), applying an equilateral-triangle transect with 10 m sides, centred within each plot. Herbaceous and shrub species height was measured every 2 m along each side of the triangular transect (15 sampling points in total) to estimate plot-level biomass following Ascoli et al. (2020). Litter was collected in 40 cm × 40 cm subplot at the centre of each side of the triangular transect. After litter removal, soil cores (5 cm inner diameter, 0–30 cm depth) were collected using a split-tube soil corer (Eijkelkamp, The Netherlands) and its two main layers, the organic (O) and the mineral (A) horizons, were identified by colour differences in the field. After recording their thickness, they were physically cut at the boundary and stored in different bags for laboratory analysis.

Vegetation surveys were conducted in three 5 m × 5 m subplots randomly located within the 13 m radius plot. In each of these subplots, the percentage cover of trees, shrubs, and herbaceous layer, was visually estimated. The surveys were carried out in late spring/early summer.

2.3. Biomass and carbon stocks assessment

2.3.1. Vegetation biomass

2.3.1.1. Standing trees and their roots. The biomass of living trees was estimated with the R package *allodb* (Gonzalez-Akre et al., 2022), using the individual dendrometric data collected in the field. Total aboveground tree biomass at the plot level was then calculated as the sum of all surveyed trees and expressed as Mg per hectare [Mg ha^{-1}], considering the plot size. The root biomass per hectare of standing trees at the plot level was estimated by multiplying the aboveground tree biomass by the root-to-shoot ratio reported by Eggleston et al. (2006).

2.3.1.2. Shrubs and their roots. Shrub biomass per hectare was estimated using allometric equations for the dominant shrub species present in each plot (Riccardi et al., 2007; Smith and Brand, 1983). These species- or genus- specific equations use average shrub cover, calculated as the ratio between the number of sampling points with shrub presence and the total number of points along the transect, and mean shrub height (for more details see Alberti et al., 2024). For those lacking species-specific equations, total biomass was estimated using the general equation for macro-phanerophytes by De Cáceres et al. (2019). Shrub root biomass was calculated using the same approach as for the roots of standing living trees.

2.3.1.3. Herbaceous species and their roots. Grass and herb biomass was estimated using height-based allometric equations: the equation from Halpern et al. (1996) for herbaceous vegetation shorter than 20 cm; the equation from Bovio and Ascoli (2013) for herbaceous vegetation between 20 cm and 40 cm; and the one from Mou (2015) for herbaceous vegetation taller than 40 cm. Grass and herb root biomass was calculated using a root-to-shoot ratio of 4, as suggested by Eggleston et al. (2006) for cold temperate and warm temperate wet grasslands.

The total vegetation biomass [Mg C ha^{-1}] was then obtained as the sum of the aboveground and belowground components of standing trees, shrubs, and herbaceous species.

2.3.2. Deadwood biomass

2.3.2.1. Snags, stumps, and their roots. Snag and stumps' biomass was quantified applying a biomass reduction factor to correct the potential overestimation resulting from lower wood density in different decay stages, following Bitunjac et al. (2023). The biomass of snag and stump roots was determined by applying the root-to-shoot ratio from Eggleston et al. (2006) on the biomass of a tree of DBH equal to the diameter of the snag or stump calculated using the *allodb* R package.

2.3.2.2. Lying deadwood and woody debris. The biomass of lying logs with a diameter > 10 cm was quantified using a formula based on the equation of a truncated cone, also considering the basic density of lying deadwood decay class retrieved from Bitunjac et al. (2023).

The biomass of woody debris (diameter>2.5 cm and < 10 cm;) was calculated following Harmon and Sexton (1996), using data surveyed using the line-intersect method in the field (three linear transects of 10 m each arranged as a triangle in the centre of the plot).

After scaling all the biomass data to the hectar, the total deadwood biomass $\left[\mathrm{Mgha}^{-1}\right]$ was calculated by summing all the individual components, namely snags and stumps (including their roots), lying logs, woody debris.

2.3.3. Vegetation and deadwood carbon stock quantification

Vegetation C stocks [Mg C ha^{-1}] were obtained by applying a conversion factor of 0.47 to vegetation biomass, corresponding to the average C content of living trees (Eggleston et al., 2006).

Considering that the C fraction remains largely constant across decay stages, an average conversion factor of 0.475 for broadleaves and 0.505 for conifers was used to obtain deadwood carbon stock [Mg C ha^{-1}] from the total deadwood biomass (Bitunjac et al., 2023).

2.3.4. Soil carbon stock quantification

Soil C stocks were quantified separately for organic and mineral soil horizons. Bulk density was determined from soil cores by recording the fresh weight of the entire sample and separating the coarse fraction (>2 mm) from the fine earth fraction through sieving. A subsample of the fine earth fraction was oven-dried at 70 °C for 48 h to determine soil moisture content by gravimetric method (FAO., 2023). Bulk density was then calculated by relating the oven-dry mass of the fine earth fraction to the volume of the sampled soil horizon.

From each fine earth subsample, a portion was pulverized with a ball mill and analysed for carbon concentration (%C) using a CHN elemental analyser (Elementar Italia S.r.l.; Vario Micro Tube CHNSO). Prior to analysis, samples were treated with HCl (1:2 v/v) to remove carbonates (Nieuwenhuize et al., 1994). Each measurement was performed in triplicates. Soil carbon stocks for each horizon were calculated by combining bulk density, horizon thickness, and measured carbon concentration, and expressed on an area basis.

Full details of procedures and equations used are provided in the Supplementary Materials 2 (SM2).

2.4. Plant diversity indices

After averaging cover values of the three subplots recorded for each plot, three α diversity indices, namely species richness (S), Shannon diversity (H) and Pielou's evenness (J), were calculated for the herbaceous plant species using the 'diversity' function in the *vegan* R package (Oksanen et al., 2001).

2.5. Statistical analysis

All statistical analyses were performed in R environment (R Core Team, 2024). To account for the hierarchical sampling design, we used linear mixed-effects models (LMMs) and generalized linear mixed-effects models (GLMMs), including the chronosequence as a random effect in all models. Vegetation and total C stocks displayed heteroscedasticity and skewed distributions; therefore GLMMs with a Gamma distribution and log-link function were fitted, following the recommendations of Wilson et al. (2025). Deadwood C stocks also showed heteroscedasticity and deviations from normality; since a Gamma GLMM did not provide an adequate fit, this variable was modelled using a log-transformed LMM. By contrast, soil C stocks displayed an approximately symmetric distribution with homogeneous variance, making Gaussian LMM appropriate. Diversity indices (species richness, Shannon diversity, and Pielou's evenness) were modelled using Gaussian LMMs, as residual inspection indicated no strong deviation from normality. For all response variables, Successional stages (five classes: 0, I, II, III, and IV) and Site (Friuli Venezia Giulia, Tuscany, Abruzzo, Basilicata) were included as fixed effects, along with their interaction (Successional stages × Site). Model assumptions were checked using the DHARMa package (Hartig, 2024). Post-hoc comparisons among successional stages within each site, and among sites within each successional stage, were performed using estimated marginal means (*emmeans* package; Lenth, 2024) with Sidak adjustment for multiple testing. The significance of the fixed effects on C stocks and diversity indices was assessed using ANOVA based on F-tests for LMMs and Wald χ^2 tests with type-III analysis of variance for GLMMs, allowing evaluation of the relative contribution of predictors and their interactions to observed successional patterns.

To explore the relationship between herbaceous plant diversity indices and total C stock, orthogonal second-degree polynomial regression models were fitted separately for each site following Van de Perre et al. (2018). This approach enabled testing whether the relationship was best described by a linear or a quadratic form. When only the linear term was significant, the linear model was reported; when the quadratic term was significant, the polynomial model was reported. Model fit was evaluated using the coefficient of determination (R^2) and the significance of regression terms.

3. Results

3.1. Carbon stocks

Excluding the managed stage (stage 0), where SOC is the dominant pool, living trees represented the main C compartment across all successional stages (Fig. 2), particularly in old forests, where mean values reached the maximum of 247 Mg C ha^{-1} in Basilicata. Soil C was the second largest contributor throughout succession, while herbaceous vegetation contributed substantially only to the earlier successional stages and declined sharply in later successional stages. Deadwood C increased with stand age but remained, together with shrubs, a minor component throughout.

Total ecosystem C stocks increased across successional stages in all sites (Successional stage effects: $\chi^2 = 81.8$, df = 4, p-value < 0.001; Fig. 3 E; Table S4.2). Significant effects were also detected for Site ($\chi^2 = 24.6$, df = 3, p-value < 0.001; Table S4.2), and for Site × Successional stage interactions ($\chi^2 = 59.9$, df = 12, p-value < 0.001; Table S4.2). Post-hoc comparisons showed that, at stage 0, the Basilicata site started from significantly lower C stocks than Friuli Venezia Giulia and Abruzzo (p-value = 0.0001 and p-value = 0.0002 respectively), while Tuscany displayed intermediate values. At later successional stages, Basilicata reached significantly higher vegetation C stocks than Abruzzo (p-value = 0.0062), with Friuli Venezia Giulia and Tuscany occupying intermediate positions. Basilicata showed the steepest accumulation, reaching nearly 290 Mg C ha^{-1} in stage IV.

Vegetation C was the largest C pool - showed significant effects of Successional stage ($\chi^2 = 105.9$, df = 4, p-value < 0.001; Table S1.2), Site ($\chi^2 = 11.7$, df = 3, p-value = 0.008; Table S1.2) and their interaction ($\chi^2 = 49.1$, df = 12, p-value < 0.001; Table S1.2). Estimated means increased from stage 0 to the oldest stage of the chronosequence (Fig. 3A). Significant differences in deadwood C across the chronosequence were only found in Tuscany, where dead organic matter increased progressively. Across sites, significant differences emerged only in successional stages I and II, with Friuli Venezia Giulia displaying higher predicted values (Fig. 3 B; Table S2.3).

Soil C displayed a distinct pattern. Successional stage alone had no significant effect (F = 1.90, p-value = 0.13; Table S3.2), whereas the effect of Site (F = 15.8, p-value < 0.001; Table S3.2) and Site × Successional stage were significant (F = 2.56, p-value = 0.011; Fig. 3 C; Table S3.2). Across successional stages, Friuli Venezia Giulia and

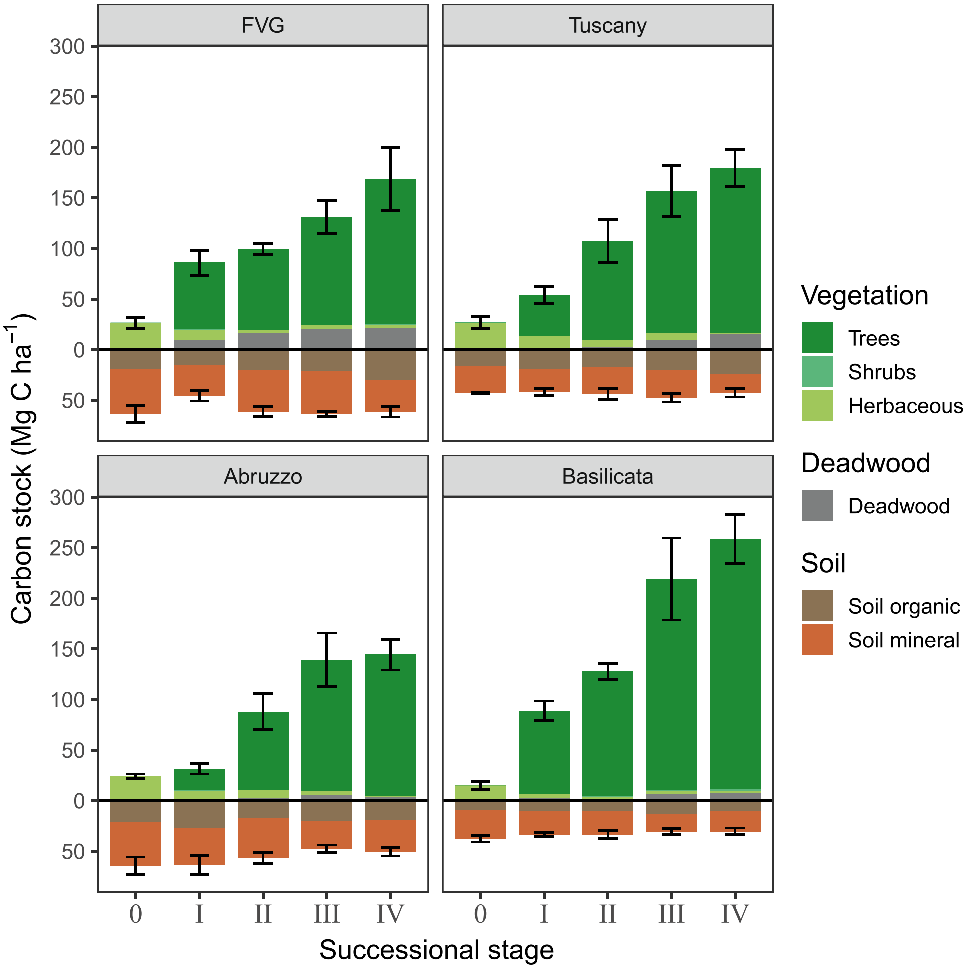

Fig. 2. Barplots of mean C stocks partitioned among different pools across successional stages in the four study sites: Friuli Venezia Giulia (FVG), Tuscany, Abruzzo, and Basilicata. Positive values represent vegetation and deadwood C compartments: living trees (including roots), shrubs (including roots), herbaceous species (including roots), and deadwood (coarse and fine woody debris, dead trees, and stumps). Negative values, plotted symmetrically for visualization, correspond to soil C pools: soil C in the organic horizon (soil organic) and soil C in the mineral horizon (soil mineral). Black bars represent aggregated standard error for vegetation and soil C pools. Shrub C stocks are not visually apparent in the barplots due to their low contribution.

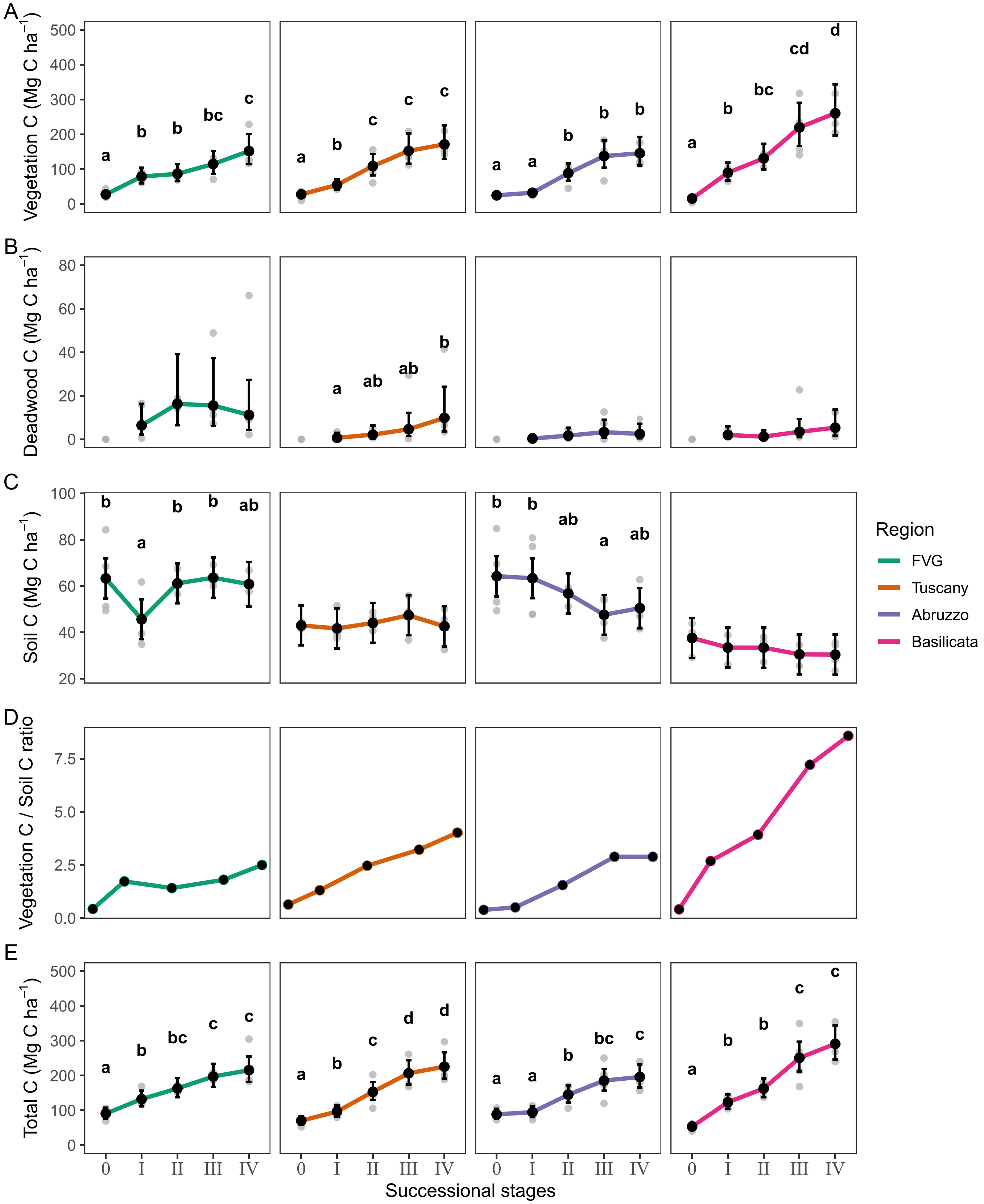

Fig. 3. Trends in vegetation (A), deadwood (B), soil (C), and total ecosystem C stocks (E) [Mg C ha^{-1}] across chronosequences in the four study sites. Values represent predicted means (± 95 % confidence intervals) derived from generalized linear mixed-effects models (vegetation and total ecosystem C) and linear mixed-effects models (deadwood and soil C). Lowercase letters denote significant pairwise differences among stand ages within each study site (Sidak-adjusted post-hoc tests). Grey points represent raw plot-level observations. The ratio between vegetation and soil C predicted values is also shown (D). Site-specific trends are represented by different colours: Friuli Venezia Giulia (FVG; green), Tuscany (orange), Abruzzo (blue), and Basilicata (purple).

Abruzzo generally maintained the highest soil C stocks, Tuscany had intermediate values, and Basilicata consistently had the lowest. In Friuli Venezia Giulia, soil C showed a marked trajectory: a significant decrease from stage 0 to stage I ($p\text{-value} < 0.05$), followed by a recovery to values comparable to the initial level in later successional stages (about 60 Mg C ha^{-1}). The ratio between vegetation and soil C stocks generally increased along the succession, indicating greater accumulation in living biomass compared to soil (Fig. 3 D). While this ratio typically reached values of about 2.5 – 4 in the stage IV, the Basilicata site showed a much stronger imbalance, with vegetation C stocks exceeding soil C stocks by a factor of 8.6. Full summaries of all statistical models are provided in the Supplementary Materials 1 (SM1; from Table S1.1 to Table S4.3).

3.2. *Plant diversity*

Across the four study sites, a total of 384 plant species were recorded throughout the chronosequences. Plant species richness at the site level increased from South to North, with Friuli Venezia Giulia hosting the highest number of species (197). Herbaceous species richness ranged from 106 species in Basilicata to 167 in Friuli Venezia Giulia, while shrub richness varied from 7 species in Abruzzo to 13 in Basilicata. The lowest number of tree species was found in Abruzzo (9 species), followed by Basilicata (14), with both Friuli Venezia Giulia and Tuscany hosting 17 species. Venn diagrams (Figure S1) show that the proportion of herbaceous species shared between all four sites across successional stages is relatively low (6 % of total species; 19 species). Tuscany and Abruzzo were the most similar in herbaceous species composition, whereas Basilicata and Friuli Venezia Giulia showed the lowest overlap. Friuli Venezia Giulia emerged as the site with the highest number of unique species (119), a pattern consistent across individual successional stages. Within each successional stage, the number of species shared between any two sites generally did not exceed 20, except for Tuscany and Abruzzo, which shared 31 species at stage 0, and 27 species in stages I, II, and III. The lowest levels of overlap were observed between Friuli Venezia Giulia and the other three sites in the later successional stages (II, III, and IV).

LMMs revealed significant effects of Successional stage ($F = 12.38$, $p\text{-value} < 0.001$), Site ($F = 6.08$, $p\text{-value} = 0.001$), and their interaction ($F = 1.96$, $p\text{-value} = 0.045$) on species richness (Fig. 4 A; Table S5.2). Post-hoc comparisons indicated that stage 0 supported the highest values across sites (~30 species), except Friuli Venezia Giulia, where the peak occurred in the transitional stage I (~38 species), significantly higher than in all other sites (Table S5.3). By contrast, Basilicata showed a marked decline at stage I followed by a slight increase in the later stages. At intermediate successional stages, richness converged across sites (20–23 species), whereas at stage IV values remained low, with Abruzzo

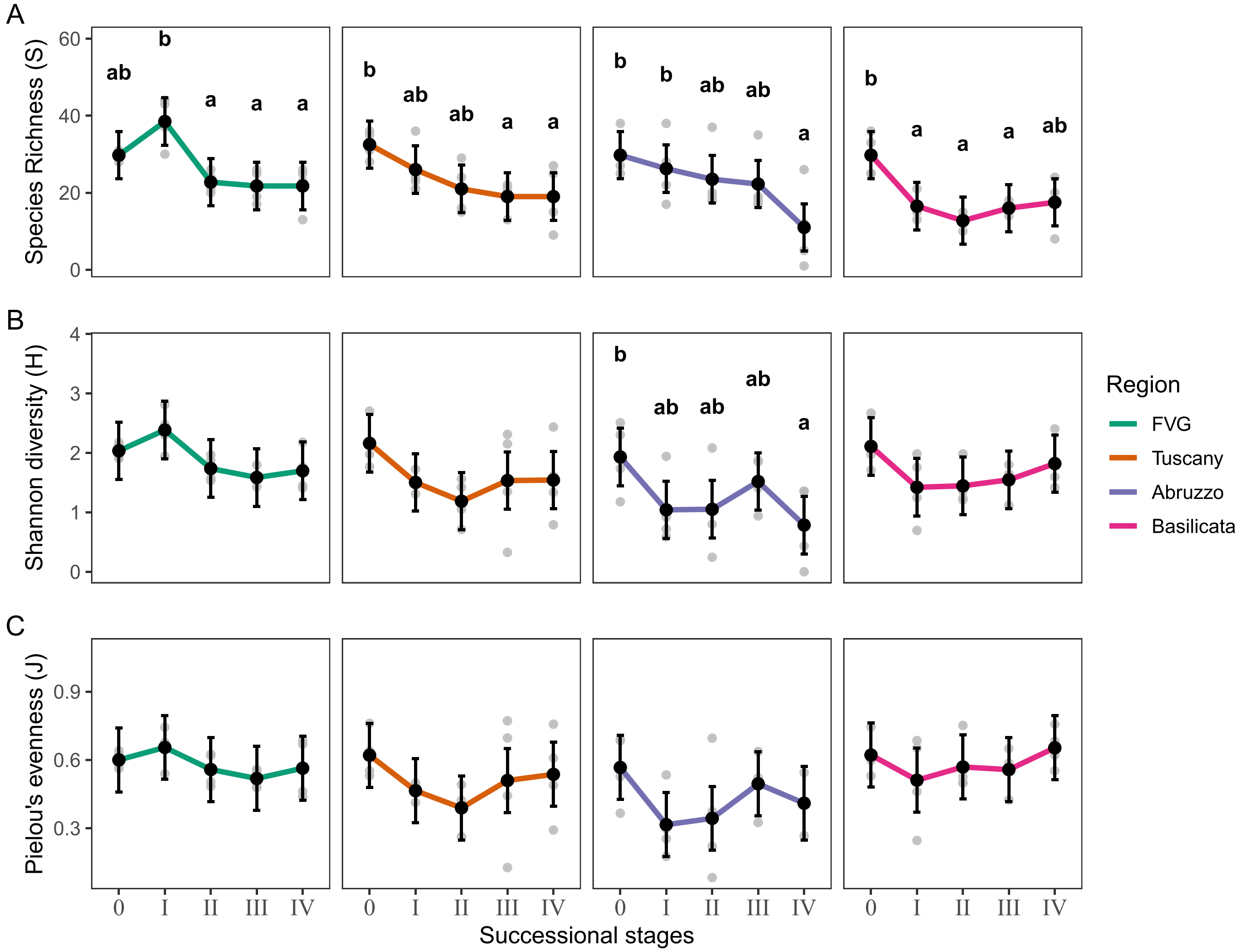

Fig. 4. Trends in herbaceous species richness (S; panel A), Shannon's entropy (H; panel B), and Pielou's evenness (J; panel C) across chronosequences in the four study sites. Values represent predicted means (± 95 % confidence intervals) from linear mixed-effects models. Lowercase letters indicate significant pairwise differences among stand ages within each site (Sidak-adjusted post-hoc tests). Grey points represent raw plot-level observations. Site trends are shown in different colours: Friuli Venezia Giulia (FVG; green), Tuscany (orange), Abruzzo (blue), and Basilicata (purple).

showing the lowest and Friuli Venezia Giulia site the highest.

For Shannon diversity, both Site ($F = 5.47$, p-value = 0.002) and Successional stage ($F = 4.81$, p-value = 0.002) were significant, while their interaction was not (Table S6.2). Abruzzo was the only site exhibiting significant shifts in Shannon's index across succession, with the highest values in stage 0 and lower in stage IV (p-value = 0.016; Fig. 4 B). Friuli Venezia Giulia maintained the highest values at stage I ($H = 2.39$), significantly higher than Abruzzo and Basilicata. At stage IV, Abruzzo showed the lowest Shannon diversity, whereas Basilicata retained higher values (Table S6.3).

Pielou's evenness was primarily influenced by Site ($F = 5.11$, p-value = 0.003), while neither Successional stage nor the interaction were significant (Fig. 4 C; Table S7.2). Significant differences among sites occurred in stage I, where Friuli Venezia Giulia displayed values significantly higher than Abruzzo, with Basilicata and Tuscany showing intermediate values (Table S7.3). Complete summaries of the statistical models are provided in the Supplementary Materials 1 (SM1; from Tabel S5.1 to Table S7.3).

3.3. Relationships between carbon stock and plant diversity

Orthogonal polynomial regressions were applied to assess linear and quadratic relationships between total ecosystem C stocks and plant diversity indices across the four study sites. Significant associations were detected between species richness and Shannon diversity and C stock, showing broadly similar patterns.

For species richness (Fig. 5), negative linear effects of C were detected in Friuli Venezia Giulia ($\beta = -15.8$, $p = 0.025$, $R^2 = 0.32$), Tuscany ($\beta = -19.7$, $p = 0.005$, $R^2 = 0.42$) and Abruzzo ($\beta = -22.1$, $p = 0.027$, $R^2 = 0.28$). By contrast, the Basilicata site exhibited a U-shaped relationship, driven by a strong positive quadratic component ($\beta = 21.6$, $p < 0.001$, $R^2 = 0.67$).

Shannon diversity (Figure S1 B) showed weaker but comparable trends: a negative relationship with C stocks in Friuli Venezia Giulia site ($\beta = -0.88$, $p = 0.019$, $R^2 = 0.33$) and a non-significant declines in Tuscany and Abruzzo, while Basilicata again displayed a non-linear response (quadratic $\beta = 1.28$, $p = 0.003$, $R^2 = 0.41$) (Figure S2 B).

By contrast, Pielou's evenness (Figure S2 C) was not significantly related to total ecosystem C stocks at any site ($p > 0.05$).

4. Discussion

4.1. Carbon stocks dynamics along succession

Our findings show that secondary succession on agricultural land with management cessation leads to an overall increase in total ecosystem C stock at all study sites. This evidence confirms our hypothesis and aligns with previous studies (Thuille and Schulze, 2006; Alberti et al., 2008; Hiltbrunner et al., 2013; Guidi et al., 2014; Pellis et al., 2019). In the stage 0, total C was predominantly stored in the soil (61 – 73 % of the total), while in later successional stages vegetation C became the dominant pool, with living trees biomass emerging as the main driver of ecosystem C accumulation over time. Total ecosystem C stocks reached up to 289 Mg C ha^{-1} in Basilicata in the oldest stands,

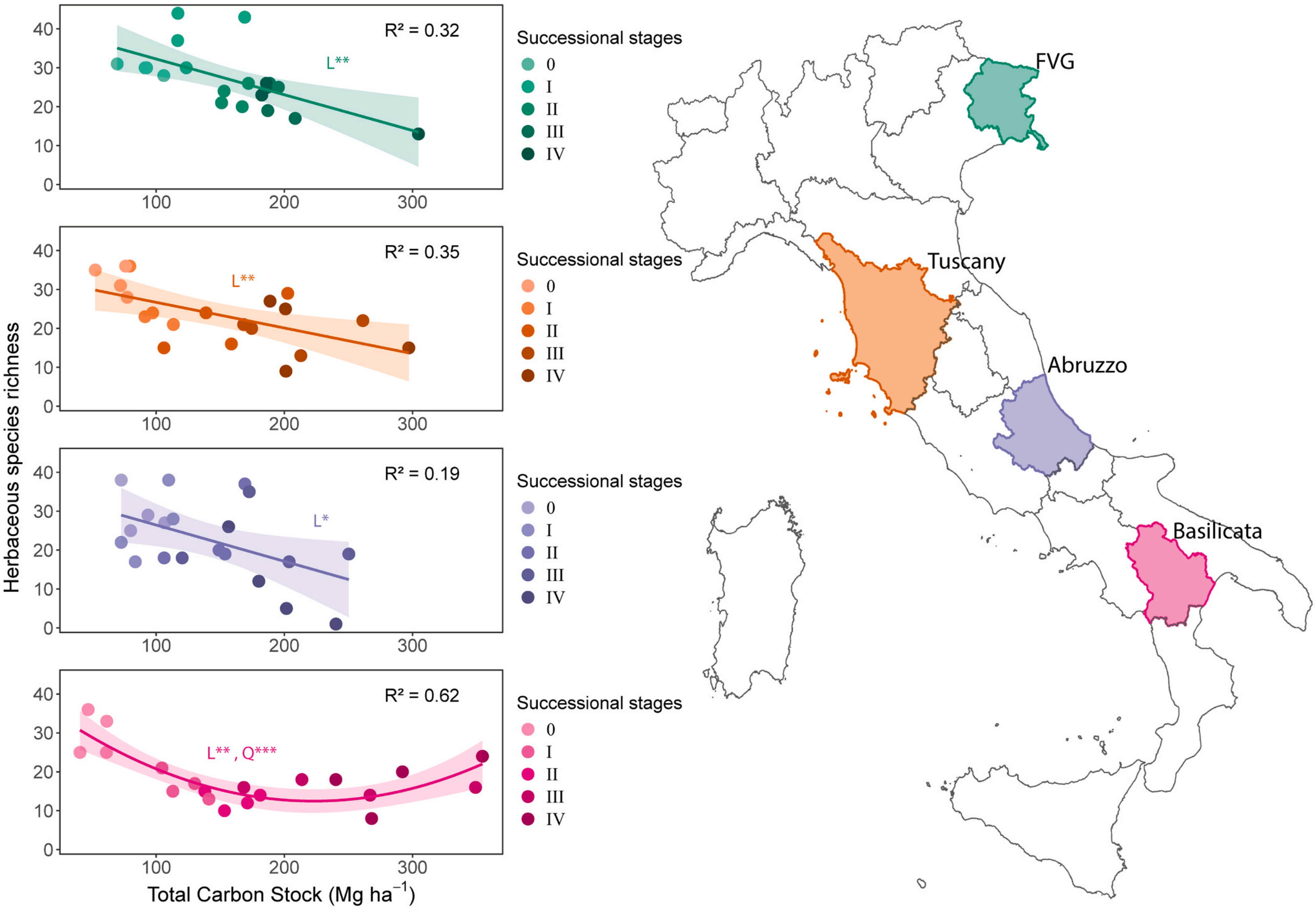

Fig. 5. Relationships between herbaceous species richness and total ecosystem C stocks across the four study sites: Friuli Venezia Giulia (FVG; green), Tuscany (orange), Abruzzo (blue), and Basilicata (purple). Each point represents a field plot, color-coded by successional stage. Regression lines correspond to either linear models or quadratic polynomial models, with shaded areas indicating 95 % confidence intervals. When significant, R^2 and significance levels for the linear (L) and quadratic (Q) components (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$) are reported within each panel.

where living trees accounted for up to 85 % of total C, while soil C always played a comparatively minor role (Alberti et al., 2008; Badalamenti et al., 2019; Weissgerber et al., 2024).

Previous meta-analyses have reported that abandoned grasslands do not show consistent SOC gains following natural reforestation, with highly variable responses across sites (Guo and Gifford, 2002; Poeplau et al., 2011). Similarly, Nezhad et al. (submitted) reported that secondary succession on abandoned grasslands contributes little to SOC sequestration in the short term, with outcomes strongly dependent on ecoregion, soil type, and forest type. Our findings partly reflect this variability. In the Basilicata and Tuscany sites, no significant differences in SOC were observed across successional stages, a pattern consistent with recent evidence from secondary succession in central France (Weissgerber et al., 2024). The absence of clear SOC changes may reflect a balance between increased C inputs from higher litter and root biomass and increased microbial decomposition and stabilization processes (Thuille and Schulze, 2006; Qiao et al., 2019). By contrast, the Friuli Venezia Giulia and Abruzzo sites showed distinct SOC trajectories. In Abruzzo, SOC decreased from stage 0 to stage III, followed by a slight recovery in the oldest forests. In Friuli Venezia Giulia, SOC dropped sharply between stage 0 and stage I and then returned to levels similar to the initial stage in later successional phases. Thuille and Schulze (2006) observed comparable SOC losses during the first 10–15 years of succession, a timeframe consistent with our age estimates for stage I stands. This decline may be linked to the dominance of r-strategist microbial communities in early succession, characterized by high respiration rates and rapid C consumption (Zhou et al., 2017), together with the fact that woody biomass does not immediately contribute to soil C in the first stages after abandonment (Alberti et al., 2011). Moreover, the loss of fine roots with rapid turnover typical of meadows and pastures reduces soil C inputs, while the replacement of arbuscular mycorrhizae typical of grasslands with ecto- and ericoid mycorrhizae may enhance organic matter oxidation, further contributing to SOC decline (Thuille and Schulze, 2006). Although our study was limited to the upper 30 cm of soil, this layer contains the largest fraction of total SOC (Jobbágy and Jackson, 2000) and is the most sensitive to C stock changes during secondary succession (Poeplau et al., 2011). Furthermore, subsoil layers generally respond to land-use change in the same direction as the topsoil (Poeplau and Don, 2013). Climate is also an important driver of soil C dynamics during secondary succession. Jackson et al. (2002) reported a negative correlation between precipitation and SOC changes in grasslands undergoing woody encroachment. In humid environments, highly productive grasslands tend to allocate more C to belowground biomass and can maintain higher SOC levels than regenerating forests, thereby limiting the potential for SOC accumulation following reforestation.

4.2. Plant diversity dynamics along succession

Plant diversity exhibited a latitudinal gradient across the study sites, with higher species richness observed at northern sites compared to southern ones. Our results highlight clear successional patterns in plant diversity across the investigated chronosequences. Managed and earlier successional stages exhibited the highest levels of species richness, followed by a progressive decline in older forests. Shannon diversity mirrored the trends of richness, although differences across successional stages were less pronounced. Pielou evenness remained relatively constant along the succession. The significant interaction between successional stage and site for species richness indicates that richness trajectories are not uniform across sites but are strongly influenced by the local conditions and land-use history. By contrast, Shannon diversity was independently affected by both site and successional stage, without a significant interaction, suggesting that while the number of species varies according to local floristic composition and environmental context, the relative distribution of abundances tends to converge as succession proceeds.

The observed loss of herbaceous diversity aligns with the classical successional theory, for which the transition from open habitats to closed-canopy forests reduces light availability and niche space for herbaceous species, favouring forest specialist species and ultimately decreasing understorey diversity (Grime, 1973; Sabatini et al., 2014; Bricca et al., 2025). This pattern was particularly evident in Tuscany and Abruzzo sites, where species richness gradually declined in older successional stages, in agreement with previous findings from other ecosystems (Höchtl et al., (2005); Amici et al., (2013); Sabatini et al., (2019); Wieczorkowski and Lehmann, (2022);. By contrast, Friuli Venezia Giulia and Basilicata exhibited distinct patterns. In Basilicata, plant diversity partially recovered in the oldest successional stage, although it did not reach the levels observed in the managed stage. This U-shaped trajectory resembles patterns reported for temperate secondary forest successions (Hilmers et al., 2018) and in beech forest chronosequences in central Italy (Bartha et al., 2020). Such recovery may result from the establishment of forest specialist species or structural changes in late succession that locally increase understory light availability. In Friuli Venezia Giulia, successional stage I showed particularly high species richness, highlighting the ecological importance of transitional habitats that combine elements of both meadow and forest flora. These environments promote coexistence between light-demanding and shade-tolerant forest species (Pornaro et al., 2013), a pattern also observed in semi-arid successional ecosystems of southern Spain (Bonet and Pausas, 2004). The distinct response in Friuli Venezia Giulia likely reflects the specific composition of the local plant community, including species adapted to transitional stages. By contrast, several studies in tropical ecosystems have reported a positive effect of succession on plant diversity (Letcher and Chazdon, 2009; Oberleitner et al., 2021; Salete Capellesso et al., 2021), highlighting how successional trajectories can vary substantially across biomes.

4.3. Carbon-diversity relationship

We found clear trade-offs between herbaceous plant diversity and total ecosystem C stocks along secondary forest successions in Italy. Similarly, Sabatini et al. (2019), in a multi-taxa analysis, reported comparable patterns between plant species richness and aboveground live C stocks in temperate forests. The observed negative relationship is likely driven by canopy closure of dominant trees, which reduces light availability for the herbaceous layer as vegetation biomass — and consequently C storage — increases (Sabatini et al., 2014).

In Basilicata, the C-plant diversity relationship follows a distinct trajectory compared to the other regions, with the lowest plant species richness occurring at intermediate C stock values and a subsequent recovery at sites with higher ecosystem C. Basilicata was also the site with the highest total C stocks in the later stages, largely driven by the substantial accumulation of living tree biomass. In this area, the environmental conditions are affected by the proximity to the Mediterranean sea, allowing a longer vegetative period, could have promoted faster tree growth (Lempereur et al., 2015; Pretzsch et al., 2018). The rapid growth of the forest stands may have led to an earlier onset of the understory reinitiation phase, which is known to host a higher number of understory species (Oliver and Larson, 1996). These local conditions likely contributed to the observed recovery of plant diversity in the late-successional stages. Additional analyses using structural metrics, such as LiDAR-derived ones, could provide deeper insights into the mechanisms driving this dynamic. The environmental conditions at the other sites did not allow stands to reach this phase within the time span of our study. The non-linear pattern observed in Basilicata may therefore represent a trajectory that could emerge in the other sites if succession continues.

At the global scale, Strassburg et al. (2010) identified strong but unevenly distributed congruence between species richness and biomass C. For instance, studies in the tropics often report congruence and co-benefits between C stocks and biodiversity (Sullivan et al., 2017; Deere et al., 2018; Matos et al., 2020; Salete Capellesso et al., 2021), likely due to the high availability of light, water and nutrients in tropical environments that can simultaneously support large plant biomass and a diverse species assemblage. These areas combining high C storage and biodiversity could be effectively protected through C-oriented conservation strategies. However, regions with high biodiversity but lower C stocks may not benefit from such approaches and could even face increased threats under C-oriented policies. Our findings support this perspective at a smaller scale: in Friuli Venezia Giulia, Tuscany, and Abruzzo, clear trade-offs emerge between promoting plant diversity and mitigating climate change through C storage. In these sites, pasture or mowing cessation leads to gradual declines in plant diversity, accompanied by a continuous accumulation of ecosystem C, offering for climate mitigation rather than plant diversity conservation. By contrast, in Basilicata, the decline in plant diversity appears temporary and is followed by recovery in late-successional forests that also store large amounts of C. This suggests that, in Basilicata, management strategies could aim to jointly maximize both plant diversity and C storage, enabling true win-win outcomes.

5. Conclusions

Our study, analysing 16 chronosequences in four distinct areas along a latitudinal gradient in Italy, demonstrates that natural forest expansion has a positive, though site-specific, effect on total ecosystem C stock during the first 75 years following land abandonment. By contrast, plant diversity peaked in more open habitats, such as meadows and pastures (Tuscany, Abruzzo, and Basilicata) or during earlier successional stage (in Friuli Venezia Giulia) and subsequently declined in three out of the four study sites as succession progressed. These divergent trajectories of C accumulation and plant diversity led to negative relationships between these two variables, except in Basilicata, where the latter partially recovered in later successional stage, though not to the initial levels, coinciding with the highest C stocks observed across all study sites.

Our findings highlight that spontaneous reforestation often entails significant trade-offs between climate change mitigation and plant diversity conservation, which should be explicitly considered in management and policy frameworks. Importantly, under favourable environmental conditions, these trade-offs may diminish over time, allowing concurrent increases in both C stocks and plant diversity. Further research is needed to assess whether similar win–win outcomes can occur in other sites. This could be addressed, for example, by investigating chronosequences extending beyond 75 years. Such insights would be highly valuable for managers and policymakers seeking to identify when and where nature-based solutions can simultaneously deliver multiple co-benefits, including climate change mitigation and biodiversity conservation.

CRediT authorship contribution statement

Gianmaria Bonari: Data curation, Investigation, Writing – review & editing. **Giacomo Trotta:** Writing – review & editing, Investigation. **Giorgio Alberti:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation. **Speranza Claudia Panico:** Writing – review & editing, Investigation. **Natalie Piazza:** Writing – review & editing, Software, Investigation, Data curation. **Alessandro Foscari:** Writing – review & editing, Investigation. **Guido Incerti:** Writing – review & editing, Supervision, Investigation. **Tommaso Chiti:** Writing – review & editing, Investigation. **Paolo Cingano:** Writing – review & editing, Investigation. **Gabriele Antoniella:** Writing – review & editing, Investigation. **Valentino Casolo:** Writing – review & editing, Supervision, Methodology. **Lorenzo Orzan:** Writing – original draft, Visualization, Software, Formal analysis, Data curation, Conceptualization. **Antonio Tomao:** Writing – review & editing, Supervision, Methodology, Investigation.

Funding

This study was mainly supported by the National Biodiversity Future Center – NBFC (project code CN_00000033) funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender no. 3138 of 16 December 2021, rectified by Decree n. 3175 of 18 December 2021 of the Italian Ministry of University and Research funded by the European Union – NextGenerationEU. G.A., A.T., and N.P. were also supported by the WILDCARD project funded by the European Climate, Infrastructure and Environment Executive Agency (CINEA – grant number: 101081177). A.F. was supported by European Union – Next Generation EU, under Mission 4, Component 2, Inv. 1.1, as part of the PRIN 2022 project "REWILDFIRE" (CUP: G53D23001360006). The views and opinions expressed are however those of the authors only and do not necessarily reflect those of the funders. Neither the European Union nor the granting authorities can be held responsible for them.

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 would like to thank the administrations of the Foreste Casentinesi National Park, Gran Sasso and Monti della Laga National Park, and Pollino National Park for their support in authorizing our field activities. We also extend our gratitude to Luca Cadez for his assistance with the field surveys and logistics, to Francesco Mascia for his contribution to the vegetation surveys, and to Giovanni Donadon, Federico Pittaro, and Daniele Segato for helping in the field survey and in soil sample pretreatment and analysis.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123527.

Data availability

Data will be made available on request.

References

Agnoletti, M., Piras, F., Venturi, M., Santoro, A., 2022. Cultural values and forest dynamics: The Italian forests in the last 150 years. For. Ecol. Manag 503, 119655. https://doi.org/10.1016/j.foreco.2021.119655.

Alberti, G., Ballesteros, M., Janečková, P., Müllerova, A., Piazza, N., Řehounková, K., Šebelíková, L., Samonil, P., Tomao, A., 2024. Deliverable 3.1: Preliminary dataset on available carbon and biodiversity across the network. Horizon Europe Project No. 101081177. European Commission, p. 43.

Alberti, G., Leronni, V., Piazzi, M., Petrella, F., Mairota, P., Peressotti, A., Piussi, P., Valentini, R., Gristina, L., La Mantia, T., Novara, A., Rühl, J., 2011. Impact of woody encroachment on soil organic carbon and nitrogen in abandoned agricultural lands along a rainfall gradient in Italy. Reg. Environ. Change 11, 917–924. https://doi.org/10.1007/s10113-011-0229-6.

Alberti, G., Peressotti, A., Piussi, P., Zerbi, G., 2008. Forest ecosystem carbon accumulation during a secondary succession in the Eastern Prealps of Italy. For. Int. J. For. Res. 81, 1–11. https://doi.org/10.1093/forestry/cpm026.

Amici, V., Santi, E., Filibeck, G., Diekmann, M., Geri, F., Landi, S., Scoppola, A., Chiarucci, A., 2013. Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. J. Biogeogr. 40, 2335–2347. https://doi.org/10.1111/jbi.12182.

Ascoli, D., Vacchiano, G., Scarpa, C., Arca, B., Barbati, A., Battipaglia, G., Elia, M., Esposito, A., Garfì, V., Lovreglio, R., Mairota, P., Marchetti, M., Marchi, E., Meytre, S., Ottaviano, M., Pellizzaro, G., Rizzolo, R., Sallustio, L., Salis, M., Sirca, C., Valese, E., Ventura, A., Bacciu, V., 2020. Harmonized dataset of surface fuels under Alpine, temperate and Mediterranean conditions in Italy. A synthesis supporting fire management. IForest Biogeosciences 13, 513. https://doi.org/10.3832/ifor3587-013.

Badalamenti, E., Battipaglia, G., Gristina, L., Novara, A., Rühl, J., Sala, G., Sapienza, L., Valentini, R., Mantia, T.L., 2019. Carbon stock increases up to old growth forest along a secondary succession in Mediterranean island ecosystems. PLOS ONE 14, e0220194. https://doi.org/10.1371/journal.pone.0220194.

Bartha, S., Canullo, R., Chelli, S., Campetella, G., 2020. Unimodal relationships of understory alpha and beta diversity along chronosequence in coppiced and unmanaged beech forests. Diversity 12, 101. https://doi.org/10.3390/d12030101.

Bell, S.M., Terrer, C., Barriocanal, C., Jackson, R.B., Rosell-Melé, A., 2021. Soil organic carbon accumulation rates on Mediterranean abandoned agricultural lands. Sci. Total Environ. 759, 143535. https://doi.org/10.1016/j.scitotenv.2020.143535.

Bitunjac, D., Ostrogović Sever, M.Z., Sever, K., Merganičová, K., Marjanović, H., 2023. Dead wood volume-to-carbon conversion factors by decay class for ten tree species in Croatia and eight tree genera globally. For. Ecol. Manag 549, 121431. https://doi.org/10.1016/j.foreco.2023.121431.

Blasi, C., Rosati, L., 2010. La Vegetazione d'Italia e la Carta delle Serie di vegetazione. In: La vegetazione d'Italia. Palombi & Partner Srl, 2010, pp. 9–15.

Bonet, A., Pausas, J.G., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecol. 174, 257–270. https://doi.org/10.1023/B:VEGE.0000049106.96330.9c.

Bovio, G., Ascoli, D., 2013. La tecnica del fuoco prescritto. ARACNE Editrice S.r.l. Italia. ⟨https://hdl.handle.net/2318/143524⟩.

Bricca, A., Zerbe, S., Fellin, H., Alessi, N., Maccherini, S., Bonari, G., 2025. Passive Rewilding of Old-Established Plantations Into Native Forests. J. Veg. Sci. 36 (6), e70085. https://doi.org/10.1111/jvs.70085.

Castillo, C.P., Kavalov, B., Diogo, V., Jacobs-Crisioni, C., Silva, F.B. e, Lavalle, C., 2018. Agricultural land abandonment in the EU within 2015-2030. European Commission, Ispra, 2018, JRC113718.

Cavanaugh, K.C., Gosnell, J.S., Davis, S.L., Ahumada, J., Boundja, P., Clark, D.B., Mugerwa, B., Jansen, P.A., O'Brien, T.G., Rovero, F., Sheil, D., Vasquez, R., Andelman, S., 2014. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. Glob. Ecol. Biogeogr. 23, 563–573. https://doi.org/10.1111/geb.12143.

Cimini, D., Tomao, A., Mattioli, W., Barbati, A., Corona, P., 2013. Assessing impact of forest cover change dynamics on high nature value farmland in Mediterranean mountain landscape. Ann. Silvic. Res. 37, 29–37. https://doi.org/10.12899/asr-771.

R. Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.R-project.org⟩.

De Cáceres, M., Casals, P., Gabriel, E., Castro, X., 2019. Scaling-up individual-level allometric equations to predict stand-level fuel loading in Mediterranean shrublands. Ann. For. Sci. 76, 87. https://doi.org/10.1007/s13595-019-0873-4.

Deere, N.J., Guillera-Arroita, G., Baking, E.L., Bernard, H., Pfeifer, M., Reynolds, G., Wearn, O.R., Davies, Z.G., Struebig, M.J., 2018. High Carbon Stock forests provide co-benefits for tropical biodiversity. J. Appl. Ecol. 55, 997–1008. https://doi.org/10.1111/1365-2664.13023.

Di Cosmo, L., Gasparini, P., Paletto, A., Nocetti, M., 2013. Deadwood basic density values for national-level carbon stock estimates in Italy. For. Ecol. Manag 295, 51–58. https://doi.org/10.1016/j.foreco.2013.01.010.

Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., 2006. IPCC guidelines for national greenhouse gas inventories. Volume 4: Agriculture, Forestry and Other Land Use. Inst. Glob. Environ. Strateg. Hayama Jpn, p. 4.

European Environment Agency (EEA). 2024. Biogeographical regions, Europe 2016. ⟨https://www.eea.europa.eu/en/analysis/maps-and-charts/biogeographical-regions-in-europe-2?activeTab=8a280073-bf94-4717-b3e2-1374b57ca99d⟩.

FAO, 2023. Standard Operating Procedure for Soil Moisture Content by Gravimetric Method. Rome.

FAO and UNEP, 2020. The State of the World's Forests 2020. Forests, biodiversity and people, The State of the World's Forests (SOFO). FAO and UNEP, Rome, Italy. https://doi.org/10.4060/ca8642en.

Fayet, C.M.J., Verburg, P.H., 2023. Modelling opportunities of potential European abandoned farmland to contribute to environmental policy targets. CATENA 232, 107460. https://doi.org/10.1016/j.catena.2023.107460.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Clim. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Fino, E., Blasi, E., Perugini, L., Pellis, G., Valentini, R., Chiti, T., 2020. Is _soil contributing to climate change mitigation during woody encroachment? A case study on the Italian Alps. Forests 11, 887. https://doi.org/10.3390/f11080887.

Frei, T., Espelta, J.M., Górriz-Mifsud, E., Hampe, A., Lefèvre, F., Martín-Forés, I., Winkel, G., 2024. Can natural forest expansion contribute to Europe's restoration policy agenda? An interdisciplinary assessment. Ambio 53, 34–45. https://doi.org/10.1007/s13280-023-01924-2.

Friedlingstein, P., O'Sullivan, M., Jones, M.W., Andrew, R.M., Hauck, J., Olsen, A., Peters, G.P., Peters, W., Pongratz, J., Sitch, S., Le Quéré, C., Canadell, J.G., Ciais, P., Jackson, R.B., Alin, S., Aragão, L.E.O.C., Arneth, A., Arora, V., Bates, N.R., Becker, M., Benoit-Cattin, A., Bittig, H.C., Bopp, L., Bultan, S., Chandra, N., Chevallier, F., Chini, L.P., Evans, W., Florentie, L., Forster, P.M., Gasser, T., Gehlen, M., Gilfillan, D., Gkritzalis, T., Gregor, L., Gruber, N., Harris, I., Hartung, K., Haverd, V., Houghton, R.A., Ilyina, T., Jain, A.K., Joetzjer, E., Kadono, K., Kato, E., Kitidis, V., Korsbakken, J.I., Landschützer, P., Lefèvre, N., Lenton, A., Lienert, S., Liu, Z., Lombardozzi, D., Marland, G., Metzl, N., Munro, D.R., Nabel, J.E.M.S., Nakaoka, S.-I., Niwa, Y., O'Brien, K., Ono, T., Palmer, P.I., Pierrot, D., Poulter, B., Resplandy, L., Robertson, E., Rödenbeck, C., Schwinger, J., Séférian, R., Skjelvan, I., Smith, A.J.P., Sutton, A.J., Tanhua, T., Tans, P.P., Tian, H., Tilbrook, B., van der Werf, G., Vuichard, N., Walker, A.P., Wanninkhof, R., Watson, A.J., Willis, D., Wiltshire, A.J., Yuan, W., Yue, X., Zaehle, S., 2020. Global Carbon Budget 2020. Earth Syst. Sci. Data 12, 3269–3340. https://doi.org/10.5194/essd-12-3269-2020.

Gasparini, P., Di Cosmo, L., Floris, A., De Laurentis, D., 2022. talian National Forest Inventory—Methods and Results of the Third Survey (Eds.). Inventario Nazionale delle Foreste e dei Serbatoi Forestali di Carbonio—Metodi e Risultati della Terza Indagine. In: I. Springer Nature. https://doi.org/10.1007/978-3-030-98678-0.

Gonzalez-Akre, E., Piponiot, C., Lepore, M., Herrmann, V., Lutz, J.A., Baltzer, J.L., Dick, C.W., Gilbert, G.S., He, F., Heym, M., Huerta, A.I., Jansen, P.A., Johnson, D.J., Knapp, N., Král, K., Lin, D., Malhi, Y., McMahon, S.M., Myers, J.A., Orwig, D., Rodríguez-Hernández, D.I., Russo, S.E., Shue, J., Wang, X., Wolf, A., Yang, T., Davies, S.J., Anderson-Teixeira, K.J., 2022. allodb: An R package for biomass estimation at globally distributed extratropical forest plots. Methods Ecol. Evol. 13, 330–338. https://doi.org/10.1111/2041-210X.13756.

Grassi, G., House, J., Dentener, F., Federici, S., den Elzen, M., Penman, J., 2017. The key role of forests in meeting climate targets requires science for credible mitigation. Nat. Clim. Change 7, 220–226. https://doi.org/10.1038/nclimate3227.

Grime, J.P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242, 344–347. https://doi.org/10.1038/242344a0.

Guidi, C., Vesterdal, L., Gianelle, D., Rodeghiero, M., 2014. Changes in soil organic carbon and nitrogen following forest expansion on grassland in the Southern Alps. For. Ecol. Manag 328, 103–116. https://doi.org/10.1016/j.foreco.2014.05.025.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Change Biol. 8, 345–360. https://doi.org/10.1046/j.1354-1013.2002.00486.x.

Halpern, C.B., Miller, E.A., Geyer, M.A., 1996. Equations for predicting above-ground biomass of plant species in early successional forests of the Western Cascade Range. Or. Northwest Sci. 70 (4), 306–320.

Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. Pub. No. 20. US Long-Term Ecol. Res. Netw. Off. Univ. Wash, Seattle, WA, p. 73.

Hartig, F., 2024. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. 10.32614/CRAN. package.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. J. Appl. Ecol. 55, 2756–2766. https://doi.org/10.1111/1365-2664.13238.

Hiltbrunner, D., Zimmermann, S., Hagedorn, F., 2013. Afforestation with Norway spruce on a subalpine pasture alters carbon dynamics but only moderately affects soil carbon storage. Biogeochemistry 115, 251–266. https://doi.org/10.1007/s10533-013-9832-6.

Höchtl, F., Lehringer, S., Konold, W., 2005. Wilderness": what it means when it becomes a reality—a case study from the southwestern Alps. In: Landsc. Urban Plan, 70. Rural Landscapes: past processes and future strategies, pp. 85–95. https://doi.org/10.1016/j.landurbplan.2003.10.006.

Jackson, R.B., Banner, J.L., Jobbágy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418, 623–626. https://doi.org/10.1038/nature00910.

Jobbágy, E.G., Jackson, R.B., 2000. The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation. Ecol. Appl. 10, 423–436. https://doi.org/10.1890/1051-0761(2000)010%255B0423:TVDOSO%255D2.0.CO;2.

Jongman, R.H.G., 2002. Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. Landsc. Urban Plan. Fragm. Land Use Plan. Anal. Beyond? 58, 211–221. https://doi.org/10.1016/S0169-2046(01)00222-5.

Kikstra, J.S., Nicholls, Z.R.J., Smith, C.J., Lewis, J., Lamboll, R.D., Byers, E., Sandstad, M., Meinshausen, M., Gidden, M.J., Rogelj, J., Kriegler, E., Peters, G.P., Fuglestvedt, J.S., Skeie, R.B., Samset, B.H., Wienpahl, L., van Vuuren, D.P., van der Wijst, K.-I., Al Khourdajie, A., Forster, P.M., Reisinger, A., Schaeffer, R., Riahi, K., 2022. The IPCC Sixth Assessment Report WGIII climate assessment of mitigation pathways: from emissions to global temperatures. Geosci. Model Dev. 15, 9075–9109. https://doi.org/10.5194/gmd-15-9075-2022.

Lempereur, M., Martin-StPaul, N.K., Damesin, C., Joffre, R., Ourcival, J.-M., Rocheteau, A., Rambal, S., 2015. Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: implications for assessing forest productivity under climate change. N. Phytol. 207, 579–590. https://doi.org/10.1111/nph.13400.

Lenth, R., 2024. emmeans: Estimated Marginal Means, aka Least-Squares Means. R. Package Version 1 (10), 4. ⟨https://CRAN.R-project.org/package=emmeans⟩.

Letcher, S.G., Chazdon, R.L., 2009. Rapid Recovery of Biomass, Species Richness, and Species Composition in a Forest Chronosequence in Northeastern Costa Rica. Biotropica 41, 608–617. https://doi.org/10.1111/j.1744-7429.2009.00517.x.

López-Moreno, J.I., Vicente-Serrano, S.M., Moran-Tejeda, E., Zabalza, J., Lorenzo-Lacruz, J., García-Ruiz, J.M., 2011. Impact of climate evolution and land use changes on water yield in the ebro basin. Hydrol. Earth Syst. Sci. 15, 311–322. https://doi.org/10.5194/hess-15-311-2011.

Malandra, F., Vitali, A., Urbinati, C., Garbarino, M., 2018. 70 Years of Land Use/Land Cover Changes in the Apennines (Italy): A Meta-Analysis. Forests 9, 551. https://doi.org/10.3390/f9090551.

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., De Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., Da Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob. Change Biol. 26, 509–522. https://doi.org/10.1111/gcb.14824.

Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. J. Appl. Ecol. 54, 12–27. https://doi.org/10.1111/1365-2664.12669.

Mou, G., 2015. Sviluppo di tecniche innovative per la gestione integrata dei combustibili nella prevenzione degli incendi boschivi in foreste mediterranee. Tesi di Laurea. Univ. à di Sassari 169. ⟨https://hdl.handle.net/11388/250643⟩.

Nadal-Romero, E., Llena, M., Cortijos-López, M., Lasanta, T., 2023. Afforestation after land abandonment as a nature-based solution in Mediterranean mid-mountain areas: Implications and research gaps. Curr. Opin. Environ. Sci. Health 34, 100481. https://doi.org/10.1016/j.coesh.2023.100481.

Nezhad, M. , Gajski, D. , Jeanroy, C. , Verburg, P. , Alberti, G. , Samonil, P. , n.d. Soil organic carbon dynamics in rewilded abandoned lands across Europe: current status and knowledge gaps. Sci. Total Environ.

Nieuwenhuize, J., Maas, Y.E.M., Middelburg, J.J., 1994. Rapid analysis of organic carbon and nitrogen in particulate materials. Mar. Chem. 45, 217–224. https://doi.org/10.1016/0304-4203(94)90005-1.

Oberleitner, F., Egger, C., Oberdorfer, S., Dullinger, S., Wanek, W., Hietz, P., 2021. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For. Ecol. Manag 479, 118580. https://doi.org/10.1016/j.foreco.2020.118580.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J.F., Weedon, J., 2001. vegan Community Ecol. Package. https://doi.org/10.32614/CRAN.package.vegan.

Oliveira, T.M., Guiomar, N., Baptista, F.O., Pereira, J.M.C., Claro, J., 2017. Is Portugal's forest transition going up in smoke? Land Use Policy 66, 214–226. https://doi.org/10.1016/j.landusepol.2017.04.046.

Oliver, C., Larson, B., 1996. Forest Stand Dynamics. John Wiley & Sons, New York.

Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., Wagner, F., 2003. Good Practice Guidance for Land Use, Land-Use Change and Forestry. Institute for Global Environmental Strategies for the Intergovernmental Panel on Climate Change, Hayama, Kanagawa, Japan.

Palmero-Iniesta, M., Pino, J., Pesquer, L., Espelta, J.M., 2021. Recent forest area increase in Europe: expanding and regenerating forests differ in their regional patterns, drivers and productivity trends. Eur. J. For. Res. 140, 793–805. https://doi.org/10.1007/s10342-021-01366-z.

Pan, Y., Birdsey, R.A., Phillips, O.L., Houghton, R.A., Fang, J., Kauppi, P.E., Keith, H., Kurz, W.A., Ito, A., Lewis, S.L., Nabuurs, G.-J., Shvidenko, A., Hashimoto, S., Lerink, B., Schepaschenko, D., Castanho, A., Murdiyarso, D., 2024. The enduring world forest carbon sink. Nature 631, 563–569. https://doi.org/10.1038/s41586-024-07602-x.

Panico, S.C., Alberti, G., Foscari, A., Sciabbarrasi, G.L., Tomao, A., Incerti, G., 2025. Bacterial and Fungal Communities Respond Differently to Changing Soil Properties Along Afforestation Dynamic. Microb. Ecol. 88 (1), 2. https://doi.org/10.1007/s00248-025-02500-9.

Pellis, G., Chiti, T., Rey, A., Curiel Yuste, J., Trotta, C., Papale, D., 2019. The ecosystem carbon sink implications of mountain forest expansion into abandoned grazing land: The role of subsoil and climatic factors. Sci. Total Environ. 672, 106–120. https://doi.org/10.1016/j.scitotenv.2019.03.329.

Pickett, S.T.A., 1989. Space-for-Time Substitution as an Alternative to Long-Term Studies. In: Likens, G.E. (Ed.), Long-Term Studies in Ecology: Approaches and Alternatives. Springer, New York, pp. 110–135. https://doi.org/10.1007/978-1-4615-7358-6_5.

Poeplau, C., Don, A., Vesterdal, L., Leifeld, J., Van Wesemael, B., Schumacher, J., Gensior, A., 2011. Temporal dynamics of soil organic carbon after land-use change in the temperate zone – carbon response functions as a model approach. Glob. Change Biol. 17, 2415–2427. https://doi.org/10.1111/j.1365-2486.2011.02408.x.

Poeplau, C., Don, A., 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. Geoderma 192, 189–201. https://doi.org/10.1016/j.geoderma.2012.08.003.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y., Rodríguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328. https://doi.org/10.1111/geb.12364.

Pornaro, C., Schneider, M.K., Macolino, S., 2013. Plant species loss due to forest succession in Alpine pastures depends on site conditions and observation scale. Biol. Conserv 161, 213–222. https://doi.org/10.1016/j.biocon.2013.02.019.

Potter, K.M., Woodall, C.W., 2014. Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across U.S. forests. For. Ecol. Manag. Mech. Predict. Ecol. Change Manag. For. A Sel. Pap. Second Int. Conf. Biodivers. For. Ecosyst. Landsc. 321, 117–129. https://doi.org/10.1016/j.foreco.2013.06.026.

Prangel, E., Kasari-Toussaint, L., Neuenkamp, L., Noreika, N., Karise, R., Marja, R., Ingerpuu, N., Kupper, T., Keerberg, L., Oja, E., Meriste, M., Tiitsaar, A., Ivask, M., Helm, A., 2023. Afforestation and abandonment of semi-natural grasslands lead to biodiversity loss and a decline in ecosystem services and functions. J. Appl. Ecol. 60, 825–836. https://doi.org/10.1111/1365-2664.14375.

Pretzsch, H., Biber, P., Schütze, G., Kemmerer, J., Uhl, E., 2018. Wood density reduced while wood volume growth accelerated in Central European forests since 1870. For. Ecol. Manag 429, 589–616. https://doi.org/10.1016/j.foreco.2018.07.045.

Pugh, T.A.M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., Calle, L., 2019. Role of forest regrowth in global carbon sink dynamics. Proc. Natl. Acad. Sci. 116, 4382–4387. https://doi.org/10.1073/pnas.1810512116.

Qianwen, G., Arif, M., Zhongxun, Y., Jie, Z., Xinrui, H., Dongdong, D., Fan, Y., Changxiao, L., 2022. Plant species composition and diversity along successional gradients in arid and semi-arid regions of China. For. Ecol. Manag 524, 120542. https://doi.org/10.1016/j.foreco.2022.120542.

Qiao, N., Wang, J., Xu, X., Shen, Y., Long, X., Hu, Y., Schaefer, D., Li, S., Wang, H., Kuzyakov, Y., 2019. Priming alters soil carbon dynamics during forest succession. Biol. Fertil. Soils 55, 339–350. https://doi.org/10.1007/s00374-019-01351-0.

Řehounková, K., Tichý, L., Prach, K., 2024. Succession in abandoned fields: Chronosequence data verified by monitoring of semi-permanent plots. J. Veg. Sci. 35, e13303. https://doi.org/10.1111/jvs.13303.

Riccardi, C.L., Prichard, S.J., Sandberg, D.V., Ottmar, R.D., 2007. Quantifying physical characteristics of wildland fuels using the Fuel Characteristic Classification SystemThis article is one of a selection of papers published in the Special Forum on the Fuel Characteristic Classification System. Can. J. For. Res. 37, 2413–2420. https://doi.org/10.1139/X07-175.

Sabatini, F.M., de Andrade, R.B., Paillet, Y., Ódor, P., Bouget, C., Campagnaro, T., Gosselin, F., Janssen, P., Mattioli, W., Nascimbene, J., Sitzia, T., Kuemmerle, T., Burrascano, S., 2019. Trade-offs between carbon stocks and biodiversity in European temperate forests. Glob. Change Biol. 25, 536–548. https://doi.org/10.1111/gcb.14503.

Sabatini, F., Jiménez-Alfaro, B., Burrascano, S., Blasi, C., 2014. Drivers of herb-layer species diversity in two unmanaged temperate forests in northern Spain. Community Ecol. 15, 147–157. https://doi.org/10.1556/comec.15.2014.2.3.

Salete Capellesso, E., Cequinel, A., Marques, R., Luisa Sausen, T., Bayer, C., Marques, M. C.M., 2021. Co-benefits in biodiversity conservation and carbon stock during forest regeneration in a preserved tropical landscape. For. Ecol. Manag 492, 119222. https://doi.org/10.1016/j.foreco.2021.119222.

Seddon, N., Chausson, A., Berry, P., Girardin, C.A.J., Smith, A., Turner, B., 2020. Understanding the value and limits of nature-based solutions to climate change and other global challenges. Philos. Trans. R. Soc. B Biol. Sci. 375, 20190120. https://doi.org/10.1098/rstb.2019.0120.

Shin, Y.-J., Midgley, G.F., Archer, E.R.M., Arneth, A., Barnes, D.K.A., Chan, L., Hashimoto, S., Hoegh-Guldberg, O., Insarov, G., Leadley, P., Levin, L.A., Ngo, H.T., Pandit, R., Pires, A.P.F., Pörtner, H.-O., Rogers, A.D., Scholes, R.J., Settele, J., Smith, P., 2022. Actions to halt biodiversity loss generally benefit the climate. Glob. Change Biol. 28, 2846–2874. https://doi.org/10.1111/gcb.16109.

Smith, W.B., Brand, G.J., 1983. Allometric Biomass Equations for 98 Species of Herbs, Shrubs, and Small Trees. Res. Note NC-299. St Paul MN US Dept Agric. For. Serv. North Cent. For. Exp. https://doi.org/10.2737/NC-RN-299.

Strassburg, B.B.N., Kelly, A., Balmford, A., Davies, R.G., Gibbs, H.K., Lovett, A., Miles, L., Orme, C.D.L., Price, J., Turner, R.K., Rodrigues, A.S.L., 2010. Global congruence of carbon storage and biodiversity in terrestrial ecosystems. Conserv. Lett. 3, 98–105. https://doi.org/10.1111/j.1755-263X.2009.00092.x.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S., de Almeida, E.C., de Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, C., Baker, G.A., Balinga, T.R., Banin, M., Baraloto, L.F., Bastin, C., Berry, J.-F., Bogaert, N., Bonal, J., Bongers, D., Brienen, F., Camargo, R., Cerón, J.L.C., Moscoso, C., Chezeaux, V.C., Clark, E., Pacheco, C.J., Comiskey, Á.C., Valverde, J.A., Coronado, F.C., Dargie, E.N.H., Davies, G., De Canniere, S.J., Djuikouo, C., M.N, K., Doucet, J.-L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukasu, F.M., Makana, J.-R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsoedin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 39102. https://doi.org/10.1038/srep39102.

Thompson, I.D., Okabe, K., Tylianakis, J.M., Kumar, P., Brockerhoff, E.G., Schellhorn, N. A., Parrotta, J.A., Nasi, R., 2011. Forest biodiversity and the delivery of ecosystem goods and services: translating science into policy. BioScience 61, 972–981. https://doi.org/10.1525/bio.2011.61.12.7.

Thuille, A., Schulze, E.-D., 2006. Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. Glob. Change Biol. 12, 325–342. https://doi.org/10.1111/j.1365-2486.2005.01078.x.

Van de Perre, F., Willig, M.R., Presley, S.J., Bapeamoni Andemwana, F., Beeckman, H., Boeckx, P., Cooleman, S., de Haan, M., De Kesel, A., Dessein, S., Grootaert, P., Huygens, D., Janssens, S.B., Kearsley, E., Kabeya, P.M., Leponce, M., Van den Broeck, D., Verbeeck, H., Würsten, B., Leirs, H., Verheyen, E., 2018. Reconciling biodiversity and carbon stock conservation in an Afrotropical forest landscape. Sci. Adv. 4 (3), eaar6603. https://doi.org/10.1126/sciadv.aar6603.

van der Sande, M.T., Poorter, L., Derroire, G., do Espirito Santo, M.M., Lohbeck, M., Müller, S.C., Bhaskar, R., van Breugel, M., Dupuy-Rada, J.M., Durán, S.M., Jakovac, C.C., Paz, H., Rozendaal, D.M.A., Brancalion, P., Craven, D., Mora Ardilla, F., Almeida, J.S., Balvanera, P., Becknell, J., Finegan, B., César, R.G., Hernández-Stefanoni, J.L., Kennard, D., Letcher, S.G., Marín-Spiotta, E., Muñoz, R., Reyes-García, C., Sanaphre-Villanueva, L., Utrera, L.P., Fernandes, G.W., Álvarez, F. S., Andrade, J.L., Arreola, F., Boukili, V., Cabral, G.A.L., Chave, J., Chazdon, R., Colletta, G., das Dores Magalhães Veloso, M., de Jong, B., Lebrija-Trejos, E., de Souza Moreno, V., Dent, D.H., DeWalt, S., García, E.D., Ferreira Nunes, Y.R., Granda, V., Hall, J., Lobo, R., Lopez, O., Martínez Ramos, M., Meave, J.A., Ochoa-Gaona, S., Sampaio, E.V.S.B., Sanchez-Azofeifa, A., Teixeira, H.M., Toledo, M., Uriarte, M., Wright, S.J., Zanini, K., Bongers, F., 2024. Tropical forest succession increases tree taxonomic and functional richness but decreases evenness. Glob. Ecol. Biogeogr. 33, e13856. https://doi.org/10.1111/geb.13856.

Verburg, P.H., Overmars, K.P., 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landsc. Ecol. 24, 1167–1181. https://doi.org/10.1007/s10980-009-9355-7.

Weissgerber, M., Chanteloup, L., Bonis, A., 2024. Carbon stock increase during post-agricultural succession in central France: no change of the superficial soil stock and high variability within forest stages. New 55, 1533–1555. https://doi.org/10.1007/s11056-024-10044-y.

Wieczorkowski, J.D., Lehmann, C.E.R., 2022. Encroachment diminishes herbaceous plant diversity in grassy ecosystems worldwide. Glob. Change Biol. 28, 5532–5546. https://doi.org/10.1111/gcb.16300.

Wilson, E.R., Leroux, S.J., Moran, R., Whitaker, D., Wiersma, Y., 2025. Predicting carbon storage in North American maritime boreal forests under combined disturbances. Landsc. Ecol. 40, 131. https://doi.org/10.1007/s10980-025-02145-6.

Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X., Fang, J., 2015. The relationship between species richness and biomass changes from boreal to subtropical forests in China. Ecography 38, 602–613. https://doi.org/10.1111/ecog.00940.

Yang, L., Luo, P., Wen, L., Li, D., 2016. Soil organic carbon accumulation during post-agricultural succession in a karst area, southwest China. Sci. Rep. 6 (1), 37118. https://doi.org/10.1038/srep37118.

Zhou, Z., Wang, C., Jiang, L., Luo, Y., 2017. Trends in soil microbial communities during secondary succession. Soil Biol. Biochem 115, 92–99. https://doi.org/10.1016/j.soilbio.2017.08.014.