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ORIGINAL RESEARCH PAPER

Changes in forest cover in Sudety Mountains during the last 250 years: patterns, drivers, and landscape-scale implications for nature conservation

Tomasz Henryk Szymura[1]*, Sandra Murak[1], Magdalena Szymura[2], Małgorzata Wiktoria Raduła[1]

[1] Department of Ecology, Biogeochemistry and Environmental Protection, University of Wrocław, Kanonia 6/8, 50-328 Wrocław, Poland
[2] Institute of Agroecology and Plant Production, Faculty of Life Sciences and Technology, Wrocław University of Environmental and Life Sciences, pl. Grunwaldzki 24A, 50-363 Wrocław, Poland

* Corresponding author. Email: tomasz.szymura@uwr.edu.pl

Abstract
Historical ecology gives a reference point to explain the contemporary state of particular ecosystems as well as entire landscapes. In this study, we examined the quantitative changes in forest cover in the central part of the Sudety Massif (area ca. 1,120 km^2) during the last 250 years. The information regarding forest patch distribution and its changes was derived by comparison of maps from 1747 and the 1970s drawn at scales of 1:33,000 and 1:25,000, respectively. To examine the effect of environmental variables (topography and soil conditions) and human population density on forest patch distribution and its changes (afforestation, deforestation), a set of 100 circular plots with a diameter of 1 km was established. The influence of explanatory variables was examined using regression tree methods. Changes at the level of the entire landscape were tested using a set of 25 landscape windows (5 × 5 km each). We found that the overall forest cover increased to 36.4% in the twentieth century from 30.4% in the middle of the eighteenth century. The ancient forests constituted 59% of the total forest area existing more recently. The forests in the eighteenth century occurred mostly on steep slopes, deep valley bottoms, and summits. The land relief explains more than half of the total variation in forest distribution ($R^2 = 0.56$). The effects of soil type and human population density were negligible. The contemporary forest pattern results from both land relief and the historical pattern of human population density in the middle of the eighteenth century ($R^2 = 0.64$), while the effect of soil type was negligible. The pattern of deforestation ($R^2 = 0.53$) and afforestation ($R^2 = 0.36$) results from both land relief as well as recent and nineteenth-century human population density. About 83% of the recent forest area is in physical contact with patches of the ancient forest, which provides an optimistic outlook for the migration of ancient forest species into new areas. Furthermore, changes in landscape structure reveal increased connectivity among forest patches, with potential benefits for the migration of forest species with long-range dispersal.

Keywords
ancient forests; deforestation; historical ecology; landscape fragmentation; recent forests

Introduction

Fragmentation and habitat loss are among the most influential factors causing recent declines in biodiversity [1,2]. To understand the recent landscape structure better, it is important to recognize how it has changed from a historical point of view. Studies on historical ecology assess the magnitude, character and dynamics of landscape changes, and thus they provide reference points when attempting to identify the contemporary state of a landscape [3,4]. They can also reveal whether natural or anthropogenic factors have changed over space and time and how they affect particular habitats. Moreover, understanding the past helps us to predict future changes in a landscape structure [3–6]. From a practical point of view, historical ecology provides a valuable template for nature conservation and restoration planning: firstly, the ecological continuity of habitats affects recent biodiversity levels [7,8], and secondly, historical ecology allows the setting of restoration references and targets as well as providing an insight into the appropriate location and distribution of habitats to develop landscape-level conservation strategies [3,9,10]. Thirdly, historical land use legacies (e.g., changes in chemical properties of soil) influence site properties by determining their potential for restoration [7,9,11,12].

In Central Europe, one of the most pronounced landscape changes has involved changes in the extent of forest cover over the last millennium [6,13]. The average forest cover on land suitable for agriculture in Central and Western Europe declined from 77% in 1000 BC to 6% in 1850 AD [13]. Because forests create a specific environment for plants and animals, a group of species typical of forests can be distinguished. Species in this group are commonly found in long-lasting patches of forest but are virtually absent in recently afforested lands, often due to their limited long-range dispersal ability [8,14–16]. This phenomenon is well known in nature conservation, thus for practical reason an "ancient forest" has been defined as an area continuously forested since some threshold date [10,17–19]. The threshold is related to the availability of documentation and varies from ca. 1600 in England and Wales to ca. 1780 in Poland and Germany [17,19,20]. Patches of ancient forest are considered as more valuable for nature conservation than recent forests (that is, forest created artificially on previously nonforested grounds). Therefore, sites intended for afforestation should be placed next to patches of ancient forests in order to enable ancient forest species migration [7,14,21,22]. Due to the phenomenon of extinction debt, the actual species richness in a patch can be influenced by past events. In Central European forests, the recent species richness still reflects episodes that occurred in the previous century, such as forest patch shrinkage or loss of connectivity between forest patches [23,24]. Therefore, historical knowledge regarding forest distribution is necessary for understanding the recent species richness distribution, as well as for conservation management planning [11,25].

The changing distribution of forests alters the opportunity for migration of forest species, both plants and animals, not only in terms of colonization of a recent forest by an ancient forest species, but also by changing the opportunity for migration at the entire landscape scale [26]. Conservation planners need to preserve resilient habitat networks, and this requires identification of habitat patches and corridors that are crucial for maintaining or establishing the connectivity of fragmented populations [25–27]. Changes in the landscape structure also affect the mutualistic relationships between plants and pollinating insects, which may, among others, limit the availability of pollen and consequently decrease the viability of plant populations [28]. It is well known that changes in landscape connectivity affect species distribution, and therefore knowing the historical pattern is crucial for better understanding recent patterns of biodiversity [29–31]. Such knowledge also improves management plans at the landscape scale [10,32].

The examination of landscape changes requires historical maps. Nowadays, GIS techniques allow us to quantitatively analyze historical data [33]. In Poland, access to historical maps is limited [34], and therefore the usefulness of such historical maps in ecological studies is rather restricted [21,35–37]. The historical analysis has concentrated mostly on the Carpathian region [38–41]. As a consequence, there is a lack of available data regarding ancient forest distribution, drivers of land use/land cover changes, as well as the historical structure of the landscape. Therefore, there is a lack of available data for assessing recent processes and patterns. Moreover, previous studies did not directly test the effect of human population density changes, which is potentially a significant driver of changes in forest cover [42,43].

The Silesian part of the Sudety Massif is a region that has been dramatically altered by human activities [44]. However, some surviving forest complexes have retained a high level of biodiversity [44–46], and the return of some forest animals, e.g., large predators such as the wolf *Canis lupus* and lynx *Lynx lynx*, to formerly inhabited areas, has recently been observed [47]. These patterns and ecological processes can be explained by considering historical changes in landscape structure, and such historical knowledge seems to be valuable for nature conservation planning.

In this study, we reconstructed forest distributions in the middle of the eighteenth century. We delimited patches of ancient forest, recent forest, as well as deforested areas by comparison with contemporary forest cover. Using this data, we focused on: (***i***) finding social and environmental drivers of forest distribution in the eighteenth century and recently, (***ii***) defining factors influencing the deforestation and afforestation process over the centuries, and (***iii***) examining changes in forest landscape structure over the last 250 years in a quantitative fashion.

Material and methods

Study area

The study was performed in five regions in the Polish part of the Sudety Massif: Brama Lubawska, Góry Kamienne, Góry Wałbrzyskie, Pogórze Wałbrzyskie, and Rudawy Janowickie, in total covering ca. 1,120 km^2. The study area is found at low elevation in the Central European mountains, mountain valleys, and foothills (altitude ranging from 280 to 809 m a.s.l.) (Fig. 1A). The average annual temperature is about 6.2°C, the annual total precipitation is 688.4 mm, and almost 40% of the rainfall (274 mm) falls during the summer season [48].

The study area was settled at least in the Bronze Age, with the first serious forest clearings being noted in the thirteenth century [49,50]. In the Middle Ages and in the Early Modern Period, the region was relatively densely populated and industrially well developed, mostly due to textile production and metal mining [49–51]. In the early nineteenth century, rural areas were highly overpopulated [50,51]. The development of coal mining and industry caused a further increase in the human population and its movement to towns and cities in the nineteenth century [50,51]. This phenomenon led to the depopulation of rural areas, and this trend continued after World War II [49–51].

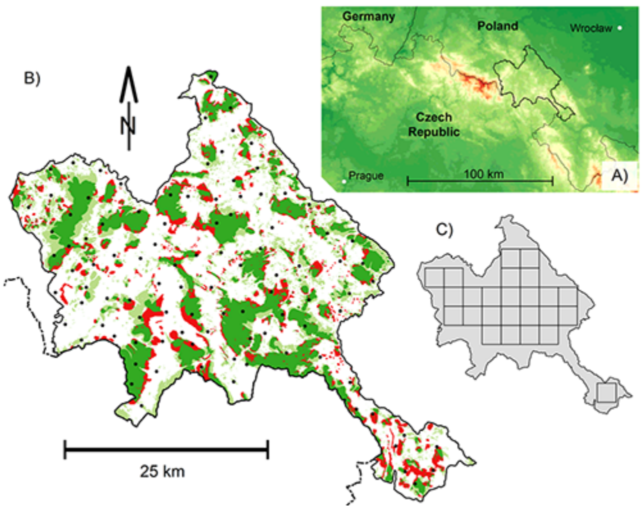

Fig. 1 Location of study area (solid black line) in terms of altitude (**A**); the study plots (black dots) on a background of ancient forest (dark green), recent forest (light green), and deforestation (red) (**B**); and location of 5 × 5 km squares for landscape analysis (**C**).

Studied forest

The natural potential vegetation of the study area varies from alluvial forest in valleys, through oak-hornbeam and eutrophic beech forests on mesic and eutrophic soils to acidophilus beech and oak forest on poor soils. On slopes of steep valleys, ravine forests with lime and maple are considered as natural potential vegetation [52]. Through the centuries, the forests have been altered by different human activities. There has been no detailed study devoted strictly to the study area, but the use of forest was most probably multipurpose, based on information for the whole of Silesia. The forest was used for bee-keeping, pannage, litter-racking, and cattle pasturing, and management has ranged from coppicing with standard techniques to large-size timber production by clear cutting and partial cutting [49,53,54]. Rational silviculture (i.e., partial cutting with different rotation periods for softwood and hardwood species and dividing forests into compartments) began as early as the sixteenth century [49]. Large-scale modern forestry with artificial afforestation and the promotion of Norway spruce (*Picea abies*) plantations started in the middle of the eighteenth century, alongside the start of the Prussian administration of Silesia [49,53]. Very little data is available regarding the species composition of forests in the eighteenth century, making it impossible to reconstruct the stand structure [49,54]. Recently, the stands have consisted mostly of Norway spruce (*Picea abies*) plantations, which dominate the forest, with a small proportion of beech (*Fagus sylvatica*), oaks (*Quercus petrea* and *Q. robur*), birch (*Betula pendula*), and larch (*Larix decidua*) [55,56].

Cartographic sources and explanatory variables

Forest distribution in the middle of the eighteenth century was reconstructed on the basis of the "Kriegeskarte von Schlesien" (hereafter called "Kriegskarte"), a set of maps at 1:33,000 scale prepared by Prussian military cartographers in 1747. On the margins of each map sheet, there is a list of settlements shown on the map and the number of inhabitants. Detailed descriptions of this map set were given by Janczak [57] and Szymura et al. [34]. Individual sheets of the Kriegskarte were calibrated and registered in the Polish State Geodetic Coordinate System 1992 using the control points method [58]. The median value of the residual mean square error of map calibration is 123 m. The recent distribution of forests was determined from topographic maps at 1:25,000 scale prepared in the Polish coordinate system "1965"; the map sheets show the situation in 1977. The latter maps were chosen due to their scale, which corresponds to that of the Kriegskarte. The contemporary topographical maps were also registered in the coordinate system "1992". Then, the forest patches present on both map sets were digitized manually using the "on screen" method. Two types of land use were distinguished: forests and nonforests. The smallest forest patch on the Kriegskarte had an area of 0.3 ha, while on the topographic maps the smallest patch was 0.03 ha.

A set of data including altitude, land relief, topsoil properties, and human population density was collected. A digital elevation model from the Shuttle Radar Topography Mission [59], with a resolution of 90 × 90 m, was used to calculate the primary and secondary topographic metrics. Data stored in the Harmonized World Soil Database v. 1.2 (HWSD) [60] were used to calculate soil characteristics (database spatial resolution of 30 arc seconds, ca. 1 × 1 km). The base soil mapping unit (SMU) used in HWSD contains data on the dominant and associated soil types, including the percentage of different soil types that they share within the SMU. For each SMU, we calculated the average value of particular soil characteristics, weighted by percentage of a given soil type. Additionally, we acquired data on the dominant soil type within entire mapping units. The results of these calculations were converted to a set of raster maps with a resolution of 1 × 1 km. The population size in settlements was obtained from the Kirgskarte (for the eighteenth century), Kartenmeister Database [61] (1840 and 1930), and from the Polish Geographical Object Database [62] (for recent population size). A detailed description of explanatory variables, including data sources, is given in Appendix S2.

Analytical methods

The digitalized maps were rasterized to a grid with a resolution of 20 × 20 m. Grids representing historical and recent forest distribution were used to delimit the area of ancient forests (that is forest patches present in the study region since 1747), recent forests (forests planted after 1747), and deforestation (patches of land deforested after 1747). The map, presented in GeoTIFF format (Appendix S1), was used to calculate the overall percentage of forest cover and its changes. The number and area of recent forest patches that were adjacent to ancient forest patches were also calculated.

To find the main explanatory variables for forest percentage cover and its changes, a set of 100 random sampling plots was established (Fig. 1B) using the "random points" tool in QGIS software. Each plot was circular with a 0.5-km radius (area 77 ha). The dimension of the plots was adjusted to local topography, in order to sample a relatively uniform environment and to reflect forest patch size at the landscape scale. The percentage of forest cover and forest cover changes, as well as the average or dominant values of explanatory variables, were used to characterise each plot. The effect of human population density was calculated as the sum of the human population in circular buffers with 1-km, 2-km, and 5-km radius from the center of each sampling point. A list of explanatory variables used for modelling and their descriptive statistics is presented in Tab. 1.

To examine changes in landscape pattern during the studied period, a net of 5 × 5-km squares was established. The size of the squares was adjusted to the acreage and shape of the study area, and to the size used for landscape scale-studies in Central Europe [63,64]. For 25 squares placed within the study area (Fig. 1C), a set of principal landscape metrics, robust for habitat area changes, was calculated for both study periods [65,66]. At the patch level, we examined changes in: patch area, shape, and isolation. The following metrics were calculated:

- Area weighted average area (AREA_AM) – this is the average patch area, but instead of a simple arithmetic mean, the average is weighted by patch size. As a result, the influence of the largest patches on this metric is stronger than that of smaller forest patches. This metric provides a landscape-based perspective of patch structure because it reflects the average conditions of a pixel chosen at random or the conditions that an animal dropped at random into the landscape would experience.
- Perimeter-area fractal dimension (PAFRAC) – this provides an index of patch shape complexity across a wide range of patch sizes. Specifically, it describes the power relationship between patch area and perimeter, and thus describes how patch perimeter increases per unit increase in patch area.
- As a measure of patch isolation, the area weighted average proximity index (PROX_AM) was calculated – this quantifies the spatial context of a patch in relation to its neighbors; specifically, the index distinguishes sparse distributions of small habitat patches from configurations where the habitat forms a complex cluster of larger patches [65,66].

As a measurement of entire landscape fragmentation, subdivision metrics (in the sense of McGarigal [65]) were used: clumpiness (CLUMPY) and number of patches (NP). The CLUMPY is a normalized index depicting the deviation from a random distribution, i.e., distinguishing distributions that are more uniform than random and more aggregated [65,66].

The explanatory ability of topographic and soil variables, as well as human population data, was checked using the regression tree method. The model was evaluated using the V-fold cross validation ($V = 3$) according to rule of 1 standard deviation [67,68]. The difference between the eighteenth and twentieth century in terms of forest cover and landscape patterns was tested using the Wilcoxon signed-rank test. All work with maps and the spatial and statistical analyses were done using the QGis and SAGA software, with the exception of the landscape analysis, for which Fragstat was used.

Results

The distribution of ancient forest, recent forest and deforestation is shown in Fig. 1B. The high-resolution map, which can be used in most GIS software, is presented in Appendix S1. The forest covered 30.4% (342 km^2) of the study area in the eighteenth century, and 36.4% (408 km^2) in the twentieth century. The ancient forest constituted 58.8% (240 km^2), and the recent forest 41.1% (168 km^2), of the contemporary forest area (Fig. 1B). Among all patches of recent forests, less than half of them (46%) were connected with the ancient forest (that is adjacent to patches of ancient forest). However, most of the isolated afforestations were rather small in size. As a result, 83% of the recent forest acreage was joined directly to patches of ancient forest (Fig. 1B).

The forests were distributed unevenly throughout the study area, resulting in large variations in percentage forest cover in particular plots, ranging from 0% to 100% in both studied periods (Tab. 2). The average percentage of forest cover in the twentieth century was higher than in the eighteenth century ($T = 1808.0$, $p = 0.02$).

Tab. 1 Descriptive statistics of explanatory variables calculated for sampling plots ($N = 100$). Abbreviations of variable names are defined in Appendix S2.

Variable	Abbreviation	Unit	Average	*SD*	Median	Lower quartile	Upper quartile	Minimum	Maximum
Elevation	Alt.	m a.s.l.	523	110	514	450	594	280	809
Slope	Slope	°	6.8	3.4	6.5	3.9	9.1	0.9	15.4
Diurnal anisotropic heating	DAH	-	0.00	0.05	−0.007	−0.036	0.03	−0.173	0.1
Topographic roughness index	TRI	-	26.6	13.2	25.1	16.5	36.1	4.0	62.1
Topographic wetness index	TWI	-	12.03	0.64	11.974	11.581	12.47	10.800	13.8
Topographic position index	TPI	-	2.99	28.36	0.840	−16.680	21.47	−69.660	98.1
Soil depth	Depth	cm	79.7	19.2	93.0	56.0	93.0	0.0	100.0
Organic carbon	OC	%	1.47	0.37	1.270	1.270	1.70	0.000	2.0
pH	pH	-	5.72	0.94	6.270	5.120	6.27	0.000	7.0
Sand fraction	Sand	%	44.7	16.0	34.8	32.5	62.6	0.0	71.7
Number of citizens in settlement in 2000 in 5-km buffer	N_2000_5	-	15,372	26,500	6,397	3,505	14,100	293	135,562
Number of citizens in settlement in 1905 in 5-km buffer	N_1905_5	-	7,948	5,510	6,061	3,687	10,281	1,025	29,559
Number of citizens in settlement in 1840 in 5-km buffer	N_1840_5	-	5,465	1,824	5,339	4,245	6,669	1,134	9,935
Number of citizens in settlement in 1746 in 5-km buffer	N_1746_5	-	677	260	650	491	814	211	1,621
Number of citizens in settlement in 2000 in 2-km buffer	N_2000_2	-	7,367	19,752	1,496	772	5,056	0	112,702
Number of citizens in settlement in 1905 in 2-km buffer	N_1905_2	-	3,340	3,769	1,750	1,082	4,286	0	16,435
Number of citizens in settlement in 1840 in 2-km buffer	N_1840_2	-	2,138	1,275	1,897	1,140	2,717	0	6,638
Number of citizens in settlement in 1746 in 2-km buffer	N_1746_2	-	260	155	232	166	332	0	865
Number of citizens in settlement in 2000 in 1-km buffer	N_2000_1	-	353	2,083	0	0	93	0	20,386
Number of citizens in settlement in 1905 in 1-km buffer	N_1905_1	-	379	1,491	0	0	264	0	13,018
Number of citizens in settlement in 1840 in 1-km buffer	N_1840_1	-	217	419	0	0	347	0	2,230
Number of citizens in settlement in 1746 in 1-km buffer	N_1746_1	-	34	81	0	0	67	0	674

Tab. 2 Descriptive statistics of historical and contemporary forest cover, as well as deforestation, afforestation, and ancient forest percentage in sampling plots (N = 100).

Variable	Unit	Average	*SD*	Median	Lower quartile	Upper quartile	Minimum	Maximum
Forest in eighteen century	%	32.9	36.2	12.4	0.1	66.7	0.0	100.0
Forest in twentieth century	%	39.4	35.6	30.2	4.1	71.3	0.0	100.0
Deforestation	%	9.1	14.2	2.9	0.0	11.6	0.0	67.8
Recent forests (afforestation)	%	15.5	19.5	5.9	0.6	25.1	0.0	78.7
Ancient forests	%	23.8	32.7	4.3	0.0	42.7	0.0	100.0

The descriptive statistics of explanatory variables are shown in Tab. 1. The study area is dominated by Eutric Cambisols (51%), and then the following soils: Umbric Leptosols (21%), Dystric Cambisols (18%), Eutric Fluvisols (8%), and Urban soils (2%). Environmental and demographic data explained a significant amount of the variation regarding the pattern of percentage forest cover and its changes over time. The percentage of forest cover in the eighteenth century was related exclusively to land relief features and altitude. The highest percentage of forest was observed on steep slopes (inclination >8.1°), especially on hilltops and valley bottoms (Fig. 2A). The contemporary distribution of forest was explained by land relief and human population density in the eighteenth century. In summary, contemporary forest patches are found in areas with rough terrain that had a low population density in the middle of the eighteenth century (Fig. 2B). The patterns of deforestation and afforestation were best explained by the complex interaction of human population density, land relief, and altitude. Deforestation was high in areas with high contemporary human population density, while afforested areas were rather wet areas. Relatively low deforestation and high afforestation at lower altitudes (around 500 m a.s.l) were also observed (Fig. 2C,D). The soil traits did not explain the patterns of distribution.

From the landscape perspective, the changes included establishing numerous small forest patches, as well as increasing the area of large forest patches (Fig. 1A, Fig. 3, Tab. 3). As a result of these two processes, the area-weighted mean patch area did not change significantly between the two study periods (Fig. 3, Tab. 3), but the shape of forest patches has become more complex than in the eighteenth century, as denoted by the higher values of PAFRAC. Forest patches have also become less isolated, as indicated by the higher PROX_AM index. Forest patches in the eighteenth century were more aggregated than they were more recently and the increasing number of patches suggests that the modern landscape is less fragmented than the historical one (Tab. 3).

Discussion

Forest cover and global drivers of changes in forest cover

The historical level of forest cover (average 30.4%) in the study area was relatively low compared to other European mountain areas. The average forest cover of eighteenth-century Europe was 42%, the forest cover in Carinthia (Alps) was 41%, while in Transylvania (Carpathians) it was 48% [4,69]. During the same period, the percentage of forest cover in the Karkonosze Mts (Sudety) was 45% [34] and, at the very beginning of the nineteenth century, it was 41% in the Świętokrzyskie Mts [70]. The rather low forest cover of the study area was attributed to the relatively low altitude of the region, which increases its agricultural potential and the density of the human population. Moreover, the study area was located in a densely populated and well-developed region between Bohemia and Silesia. However, given the altitude and human population density of comparable mountainous regions, such as the Belgian Ardennes, the forest cover in the eighteenth century could have been as low as 18% [71]. At that time, the forest cover in the lowlands could have been even lower: in Bohemia, in the vicinity of Kutna Hora,

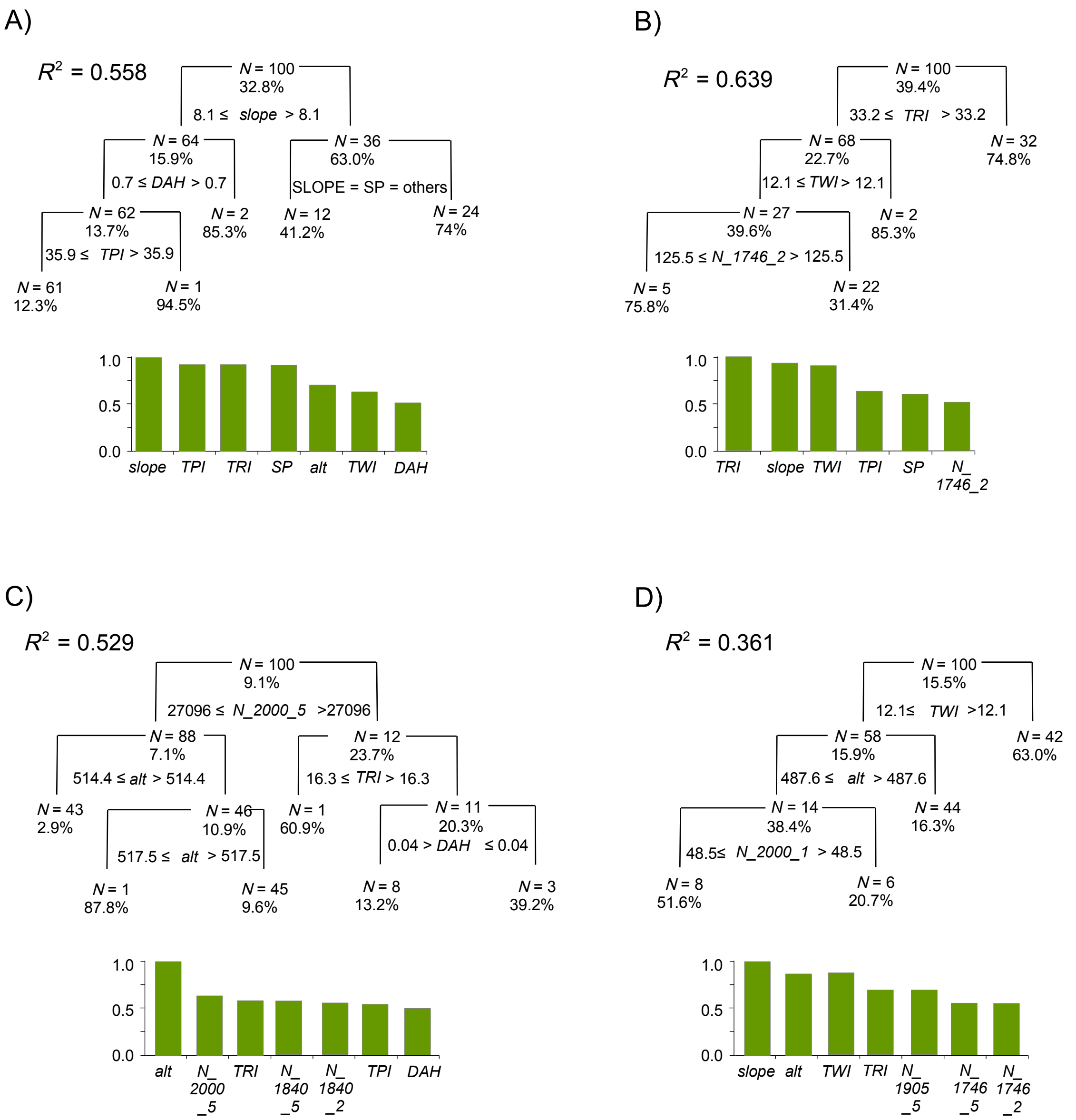

Fig. 2 Results of regression trees for forest cover in the eighteenth (**A**) and twentieth century (**B**), deforestation (**C**), and afforestation (**D**). The amount of variation explained by models (R^2) and importance values of factors are shown besides the regression trees. Only variables with the highest importance value for a particular model are shown. Abbreviations: alt – elevation; DAH – diurnal anisotropic heating; N_1746_2 – number of citizens in settlement in 1746 in 2-km buffer; N_1746_5 – number of citizens in settlement in 1746 in 5-km buffer; N_1840_2 – number of citizens in settlement in 1840 in 2-km buffer; N_1840_5 – number of citizens in settlement in 1840 in 5-km buffer; N_1905_5 – number of citizens in settlement in 1905 in 5-km buffer; N_2000_1 – number of citizens in settlement in 2000 in 1-km buffer; N_2000_1 – number of citizens in settlement in 1840 in 1-km buffer; SP – slope position; TPI – topographic position index; TRI – topographic roughness index.

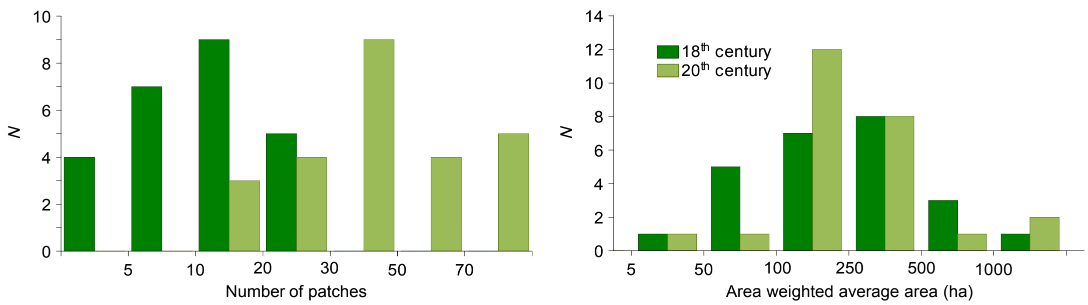

Fig. 3 Distribution of patch number (left graph) and area weighted average patch area (right graph) of forest in 5 × 5-km squares in the eighteenth and twentieth century.

Tab. 3 Basic statistics and results of landscape metrics comparison (T, p) in the eighteenth and twentieth centuries. Statistically significant differences are indicated in bold. The abbreviations are defined in the "Material and methods" section.

Metrics	Abbreviation	Time period	Average	SD	Median	Lower quartile	Upper quartile	Minimum	Maximum	T	p
Number of patches	NP	18	12.56	6.72	11.00	7.00	17.00	4.00	26.00	**0.000**	**0.000**
		20	45.56	22.29	39.00	30.00	60.00	11.00	90.00		
Area weighted average patch area	AREA_AM	18	315.9	265.8	249.8	101.0	411.0	39.8	1142.7	157.00	0.882
		20	325.5	281.9	223.2	156.3	385.1	37.9	1210.6		
Perimeter-area fractal dimension	PAFRAC	18	1.160	0.076	1.156	1.126	1.197	0.994	1.312	**17.000**	**0.015**
		20	1.235	0.059	1.238	1.191	1.264	1.135	1.361		
Area weighted average proximity index	PROX_AM	18	40.53	26.62	45.19	5.48	52.94	0.22	152.04	**23.000**	**0.001**
		20	290.34	101.13	638.68	52.72	250.40	3.49	3126.92		
Clumpiness	CLUMPY	18	0.966	0.011	0.967	0.959	0.974	0.944	0.983	**0.000**	**0.000**
		20	0.928	0.024	0.933	0.921	0.943	0.865	0.965		

forest cover reached 16.6% [72], while in Flanders (northern Belgium) it was only 9.7% [10].

The main determinants of land-use shift are global changes, which are amplified or attenuated by the effect of local factors [73]. In the context of this study, the low forest cover in the eighteenth-century Europe led to a shortage of wood, which was considered a strategic problem throughout European countries [74]. To overcome this shortage, a plan to increase the forest cover in Silesia, along with modern effective forest management, was implemented by Fredric the Great, the king of Prussia. Particular attention was paid to the forests of Sudety, for the management of which a special royal commission was established in 1777 [49,53]. This new Prussian forest policy was very effective and led to an increase in forest cover from 45% to 69% in the Karkonosze Mts in the period 1747–1824 [34]. The politics of forest management generally continued through the nineteenth and twentieth century and led to stable wood production and an increase in forest cover [49,53].

Local drivers of changes in forest cover

The forests in the eighteenth century were unevenly distributed. The results suggest that land relief was a major driver of the land-use system: forest persisted mostly on slopes, v-shaped valley bottoms, and convex hilltops (Fig. 2A), while flatlands were usually deforested. This could be attributed to timber transport difficulties and the high risk of erosion that would make such sites less suitable for agriculture. The results did not show a role for soil properties or population density as drivers of forest cover in the eighteenth century. An effect of soil properties on forest cover was shown for the Central European lowlands [36,42,43], where more fertile soils were usually deforested. Similarly, Ciupa et al. [70] found a higher deforestation rate on soil suitable for agriculture in the Świętokrzyskie Mts, however this was not tested statistically. We assume that in the studied region a relatively complex land relief caused the patchy distribution of forest and agricultural lands (Fig. 1B), and that the land relief effect overrides the influence of soil type. Moreover, Wulff et al. [43] found that soil condition had contrasting effects: deforested soils were fertile and in high demand by farmers (Phaeozems), while forest was restricted to low productivity sandy soils. In our study, the differentiation among soil types was not as extreme, because the Eutric Cambisols with moderate agricultural usefulness were the most productive soil types in our study area.

The influence of land relief on forest distribution is also visible more recently: the highest percentage of forest was observed in areas with high land surface roughness. However, recent forest cover has also been affected by historical legacies of human population density. Areas with a higher population density in the middle of the eighteenth century are currently less forested than areas with a lower historical human population density. We related this to economic acceleration, which began in Silesia in the second part of the eighteenth century, as a result of Frederic the Great's policies. Thus, while preindustrial human settlements did not significantly influence the pattern of forest cover in the eighteenth century, the effect of population density from the beginning of the industrial revolution is still visible. Deforestation can be attributed to the recent human population density pattern related to post-WWII industry and mining development, and further modified by land relief. The lack of effect of soil type was also attributed to industrial development, which contrary to agriculture, is not related to soil productivity. The pattern of lower deforestation and higher afforestation at lower altitudes is interpreted as a kind of historical dependency. At lower altitudes, the forest had already been felled, and thus there was a high potential for afforestation and only limited potential for deforestation.

Landscape scale processes

The results of the landscape-scale analysis revealed that contemporary forests are less fragmented than in the eighteenth century. Therefore, we hypothesize that there has been more opportunity for species migration, with effective long-range dispersion, recently than there was historically. However, the migration of forest species is also influenced by other factors that were not analyzed here: habitat quality, increased landscape resistance caused by human population grow, and/or increasing density of roads and traffic intensity [75]. In the case of organisms with limited dispersal ability, the current landscape structure is quite favorable because most of the recent forests' acreage (83%) is adjacent to ancient forest. De Keersmaeker et al. [10] showed that in Flanders, only 13.6% of recent forest is physically connected with ancient forests. The favorable pattern of recent forest distribution can be attributed to the effect of land relief on afforestation. Afforested areas were less suitable for agriculture due to land relief. Usually in nearby areas with unsuitable for agriculture land relief, the forest cover in the eighteenth century was already high. This spatial pattern caused as the creation of large, solid forest complex. Such an interaction does not exist in the lowlands, and thus de Keersmaeker et al. [10] found that the percentage of recent forest adjoining ancient forest was much lower.

Summary

This study reveals the primacy of land relief over soil type as a factor controlling the historical pattern of forest cover. The complex land relief also causes high spatial variability in historical forest cover. Changes in forest cover began in the eighteenth century and included both substantial deforestation and afforestation; however, the entire process was dominated by afforestation. The pattern of forest cover was again driven by land relief but with a significant influence from local human population density, while soil type was not decisive. These processes resulted in the highly diversified spatial pattern of forest cover observed nowadays, where more than 50% of the total forested area is comprised of ancient forests, which are potentially valuable for nature conservation. From the landscape-scale perspective, the changes have increased landscape connectivity for forest species, including species with efficient long-range dispersal, as well as typical ancient forest species with limited dispersal ability. From the practical point of view, maps of ancient forest distribution, such as those presented here, should be used by conservationists to prioritize conservation efforts. At the landscape scale, it would be ideal if lands designated for afforestation were placed next to ancient forest to enhance migration opportunities.

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Supplementary material

The following supplementary material for this article is available at http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.3576/0:

Appendix S1 Map of ancient forest distribution, recent forest and deforestation. The map is in GeoTIFF format registered in Polish PUWG 1992 coordinate system (EPSG code 2180). The cell size is 20 × 20 m. Deforestation code – 1; recent forest code – 2; ancient forest code – 3; nonforests – 0.

Appendix S2 Description of explanatory variables.

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