

Widespread expansion of tree cover compromises European biodiversity capacity

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Patterns, drivers and potential biodiversity consequences of widespread tree-cover expansion in Europe

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Expanding tree cover is widely seen as a nature-based solution for climate mitigation and biodiversity conservation. However, widespread increases in tree cover can unintentionally reduce habitat heterogeneity or replace open ecosystems, thereby posing risks to biodiversity. Here, we developed a framework integrating measures of tree cover, connectivity, and heterogeneity, and quantified the dynamics in these measures in Europe from 2001 to 2021. We also explored potential drivers of tree dynamics, including land management, natural disturbance, climate, and human activities. We found that 23% of the European land area experienced widespread increases in tree cover and connectivity, accompanied by a decline in heterogeneity. Importantly, former cropland areas were linked to considerable tree-cover expansion and improved tree connectivity. Our findings indicate widespread densification and homogenization of vegetation, which will compromise the capacity of European ecosystems to support biodiversity. Restoring natural disturbance processes, including herbivory and fire, is essential to fully capitalize on the biodiversity potential of nature recovery in Europe.

Introduction

Trees play an important role in regulating biosphere processes and supporting biodiversity in terrestrial ecosystems. For example, tree biomass and cover are strongly linked to key climate forcings such as carbon exchange^{1,2} and albedo^{3,4}. Similarly, trees serve as habitat modifiers, and construct niches for many other species and therefore have a disproportionate impact on local assemblages and interactions in food webs⁵. The dual impact of trees on climate and biodiversity explains why nature-based solutions to the global climate and biodiversity crises strongly revolve around maintaining forests and expanding tree cover⁶. However, increasing tree cover does not universally generate positive, synergistic effects on climate and biodiversity.

Several implicit assumptions are often overlooked when promoting large-scale tree planting and forest restoration. For example, tree expansion may transform open ecosystems, such as grassland and savanna, to closed-canopy forests, which would result in biodiversity degradation or loss by diminishing resources and habitats for light-demanding plants, grazing herbivores, or bird species that rely on open habitats⁷⁻¹⁰. Also, continuous closed-canopy forests are not the historical pre-human ecosystem state across much of Europe, including in areas that currently support forests, or that did so earlier in the Holocene¹¹⁻¹³. Large-scale tree planting in such areas would therefore amount to a form of geoengineering rather than ecosystem restoration. Moreover, in vegetation types where crown fires occur naturally, such as in Mediterranean woodlands or Boreal forests, an increase in tree cover density results in a higher and more continuous fuel load, thus leading to larger, hotter, and typically more destructive fires¹⁴.

Beyond total tree cover, the structural configuration of trees, both horizontally and vertically, is a critical determinant of ecosystem function and biodiversity. Tree cover, connectivity, and heterogeneity are key structural attributes that shape habitat availability, landscape permeability, and ecological niche diversity. For example, tree connectivity facilitates movement and genetic exchange for forest-adapted species^{15,16}, but may hinder the dispersal of species reliant on open habitats^{17,18}. Vertical heterogeneity increases habitat complexity by expanding niche space, providing refuges, and supporting species with diverse functional traits^{19,20}. At the same time, spatial variation in canopy

density and productivity influences light availability and shapes community assembly, particularly in understory plant communities^{7,10}. Evaluating these three dimensions together is therefore essential for understanding how tree dynamics affect biodiversity and for guiding effective conservation and land management decisions.

In Europe, multiple drivers are reshaping tree covers, including forest management, natural disturbances, and farmland abandonment. European forests experience the highest intensity of management, about 85% of forests under some form of management²¹, shaping tree cover in major ways. For instance, new plantations can rapidly increase tree cover, while logging can alter connectivity and heterogeneity. Similarly, disturbances such as wildfires, windstorms, bark beetle outbreaks, and droughts have led to widespread tree mortality in Europe recently^{22,23}, exerting extensive influences on tree cover. Finally, Europe has experienced widespread farmland abandonment because of structural change in agriculture, outmigration from rural areas, and an increasing outsourcing of agricultural production to areas outside of Europe²⁴⁻²⁸. Such abandonment provides substantial opportunities for natural regeneration, potentially creating space for tree regeneration and expansion. While numerous studies have addressed how forest management and natural disturbances affect tree cover^{23,29}, critical knowledge gaps remain regarding their impact on tree cover connectivity and heterogeneity, key aspects influencing ecosystem functioning and biodiversity. Identifying and quantifying these patterns and their spatial distribution are central contributions that are essential for evaluating the potential trade-offs and synergies between climate mitigation and biodiversity conservation.

Here, we quantified the trends in tree cover, tree cover connectivity, and tree heterogeneity across Europe from 2001 to 2021 using 30-meter resolution tree extent and height data. Based on the trends of our tree cover (TC), tree cover connectivity index (TCI), and tree heterogeneity index (THI), together with tree cover, we classified tree dynamics into eight distinct syndromes. We examined the spatial patterns of these changes across different biogeographic regions and land management contexts, including varying intensities of forest management, types of protected areas, and areas undergoing agricultural abandonment. Finally, we employed machine learning to quantify the relative contributions

of climate, topography, natural disturbances, land management, and human activities in reshaping European tree cover. Our study aims to address the following key questions: (1) What are the spatial and temporal patterns of tree dynamics in Europe when evaluated through the combined dimensions of extent, connectivity, and heterogeneity? (2) What are the dominant environmental and anthropogenic drivers of tree dynamics?

Results

Tree dynamics in Europe

We assessed trends in tree cover, connectivity and heterogeneity on a 1- km² grid across Europe from 2001 to 2021 (*Fig. 1*). Our analysis reveals widespread increases in tree cover (58.3% of the European land area) and connectivity (55.4%), particularly in southern and central Europe, with an average rate of 0.22% yr⁻¹ within these increasing areas, while 55.4% saw improved connectivity, averaging 0.002 yr⁻¹ within regions exhibiting connectivity gains. Notably, connectivity increases were most pronounced between latitudes 40° and 45°. Declines in tree cover and connectivity were primarily concentrated in Sweden, Finland, central Germany, and the Landes region of France. Areas exhibiting increasing (49.5%) and decreasing (50.5%) trends in tree heterogeneity were roughly balanced, although regional differences in spatial patterns were evident. In East-Central Europe and central parts of Fennoscandia, heterogeneity tended to increase, while in western and southern Europe and northern Fennoscandia decreases in heterogeneity predominated.

We identified eight distinct syndromes of tree cover dynamics by combining the temporal trends of cover, connectivity, and heterogeneity (*Fig. 1d*). For example, the syndrome $TC_{\uparrow}TCI_{\uparrow}THI_{\uparrow}$ represents simultaneously increasing trends across all three metrics. The most prevalent pattern (23%), characterized by increases in tree cover and connectivity alongside decreases in heterogeneity ($TC_{\uparrow}TCI_{\uparrow}THI_{\downarrow}$), suggests a shift toward denser, more homogeneous forests at the expense of more open habitats. This trajectory was spread across Europe, in some areas associated with industrial forestry, but also prevalent in e.g. the southern Apennines, the Galicia region of Spain, the Bulgarian Balkan, the southern Carpathians in Romania, eastern Latvia and Lithuania and sub-Alpine mire-forest mosaics in

north-western Sweden. Additionally, 16% of the study area exhibited increases in all three metrics ($TC_{\uparrow}TCI_{\uparrow}THI_{\uparrow}$), with hotspots predominantly located in southeastern Europe, including Bulgaria, Serbia, Bosnia and Herzegovina, and the Carpathian Mountain region of Romania (*Supplementary Fig. S1*). In contrast, 9.2% of the study area experienced simultaneous declines in all three metrics ($TC_{\downarrow}TCI_{\downarrow}THI_{\downarrow}$), with northern Fennoscandia emerging as the primary hotspot.

We also found that trends in tree cover and connectivity indices were generally consistent, with 61.8% of cases showing aligned patterns (both increasing or decreasing) and a strong linear correlation between these metrics ($R^2 = 0.42$). In contrast, the heterogeneity trends exhibited only a weak linear relationship with tree cover trends ($R^2 = 0.04$, $p < 0.001$; *Supplementary Fig. S2*), suggesting distinct drivers or mechanisms influencing changes in tree heterogeneity compared to those affecting cover extent and connectivity.

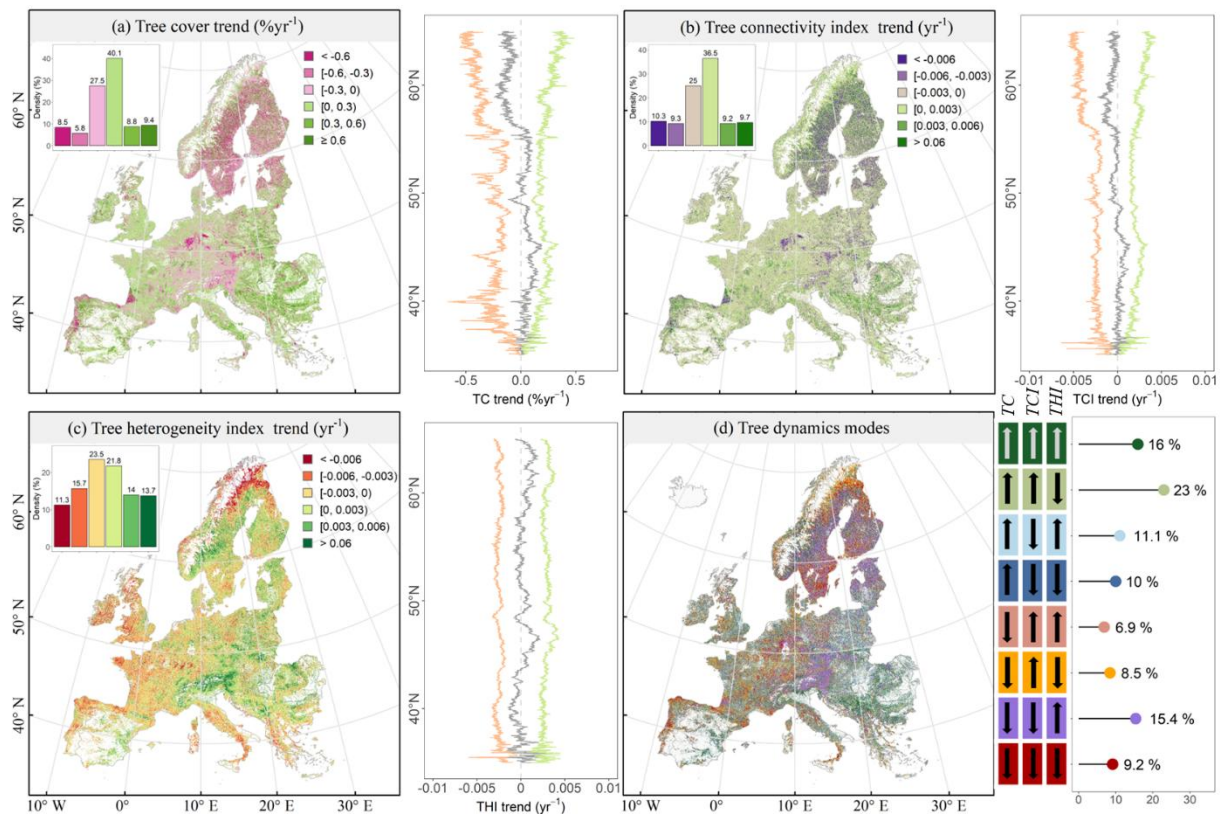


Fig.1 Tree dynamics in Europe, 2001-2021. (a) Trends in tree cover. (b) Trend in tree cover connectivity. (c) Trend in tree heterogeneity. (d) The spatial distributions and proportional composition of the eight tree dynamic syndromes are illustrated according to the combined trends of three metrics

(tree cover, connectivity, and heterogeneity). In the legend of panel (d), each row's upward arrow denotes an increasing trend in the tree metric, while the downward arrow indicates a decreasing trend. The tree dynamics within the 1km × 1 km grid were examined for trends using the PARTS approach³⁰. Here, both significant and non-significant trends are depicted, reflecting our assumption that all observed trends hold importance. The individual sub-metrics from which tree cover connectivity and tree heterogeneity were calculated are available in Supplementary Fig. S3. The average values from 2001 to 2021 for these three metrics are presented in Supplementary Fig. S4.

Tree dynamics by biogeographical region

All biogeographic regions showed an increasing trend in average tree cover except for the Boreal region (Fig. 2a). The trend in average tree cover varied between -0.12% yr⁻¹ in the Boreal and 0.19% yr⁻¹ in the Pannonian Steppe. In 2021, the Boreal region had the highest tree cover at 63.4%, while the Atlantic region had the lowest at 37.8% (Fig. 2b). The tree cover in the Boreal and Alpine regions generally exceeded the European average. Connectivity trends were largely consistent with tree cover, except for the Pannonian Steppe which saw an increase in tree cover but an overall decline in connectivity. In 2021, Connectivity in the Mediterranean (0.42) and Atlantic (0.43) regions had a distinctly lower connectivity than the European average. THI trends ranged from strongly negative to strongly positive in all regions, with overall increases in northern and eastern regions (Alpine, Boreal, Continental, and Pannonial) and declines in western and southern regions (Atlantic and Mediterranean). Average tree connectivity trends therefore matched tree cover trends in eastern regions, while going in opposite directions in western, southern and northern regions. As of 2021, tree heterogeneity values in the Mediterranean (0.46), Pannonian/ Steppe (0.50), and Atlantic (0.53) regions fall below the European average.

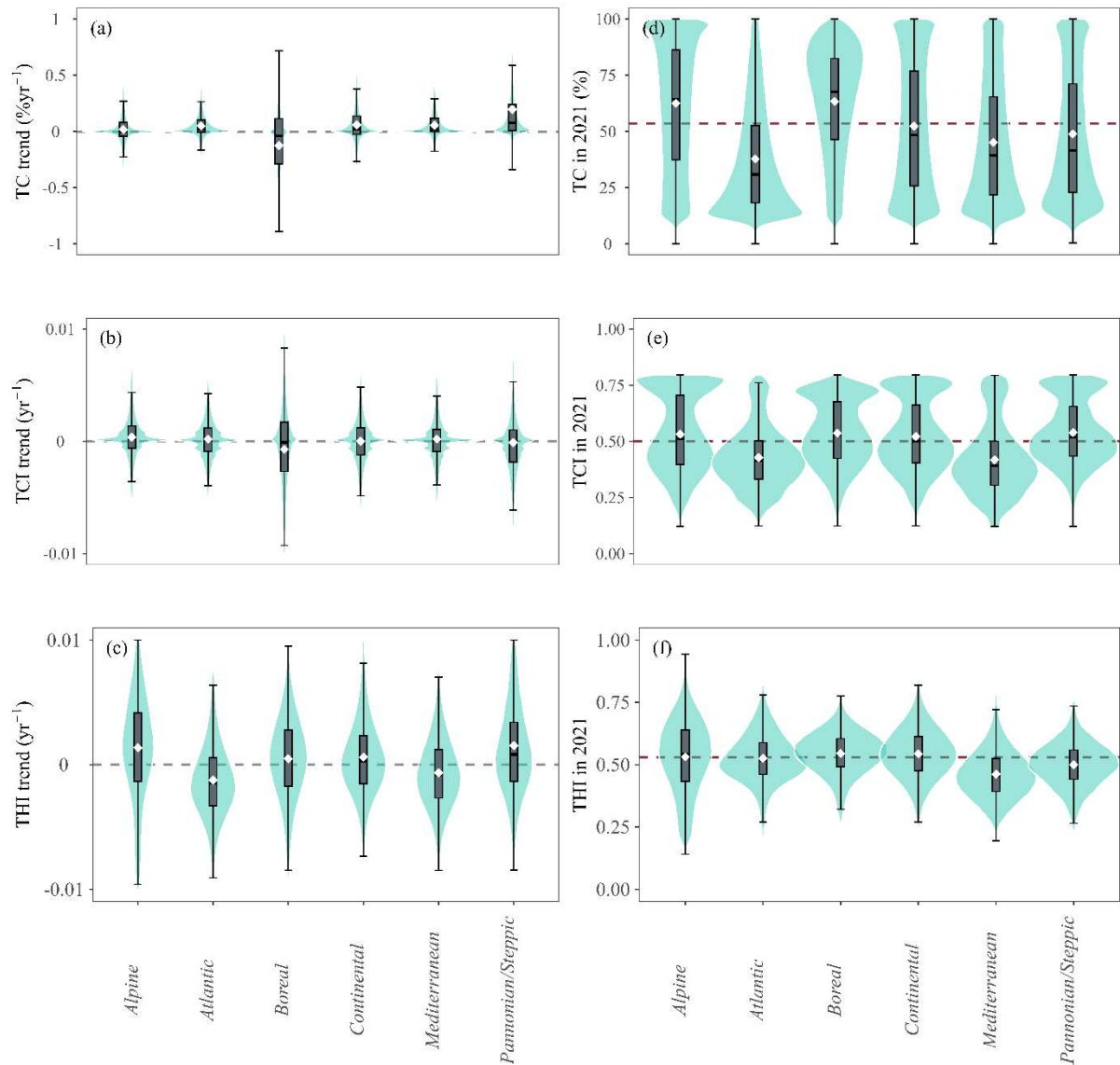


Fig.2 Trends and status (2021) of tree metrics across different biogeographic regions. (a) Tree cover (TC) trend, (b) tree connectivity index (TCI) trend, and (c) tree heterogeneity index (THI) trend, (d) TC in 2021, (e) TCI in 2021, (f) THI in 2021. This analysis included pixels with significant and nonsignificant trends from 2001 to 2021. The grey line in panels (a)-(c) denotes no trend, while the green line in panels (d)-(f) represents the average tree metric value across all biogeographic regions.

Tree dynamics across land management

Trends in tree cover vary significantly across different land management types (Fig. 3). Specifically, tree cover expanded substantially on former croplands, with an average increase of 0.24% per year, and 73% of former cropland areas exhibited an upward trend between 2001 and 2021. As forest management intensity decreases, the average tree cover trend increases, with an increase of 0.03%

per year under strict natural management to a decrease of -0.1% per year under intensive management. In 2021, forests managed at moderate intensity (i.e., those not under strict natural management or very intensive management) displayed high levels of tree cover, with averages exceeding 60%.

Trees established on former croplands exhibited the most pronounced increases in connectivity, with an average upward trend of 1.4×10^{-3} per year and increases observed in 66.2% of these areas. In contrast, forests under intensive management experienced the greatest decline in connectivity, averaging an annual decrease of -5.5×10^{-4} . In 2021, forests managed under various intensities generally maintained high connectivity levels, with average values ranging from 0.51 to 0.56. However, former croplands and strictly protected areas demonstrated relatively lower tree cover connectivity values, averaging 0.49 and 0.48, respectively.

Tree heterogeneity on average declined in the least managed vegetation, including strict protected areas, forests with strict nature management, and former croplands. Apart from forests managed at moderate intensity (i.e., those not under strict nature management or very intensive management), other land management categories exhibited a widespread decline in tree heterogeneity. Strictly protected areas showed the largest average decline trend at $-3.4 \times 10^{-3} \text{ yr}^{-1}$, followed by areas under strict nature management at $-1 \times 10^{-3} \text{ yr}^{-1}$, while former croplands exhibited an average decline of $-0.6 \times 10^{-3} \text{ yr}^{-1}$. Notably, 76% of strictly protected areas exhibited a declining trend, with extensive decreases observed in both spectral and structural heterogeneity (*Supplementary Fig. S5*). Strictly protected areas also had the lowest average tree heterogeneity, recorded at 0.38 in 2021. Similarly, tree heterogeneity declined in 62% of former cropland areas, which also exhibited comparatively low tree heterogeneity in 2021, with an average value of 0.45.

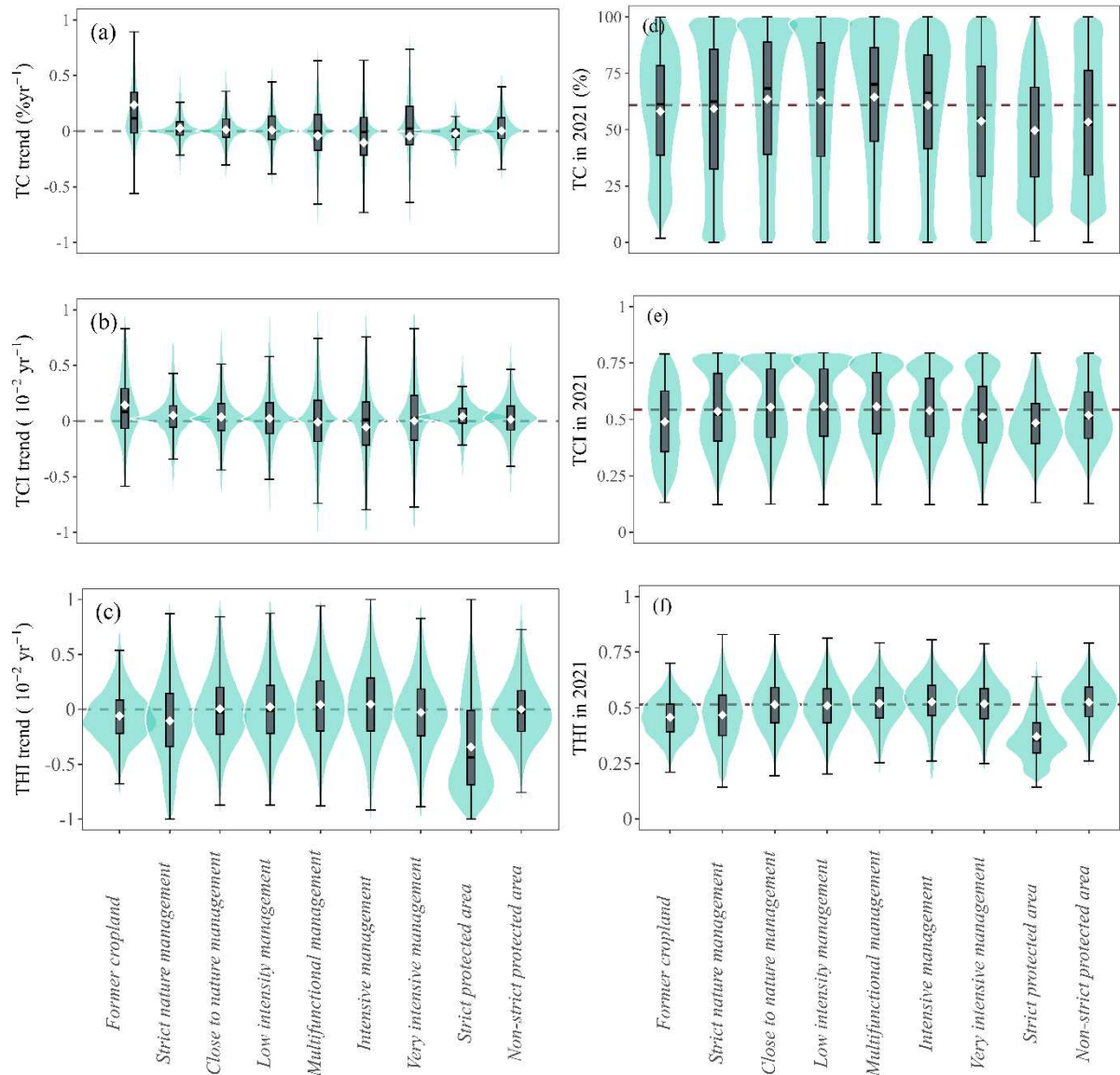


Fig.3 Trends and status of trees across land managements. **(a)** Tree cover (TC) trend, **(b)** Tree cover connectivity index (TCI) trend, and **(c)** Tree heterogeneity index (THI) trend, **(d)** TC in 2021, **(e)** TCI in 2021, **(f)** THI in 2021. This analysis included both significant and nonsignificant trends from 2001 to 2021. The grey line in panels (a)-(c) denotes a trend value of 0, while the red line in panels (d)-(f) represents the average metric value across all biogeographic regions.

Determinants of tree dynamics

Using Boosted Regression Tree (BRT) models, we examined the relative importance (Fig. 4) and relationships (Fig. 5) of various factors and our tree metrics trends. Mean annual temperature emerged as a dominant driver across all three metrics, contributing 42% to tree cover trends, 31.6% to connectivity trends, and 21.2% to heterogeneity trends. The relationships with temperature were

nonlinear and the optimal conditions for increasing tree cover and connectivity were observed in temperature climates with mean annual temperature between 8 °C and 12 °C, whereas tree heterogeneity trends increased most strongly between 0 °C and 5 °C. Partial dependence plots showed that the fraction of former cropland was strongly positively associated with increasing trends in tree cover and connectivity, with relative importances of 14.2% (the third most important factor) and 7.3%, respectively, but had little influence on trends in tree heterogeneity (1.8%; *Supplementary Fig. S7e*). Among disturbances, windstorms exerted a pronounced negative effect on tree cover trends, with relative influences of 19.7% on connectivity, 12.2% on connectivity, and 8.5% on tree heterogeneity. Accessibility to cities was the most influential variable for tree heterogeneity trends, accounting for 37.5%. Increased accessibility corresponded with a sharp decline in tree heterogeneity trends. (*Fig. 5i*). Topographic factors, such as elevation and slope, also play a substantial role in tree heterogeneity changes, with a relative importance of 11.5%. Notably, tree heterogeneity trends tended to increase as elevation rises.

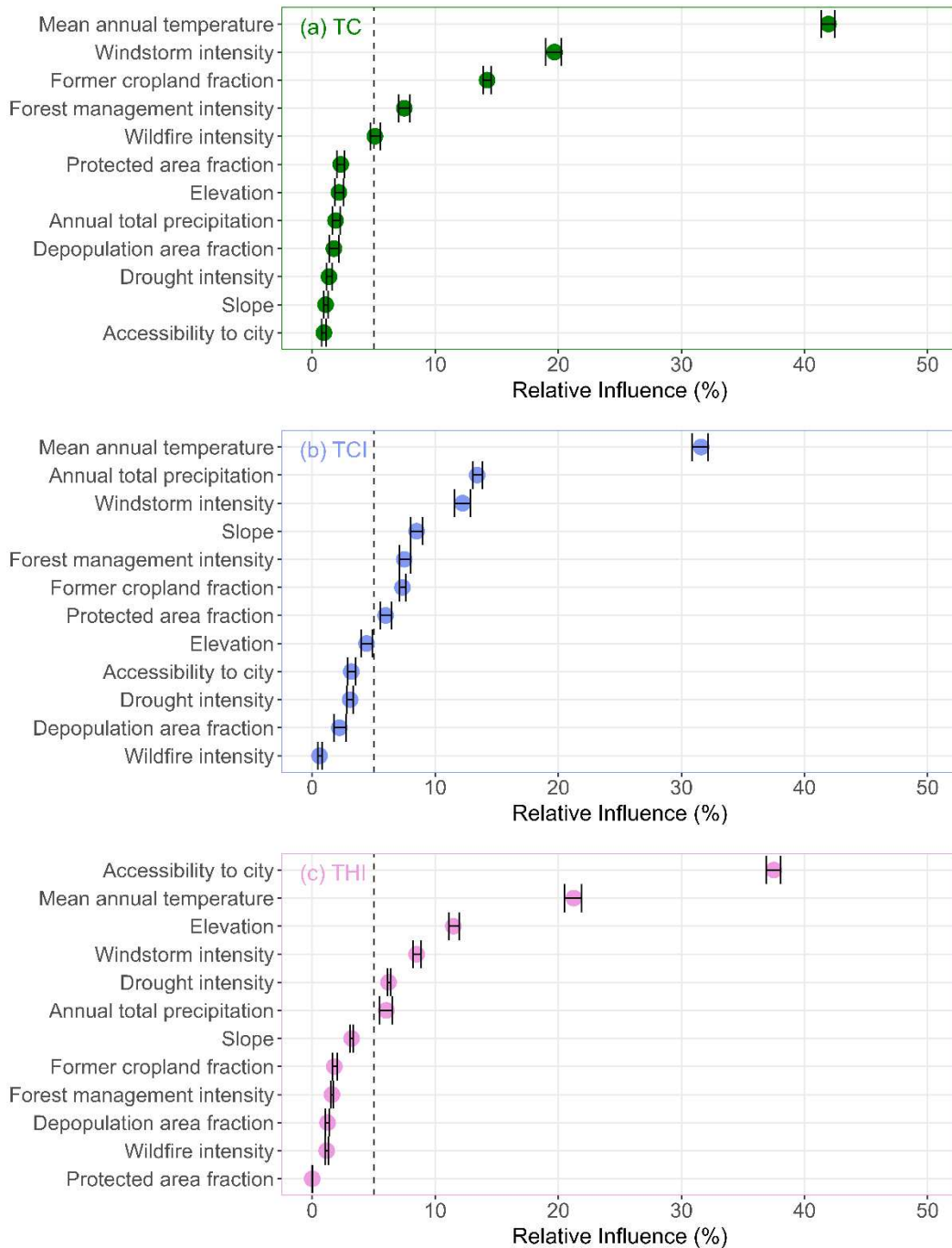


Fig 4. Relative influence of topography, climate, disturbance, land management, and human activities on changes in (a) Tree cover (TC), (b) Tree cover connectivity index (TCI), and (c) Tree heterogeneity index (THI) based on a series of BRT models. Points indicate the mean relative importance of a predictor across 99 runs of the BRT model. Bars represent the 2.5th and 97.5th percentiles of the relative influence distribution across runs. The vertical dashed line distinguishes predictors with relative influence higher or lower than the expected threshold of 5%.

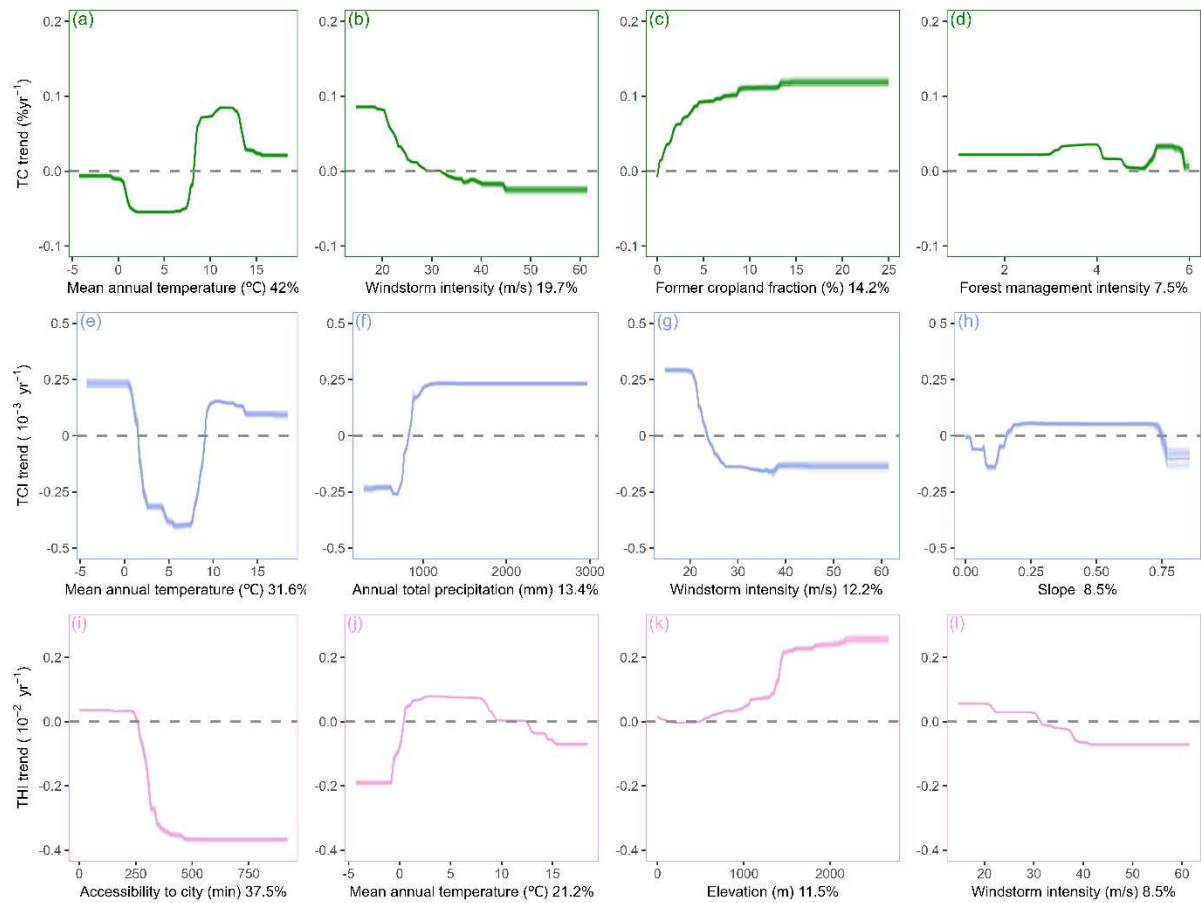


Fig 5. Partial dependence plots illustrate how the four most influential predictors affect the trends in tree cover metrics. Subfigures (a)–(d), (e)–(h), and (i)–(l) depict the relative expansion factors for the trends in tree cover (TC), connectivity (TCI), and heterogeneity (THI), respectively. Each line represents the fitted function from one of the 99 model runs. Additional partial dependence plots for the other eight predictors are provided in Supplementary Figures S6–S8.

Discussion

Tree cover increased across the majority of European land surface since 2001, with the strongest increases in Eastern, Central, and Southern Europe, and notable increases on former croplands. Increasing tree cover was associated with increased connectivity, but typically was associated with decreases in vegetation heterogeneity, indicating homogenization of vegetation structure and functioning. Our results reveal widespread succession toward increasingly dense woody vegetation that, while likely beneficial for forest-adapted taxa, can be expected to be suboptimal for overall European biodiversity, as most European taxa are adapted to semi-open and open habitats.

Tree cover increased throughout 58% of European land, which was consistent across biogeographic regions (5 out of 6) and countries (26 out of 33) (*Supplementary Fig. S2*). However, there was clear spatial patterning in tree cover dynamics with the strongest and spatially most coherent increases occurring in the Central and Eastern Europe, including in Lithuania, Poland, Slovakia, Hungary, Romania and the Balkan region. This region largely coincides with the former Eastern Bloc, where the dissolution of the former Soviet Union in 1991 marked a shift in political and socio-economic trajectories that strongly affected land-use, including widespread farmland abandonment^{25,31,32}. Parts of southern Europe also saw widespread and strong increases in tree cover, including the (southern) Apennine region in Italy and much of central and north-western Spain. These regions, along with the Eastern Alps, have experienced widespread abandonment of traditional pastoralist practices including seasonal cattle grazing of high-elevation meadows and sheep grazing on less productive and rugged terrain, partly as a result of the European Union's Common Agricultural Policy that dissuaded agricultural production in less productive regions³³⁻³⁶. To a lesser degree, large parts of France have also experienced increases in tree cover, potentially related to farmland abandonment but also discontinuation of management and harvesting on smaller, privately-owned forest plantations³⁷. Overall, the spatial patterns in tree cover increases strongly suggest a considerable contribution of natural vegetation succession toward increasingly dense and woody vegetation on land with a reduced land-use intensity.

In contrast, tree cover declines were more concentrated in space, e.g. with widespread declines related to cropping cycles of industrial forestry in Sweden and Finland. Strong, but more localized declines in tree cover took place in the hilly parts of central Germany, the Eastern Alps and the Czech Republic, consistent with bark-beetle outbreaks that predominantly kill widely planted *Picea abies* trees³⁸, the Landes region in southwestern France, consistent with storm damage and industrial forestry^{39,40}, and central Portugal, consistent with high fire activity over recent decades⁴¹.

Our analysis of potential drivers of trends in tree cover, connectivity and heterogeneity reveals that climate, natural disturbances, land management, and human activities all shape tree cover trajectories. Not surprisingly, temperature is a key determinant of woody vegetation dynamics (*Fig. 4*) as the study area spans from Mediterranean to Boreal climates and thus widely different conditions for tree and vegetation growth. Similarly, the pronounced negative influence of windstorms on all examined tree structure metrics consistent with previous research⁴². Interestingly, tree heterogeneity declined strongly with remoteness from cities (*Fig. 5i*), possibly reflecting the general global pattern that tree cover is higher on topographically complex terrain where human populations and disturbances tend to be lower⁴³.

However, the most notable potential driver were former croplands, which were strongly associated with increases in tree cover (*Fig. 3a, Fig. 5c*). This relationship may be partly explained by the afforestation of former croplands, but spontaneous vegetation succession resulting in semi-natural landscapes is the most common trajectory across Europe⁴⁴. Furthermore, our analysis was focused on croplands and did not consider land-use deintensification or abandonment of livestock grazing on rangelands and meadows, which would likely strengthen the signal of farmland abandonment in explaining tree cover increases. Finally, while tree cover increased on former croplands, decreases in heterogeneity were more common than increases (*Fig. 3c*), suggesting that vegetation succession resulted in overall homogenization of vegetation structure.

The widespread expansion of tree cover is likely to compromise the capacity of European ecosystems to sustain biodiversity and ecosystems that are resilient to ongoing climate change. The rationale for this expectation is twofold. First, the concurrent increase in tree-cover extent and

connectivity (the TC_↑TCI_↑ pattern; identified across 39% of the study area) indicates that numerous smaller tree patches arising from passive rewilding, afforestation or restoration efforts have merged into larger and denser, contiguous forest stands. While promoting habitat amount and connectivity for forest-adapted taxa, large increases in tree cover and connectivity are expected to be detrimental to taxa that are adapted to open or semi-open vegetation such as (mosaic) woodlands, shrublands and grasslands. However, the majority of the European flora and fauna are not adapted to closed-canopy forests. For example, there is comprehensive and strong evidence that most of the European flora, prefer less shading than is typical in closed-canopy forest¹⁰, extant mammal megafauna, prefer mosaic landscapes over closed canopies⁴⁵, 59% of European bird species are exclusively associated with non-forest habitats while only 14% of species is exclusively associated with forest habitats^{46,47}, and widespread arthropod groups including butterflies¹⁷ and bees⁴⁸ are strongly dependent on open habitats. The clear adaptations of European taxa to more open vegetation should be expected in light of their evolutionary history in megafauna dominated ecosystems, which prevented continuous canopy closure over large parts of Europe^{11,49-51}. The densification and homogenization of tree cover in Europe we document here thus likely risks diminishing open habitats, including woodlands, grasslands, and shrublands.

Secondly, tree-cover expansion was frequently associated with reduced habitat heterogeneity (the TC_↑THI_↓ pattern; observed in 33% of the study area). Since habitat heterogeneity and vegetation structural complexity are universally associated with high biodiversity^{19,52}, ongoing tree-cover expansion and declining heterogeneity are likely to lower the capacity of European ecosystems to support biodiversity⁵³. Restoration of fundamental ecosystem processes such as megafauna herbivory and natural fire regimes that promote ecosystem complexity and heterogeneity by suppression vegetation succession are, in turn, more likely to increase the biodiversity capacity of recovering European ecosystems^{54,55}.

One limitation of our study is that we could not provide a full attribution of tree cover dynamics in response to different forms of farmland abandonment and deintensification. First, there is uncertainty in the ESA-CCI cropland class and where we detected increased tree cover on former cropland it was not possible to determine directly if this was due to spontaneous succession or afforestation. However,

previous work has indicated that in the large majority of cases abandoned croplands in Europe experienced spontaneous revegetation⁴⁴. Second, the data did not allow for detecting deintensification or abandonment of grazing land, which have been important in promoting tree cover, as our tree-cover change maps also indicate. However, the inability to attribute tree cover change to land-use change on grazing land does not affect our main finding of widespread increases in tree cover, nor the finding that former croplands play an important role.

Our study acknowledges several uncertainties. For instance, the former cropland areas identified using ESA-CCI data may not precisely represent actual land abandonment, as it remains challenging to determine whether these lands underwent passive rewilding through natural succession, or were repurposed for short-rotation forestry, orchards, solar or wind energy installations. Each of these land trajectories could differently affect ecosystem functioning and biodiversity. Additionally, this study focused primarily on tree dynamics at the landscape scale, which might overlook the ecological roles of non-tree vegetation such as grasslands and shrublands. Future analyses should consider metrics that incorporate both tree and non-tree vegetation patches to better represent landscape functional complexity and improve our understanding of ecosystem responses⁵⁶. Furthermore, when constructing indices for tree-cover connectivity and heterogeneity, we equally weighted multiple standardized metrics to capture diverse aspects of connectivity and heterogeneity. However, the ecological implications of these individual metrics may differ, introducing uncertainty into the interpretation of our results. Finally, when examining the drivers of changes in tree metrics, data limitations restricted our ability to include certain potentially influential factors. For example, we did not account for other types of land-use de-intensification, such as pasture abandonment, or forestry land abandonment. Similarly, despite insect outbreaks being well-documented as a major natural disturbance affecting European forests⁵⁷, their impacts were not analyzed here due to the lack of consistent, long-term, large-scale datasets. Addressing these additional drivers in future studies could further clarify the complex dynamics shaping European tree-cover patterns.

We demonstrate widespread tree cover expansion across European ecosystems over the past two decades, frequently accompanied by declines in vegetation heterogeneity. These changes are

319 strongly associated with land-use deintensification and farmland abandonment, highlighting a broad
320 trend of spontaneous vegetation succession. While this trajectory offers substantial potential for climate
321 change mitigation and nature recovery, uninterrupted succession toward closed-canopy forests risks
322 reducing habitat diversity and limiting the biodiversity capacity of European landscapes. To fully realize
323 the ecological benefits of land-use deintensification, it is essential to restore natural disturbance regimes,
324 such as herbivory (via trophic rewilding)⁵⁴ and fire⁵⁸, that maintain structural complexity and promote
325 heterogeneity across scales. Without such interventions, Europe may miss a crucial opportunity to
326 support biodiverse, functionally rich, and climate-resilient ecosystems in the Anthropocene.

Online Methods

Datasets

Tree extent and height maps

Annual high-resolution (30m) tree canopy extent and height data from 2001 to 2021 in Europe⁵⁹ were used in this study to capture tree cover, connectivity and heterogeneity calculation. The tree extent and height products demonstrate high accuracy. Specifically, the root-mean-square-error (RMSE) for tree canopy height maps is ≤ 4 meters when compared to Airborne Laser Scanning and spaceborne GEDI LiDAR. Additionally, the user's and producer's accuracies for tree extent maps are both $\geq 94\%$ compared to reference samples. Forest extent and height can be obtained from https://glad.umd.edu/users/Potapov/Europe_TCH/Tree_Height/.

ESA-CCI-LC maps

ESA-CCI-LC provides an annual global land cover from 1992 to 2020 with a spatial resolution of 300 m (10 arc-second)⁶⁰. The ESA-CCI-LC dataset encompasses 37 distinct land cover classes, and we map abandonment for all six cropland classes. On a global scale, user's and producer's accuracies for cropland class were 81% and 92%, respectively, with an overall accuracy of 83%. Based on a latest published global land cover training dataset⁶¹, we conducted an assessment of cropland extent accuracy across Europe from 1999 to 2020. Results indicate mean user's and producer's accuracies of cropland were 82% and 91% in Europe, respectively, with a mean overall accuracy of 86%. (*Supplementary Table 1*). ESA-CCI-LC-based former cropland distribution can be accessed from *Supplementary Fig. S9*. ESA-CCI-LC product is accessible at <https://cds.climate.copernicus.eu/cdsapp#!/dataset/satellite-land-cover?tab=form>.

WDPA protection area

The World Database on Protected Areas (WDPA)^{62,63} offers a comprehensive global repository of marine and terrestrial protected areas. It contains six different categories of protected areas, namely strict nature reserves, wilderness areas, national parks, natural monuments, habitat/species management areas, and managed resource protected areas. When analyzing tree cover variations across land

management categories, we grouped strict nature reserves and wilderness areas into strictly protected areas, while other protected categories were classified as non-strict protected areas. This approach enabled a clearer understanding of how protection level influences tree cover dynamics. However, in the determinant analysis based on Boosted Regression Trees (BRT), all six protection categories were combined to calculate a unified "protected area fraction" within each statistical unit. We used the September 2023 version of the WDPA. The WDPA data can be retrieved from <https://www.protectedplanet.net/>.

Forest management strategies map

European forest management strategies map with 1km spatial resolution was developed based on biotic, abiotic, socio-economic and political categories and Bayesian belief network (BBN)⁶⁴. Which mapped six different forest strategies, including strict nature management, close to nature management, low intensity management, multifunctional management, intensive management, and very intensive management. We use values from 1 to 6 to represent the lowest forest management intensity to the highest management intensity.

Potential determinants

To better understand the determinants of tree dynamics in Europe, we considered five perspectives: topography, climate, disturbances, land management, and human activities. (1) We used the NASA/NGA Shuttle Radar Topography Mission (SRTM) data to extract topographical factors, accessible via the GEE data pool (CGIAR/SRTM90_V4)⁶⁵. (2) We derived climate data, namely, mean annual temperatures and annual total precipitations, from the ERA5 land reanalysis products⁶⁶. Specifically, we utilized air temperature data measured two meters above the land surface and accumulated precipitation data. These datasets are retrievable from the GEE (ECMWF/ERA5_LAND/MONTHLY_AGGR), with the ERA5 land data available at [doi:10.24381/cds.68d2bb30](https://doi.org/10.24381/cds.68d2bb30). (3) To evaluate disturbance factors, we sourced data on wildfire areas and frequencies from the MODIS burned area monthly products (MCD64A1)⁶⁷ between 2001 to 2021. Wildfire intensity was defined by combining the frequency and extent of wildfire events, calculated as the sum of the burned area multiplied by fire frequency within each statistical unit. Moreover,

windstorm intensity was defined using windstorm footprints⁶⁸ from the Copernicus Climate Change Service — Climate Data Store (<https://cds.climate.copernicus.eu#!/home>), we used maximum wind speed as an indicator of windstorm intensity, based on 60 wind footprints recorded from windstorm events between 2001 and 2021. For drought analysis, we employed the Global Standardized Precipitation Evapotranspiration Index (SPEI) dataset (0.25° spatial resolution, covering 2001 to 2021 at 360-day scales)⁶⁹ to quantify drought intensity, which can be calculated using equation 1. The SPEI dataset is accessible via <http://dx.doi.org/10.5281/zenodo.806026>. We also utilized accessibility-to-city data⁷⁰ from 2015 to represent travel time to urban centers, employing a 1 km × 1 km resolution map as one of our potential determinants (available at https://www.map.ox.ac.uk/accessibility_to_cities/). To quantify the impact of population decline on tree cover, we generated a depopulation area fraction variable based on GHS population data⁷¹ for 2000 and 2020 at a 100 m resolution. This variable is defined as the proportion of each 0.25° fishnet cell that experienced a population decrease from 2000 to 2020. The population data can be accessed via GEE (JRC/GHSL/P2023A/GHS_POP). *Supplementary Fig. S11* shows the correlation coefficients among all the used determinant factors.

$$Drought\ intensity = \sum_1^T (-SPEI_i) \quad (1)$$

where T represents the time when the SPEI is below a threshold, which in this study was defined as -2 to define extreme drought⁶⁹.

Biogeographical region

The Biogeographical Regions Europe 2016 dataset provides the official delineations defined under the Habitats Directive and used in the EMERALD network design under the Convention on the Conservation of European Wildlife and Natural Habitats. We utilized this shapefile to better understand variations in tree cover patterns and trends across different biogeographic regions. The data is available from the European Environment Agency at <http://www.eea.europa.eu/>.

403 Country administrative areas

404 The administrative boundaries of each country were obtained from the Eurostat's Nomenclature of
405 Territorial Units for Statistics (NUTS, <https://ec.europa.eu/eurostat>), we used the latest version (NUTS
406 2021) in this study.

407 Tree cover metrics

408 Tree cover (TC) serves as a metric indicating the percentage of canopy cover within each grid cell,
409 which can vary from 0 to 100%. A positive trend in TC is interpreted as an increase in the density and/or
410 extent of the tree canopy, The calculation of TC was carried out on a grid with a resolution of 1 km x 1
411 km, employing the following formula:

$$412 \quad TC = \frac{\sum_1^N A_{tree_i}}{A_0} \quad (2)$$

413 Here, $\sum_1^N A_{tree_i}$ represents the total area of trees within the grid, and A_0 represents the area of each grid
414 cell, set at 1 km² in this study.

415 Forest fragmentation is primarily characterized by edge effects, isolation effects, and patch size
416 effects^{72,73}. While these factors highlight the disruptions in forest continuity, they also serve as a
417 foundation for understanding tree cover connectivity. Therefore, to better quantify connectivity, we
418 assess these fragmentation aspects using landscape pattern metrics. Specifically, patch density (PD)
419 represents the isolation effect, patch edge density (ED) reflects the edge effect, and mean patch area
420 (MPA) captures the patch size effect. By integrating these metrics, we shift the focus from fragmentation
421 to connectivity, enabling a more comprehensive understanding of forest spatial patterns. To this end,
422 we developed a synthetic tree connectivity index (TCI) by normalizing and combining ED, PD, and
423 MPA indices using the following equations. The TCI ranges from 0 to 1, with 1 representing the highest
424 connectivity of trees. All metrics were calculated from within a 1-km grid cell using 30 m resolution
425 tree extent data by employing the "landscapemetrics" package⁷⁴ in R⁷⁵ (version 4.0.2).

$$426 \quad ED = \frac{\sum_{k=1}^m e_{ik}}{A} * 10,000 \quad (3)$$

$$PD = \frac{n_i}{A} * 10,000 * 100 \quad (4)$$

$$MPA = \text{mean}(\text{AREA}[\text{patch}_{ij}]) \quad (5)$$

$$V_{nor} = (V - Q_1)/(Q_3 - Q_1) \quad (6)$$

$$TCI = \text{Average}((1 - ED_{nor}), (1 - PD_{nor}), MPA) \quad (7)$$

where e_{ik} is the total edge length of forest patches in meters, n_i is the number of forest patches, $\text{AREA}[\text{patch}_{ij}]$ is the area of each forest patch in hectares. V represents the target variables that need to be normalized, which can be ED, PD, and MPA. V_{nor} is the value of the normalized indicator (ED, PD, or MPA). The normalized values range from 0 to 1. The lower bound, Q_1 , is calculated as the 25th percentile value minus 1.5 times the interquartile range (IQR). The upper bound, Q_3 , is calculated as the 75th percentile value plus 1.5 times the IQR. The IQR is the difference between the 75th and 25th percentile values. This normalization method accurately and intuitively represents data distribution, as landscape pattern metrics do not follow a normal distribution. To manage extreme outliers, we set pixel values that exceeded the upper and lower limits to the corresponding boundary values.

Environmental heterogeneity is a key factor influencing biodiversity due to the increased availability of ecological niches. Forest structural complexity serves as a key metric for quantifying heterogeneity within forests and has also been recognized as an important proxy for biodiversity^{76,77}. Meanwhile, the spatial variability of spectral information derived from remote sensing provides a valuable baseline for the rapid estimation of forest species diversity^{78,79}. Here, to capture these dimensions, we developed a tree heterogeneity index (THI) by integrating two critical components: structural and spectral diversity. Structural heterogeneity was quantified using the standard deviation of tree height variation, Spectral heterogeneity was evaluated using the standard deviation of annual minimum, mean, and maximum annual kernel normalized difference vegetation index (kNDVI)⁸⁰ values. We chose kNDVI over other vegetation indices as it provides a more accurate estimation of vegetation traits⁸¹. All the Landsat images (155,504 scenes) from 2001 to 2021 were used to calculate the kNDVI. All Landsat surface reflectance products were provided by Google Earth Engine⁸² (<https://developers.google.com/earth->

engine/datasets), processed for cloud removal. All metrics, representing structural, spectral, and phenological aspects, were normalized to a scale of 0 to 1 using the same method applied in the calculation of the TCI. The THI was then constructed as the average of these normalized metrics, providing a comprehensive measure of tree heterogeneity.

$$NDVI = \frac{(\rho_{nir} - \rho_{red})}{(\rho_{nir} + \rho_{red})} \quad (8)$$

$$kNDVI = \tanh(NDVI)^2 \quad (9)$$

$$THI = Average(Std_{height_{nor}}, Std_{kNDVI_{min_{nor}}}, Std_{kNDVI_{mean_{nor}}}, Std_{kNDVI_{max_{nor}}}) \quad (10)$$

where ρ_{nir} and ρ_{red} represent the red band and near-infrared band surface reflectance, respectively.

Std represents the coefficient of the indicator within $1 \text{ km} \times 1 \text{ km}$ grid.

Former cropland mapping

Using time-series data from the ESA Land Cover dataset, we identified the former cropland through a sequential classification and detection process. First, we categorized land cover into three broad classes: cropland (encompassing ESA land cover codes 10, 11, 12, 20, 30, and 40); (semi-)natural vegetation, (including codes 50, 60, 61, 62, 70, 71, 72, 80, 81, 82, 90, 100, 110, 120, 121, 122, and 130); and other land cover types. Next, we delineated historically stable cropland as areas consistently classified as cropland between 1992 and 1996, while currently (semi-)natural vegetation was defined as pixels that remained classified as (semi-) natural vegetation from 2016 to 2020. We then identified cropland abandonment events as instances where a pixel, previously classified as cropland, transitioned to a non-cropland category for at least five consecutive years, following the definition provided by the Food and Agriculture Organization of the United Nations⁸³. Finally, we defined the former cropland as areas that overlapped historically stable cropland, were classified as (semi-)natural vegetation in recent years, and had experienced at least one abandonment event between 1996 and 2016. We compared our former cropland areas with the reduction in arable cropland reported by the UN FAO crop dynamics land cover dataset from 1996 to 2021. On a national scale. This comparison revealed a significant correlation (p-value < 0.05 , $R^2 = 0.53$) (*Supplementary Fig. S8c*). We randomly selected 429 validation samples (112

former cropland and 317 non-former cropland) using high-resolution satellite images from Google Earth combined with Landsat imagery. Our accuracy assessment showed an overall accuracy of 92%, user's accuracy of 71%, producer's accuracy of 95%, and an F1-score of 0.82 for identifying former cropland areas. These results align closely with previous study⁸⁴, confirming the robustness of our classification approach.

Trends in tree cover metrics

We evaluated trends in annual TC, TCI, and THI from 2001 to 2021 using the Partitioned Autoregressive Time Series (PART) approach^{30,85}, which can consider both temporal and spatial autocorrelation. The 'remotePARTS' package in R was utilized to conduct this analysis.

Statistical modeling

To model the relationship between the selected explanatory variables and the dynamics of tree conditions, we employed boosted regression trees (BRTs). BRTs were chosen due to their ability to uncover nonlinear relationships and detect complex interactions among covariates. Moreover, they are relatively robust against overfitting⁸⁶, making them suitable for our analysis. The BRT models were constructed using the `gbm.step` routine from the `dismo` package⁸⁷, with parameters set as follows: number of trees (`n.trees`) = 1000, interaction depth = 2, and shrinkage = 0.01. For each predictor, we evaluated the relative influence and generated partial dependence plots to visualize the marginal effects of the predictors on the response variable. The response variables were the mean trends of tree cover metrics in each 0.25-degree statistic unit.

Data availability

All data are published and publicly available on Zenodo at [<https://zenodo.org/uploads/15309568>].

Code availability

The code used in this study can be found on Github at [<https://github.com/WanbenWu/EuropeanTreeDynamics>].

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