

## Article

# Past Disturbance–Present Diversity: How the Coexistence of Four Different Forest Communities within One Patch of a Homogeneous Geological Substrate Is Possible

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**Abstract:** Understanding the relationship between disturbance and forest community dynamics is a key factor in sustainable forest management and conservation planning. The study aimed to determine the main factors driving unusual differentiation of forest vegetation into four communities, all coexisting on the same geological substrate. The fieldwork, conducted on the fluvioglacial sand area in Central Poland, consisted of vegetation sampling, together with soil identification and sampling, up to depths of 150 cm. Additional soil parameters were measured in the laboratory. A Geographical Information System was applied to assess variables related to topography and forest continuity. Vegetation was classified and forest communities identified. Canonical Correspondence Analysis indicated significant effects of organic horizon thickness, forest continuity, soil disturbance and soil organic matter content on vegetation composition. We found that the coexistence of four forest communities, including two Natura 2000 habitats, a *Cladonia*-Scots pine forest and an acidophilous oak forest (codes–91T0 and 9190 respectively), resulted from former agricultural use of the land followed by secondary succession. The lowest soil-disturbance level was observed within late-successional acidophilous oak forest patches. Nearly complete soil erosion was found within the early-successional *Cladonia*-Scots pine forest. We propose that both protected habitat types may belong to the same successional sere, and discuss the possibility of replacement of the early- and late-successional forest habitat types in the context of sustainable forest management and conservation.

**Keywords:** *Cladonia*-Scots pine forest; acidophilous oak forest; Natura 2000; tillage; Central Europe; successional sere



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## 1. Introduction

### 1.1. Soil Conditions and Disturbance as Factors Influencing Forest Ecosystems

A deep understanding of forest community dynamics is essential for sustainable forest management and nature conservation planning, e.g., [1,2]. Habitat properties are among the most important primary factors influencing forest community composition [3–5] and are strongly connected with geology [6,7]. Soil conditions, such as organic matter content, reaction, nutrient availability, and moisture, affect the differentiation of forest communities [7,8]. For example, deciduous forest usually occupies more fertile habitats than coniferous forest, cfr. [8,9]. The effect of soil conditions can be modified by local topography, disturbance and forest management [10].

The most common natural disturbances are avalanches, flooding, fluctuations in moisture regime, herbivory, insect outbreaks, landslides, rockfalls, surface and crown wildfires, and windthrows [1,2]. The impact of anthropogenic disturbances (e.g., agricultural clearing, logging, anthropogenic fires) may have even greater effects on forest ecosystems [11]. Deforestation and subsequent agricultural use are the most serious disturbances to vegeta-

tion, leading to the complete disappearance of forest ecosystems, which has occurred in European lowlands since neolithic times [12].

One of the main agrotechnical operations influencing the physical, chemical and biological properties of soil is tillage [13–15]. Agricultural use greatly changes the accumulation of soil organic matter, especially in low-productivity soils [16]. It also accelerates erosion and can lead to soil truncation, degradation and transformation [17,18], thus influencing its differentiation [19].

### 1.2. Influence of Land Use Change on Oligotrophic Forest Dynamics and Forest Conservation in Central Europe

Land-use change is considered one of the main drivers of ecosystem dynamics worldwide [20]. Presently, land abandonment is the most frequent reason for landscape change across Europe [21]. This highly dynamic process is driven by a combination of socio-economic, political and environmental factors and influences biodiversity and ecosystem services [22]. It is followed by vegetation succession and seems to be a generally suitable method of ecosystem restoration, resulting mainly in the formation of secondary forests [23]. In Poland, the agriculture located on low-productivity sandy soils (called Arenosols) was largely abandoned. Nowadays they are predominantly covered by secondary pine forests [24].

Ecological succession plays an important role in shaping vegetation structure within both early- [25,26] and late-successional [27,28] ecosystems. The abandonment of traditional forest utilization and changes in anthropogenic disturbance regimes are being observed [29,30]. During the last century, many changes in Central European forest communities were observed, including the decrease in oligotrophic pine and oak forests and the expansion of more fertile forest communities, e.g., [27,31–35]. Many of the most vulnerable forest communities have been protected as Natura 2000 habitats [36]. One of the most threatened forest habitats in lowland Central Europe is the *Cladonia*-Scots pine forest *Cladonio-Pinetum* Juraszek 1927 (code: 91T0), which is in decline throughout its entire range, as described in e.g., [33,35,37]. On the other hand, acidophilous oak forest (code: 9190) in Central Europe has expanded [38,39]. While they are protected, many well-preserved patches are found in unprotected sites [40]. Both habitat types occur on sandy soils called Arenosols. Pine forest plantations can be converted into oak forest [41,42], especially on more fertile habitats. The spontaneous ingrowth of oak through forest regeneration is also possible [43], but the possibility of conversion of *Cladonia* Scots-pine forests to acidophilous oak forests has not been considered in detail. Moreover, these habitat types need different conservation management approaches, cfr. [37,44,45], and for this reason, it is necessary to decide which habitat type to protect—the early- or late-successional one.

### 1.3. Aim

A uniquely diverse forest vegetation was identified in Central Poland, on an oligotrophic sandy site near the village of Kiedrzyń. It consists of abandoned fields, initial, lichen-rich Scots-pine forests, mid-successional moss and dwarf-shrub dominated Scots-pine forests, mixed oak–pine forests and acidophilous sessile oak forests. The aim of this study was to determine the main drivers of differentiation of these forest communities occurring on the same geological substrate. Our specific goal was to assess the impact of past deforestation and soil degradation caused by tillage on the recent diversity of the described forest mosaic, including both regularly and traditionally managed patches.

## 2. Materials and Methods

### 2.1. Study Site

The study was carried out within part of a forest complex (ca. 200 ha) located in Central Poland, in the vicinity of Kiedrzyń (20°43' E 51°35' N). The area is covered by deep (up to 20 m) fluvioglacial loose sand deposits. They are partially denudated, with an admixture of loose diluvial sands in local depressions [46]. According to WBR (2015) [47]

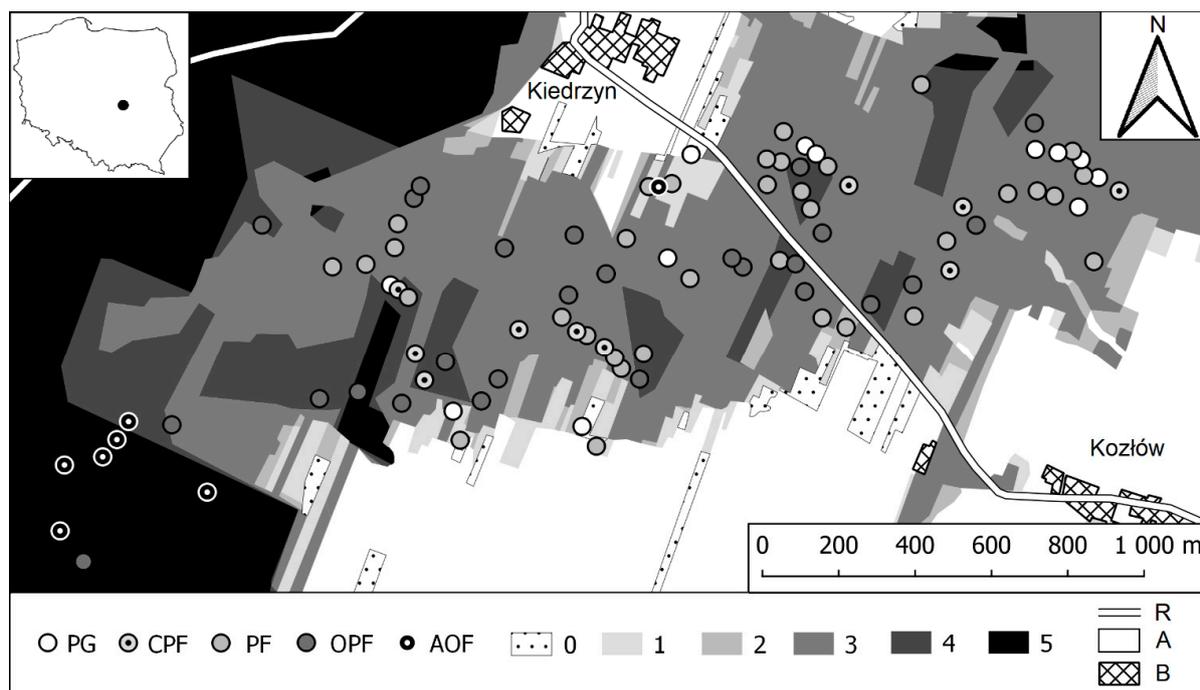
all of the soils within the research area belong to the Arenosol. At the beginning of the 20th century, the central and north-eastern parts of the site were used as arable land [48], after which most of the fields were gradually abandoned and spontaneously overgrown or planted with Scots-pine [49–51]. Many phytogenic hillocks are present within parts of the previously arable area. Such landforms are indicators of soil erosion by wind [52]. The southwestern part of the study site remained afforested during the last century. It is covered by mixed Scots-pine and sessile oak forests. The mature oak stands, located in the south-western part of the site, are managed by State Forests. According to information obtained from local forest administrators and residents, confirmed by our own observations, they are of old (around 1900 years) coppice origin. The remaining area is private property covered mainly by naturally regenerated pine forests, with single-tree cutting of Scots pine being the dominant management practice. This accelerates the natural regeneration of sessile oak, which encroach into the young secondary pine stands. Nowadays, most of the area is covered by forest, including two EU Natura 2000 habitat types, acidophilous oak forests (code: 9190) and *Cladonia* Scots-pine forests (code: 91T0) together with pine and mixed oak-pine forest communities. Abandoned fields with psammophilous grasslands (code: 2330), sparsely overgrown with Scots pine, are also admixed.

## 2.2. Fieldwork

Fieldwork was conducted during the 2016 growing season. A set of 90 circular sample plots (400 m<sup>2</sup> each) were designated within the study area (Figure 1). One sample per vegetation type in each forest subdivision was collected within State Forest lands, located in central parts of subdivisions or habitat patches. On private land the wide diversity of vegetation and local management types made it impossible to apply a regular sampling scheme. Forest division boundaries differed significantly from stand borders and habitat patches. Thus, the main aim there was to sample internally homogeneous patches, differing in vegetation structure, soil disturbance or management type. Management type was defined as traditional (natural succession, uneven stand age, single-tree cutting) or regular (planted, even age stands with regular thinning). Vegetation was sampled using the Barkman et al. (1964) [53] scale, with cover the measure of species abundance, due to the preference for pure cover scales in ecological studies [53,54]. The terrain slope angle was measured with an inclinometer. Within each plot, small soil pits (ca 50 cm deep) were made, deepened with an auger to a depth of 150 cm, and soil samples were collected at depths of 10, 30, 70 and 150 cm. In addition, soil profiles were described, soil horizons distinguished, the presence of plough disturbance determined, and the thickness of the organic matter horizon measured. The Munsell scale (2009) [55] was additionally used for color description to confirm the identification of the Bv diagnostic horizon [56], which is also a Brunic qualifier [47]. The locations of study plots were registered using GPS.

## 2.3. Laboratory Analysis

Sieving of soil samples was performed using a mesh size of 0.1 mm (fine sand), with the remaining <0.1 mm fraction representing very fine sand, silt and clay. Before chemical analysis, the collected soil samples were cleaned using a 1-mm sieve. The conductivity and pH of the samples collected at a depth of 10 cm were determined using an electronic pH/conductivity meter in a suspension of 1 part sand and 5 parts distilled water by volume (10:50) after standing for 24 h. The total organic matter content in topsoil (samples collected from a depth of 10 cm) was measured as loss on ignition at 550 °C.



**Figure 1.** Vegetation types and continuity of forest occurrence in the study area (habitat types: PG—psammophilous grassland, CPF—*Cladonia*-Scots pine forest, PF—pine forest, OPF—oak-pine mixed forest, AOF—acidophilous oak-forest; forest continuity: 0—abandoned fields, still not afforested in 2014, 1—afforested in 2014 (but not in 2001), 2—afforested since 2001 (but not in 1982), 3—afforested since 1982 (but not in 1935), 4—afforested since 1935 (but not in 1915), 5—afforested since 1915; R—main roads, A—arable land, B—built up areas).

## 2.4. Data Preparation and Analysis

### 2.4.1. Data Preparation

Vegetation data were arithmetically transformed according to Tüxen and Ellenberg (1937) [57] before analysis (Table S1 in Supplementary Materials). The forest continuity rank of the sample sites (Table 1) was estimated on the basis of historical topographical maps from the years 1915 [48], 1935 [49] and 1982 [50], as well as orthophotomaps from 2001 and 2014 [51]. Older map sheets from 1915 and 1935 required georeferencing. To do so, the entire map sheets were screen calibrated with the use of recent 1:5000 orthophotomaps [51] as a coordinate source, with 20 evenly distributed control points chosen for each dataset. Only points whose locations were assumed unchanged through time (e.g., road junctions) were used. Old maps are usually not fully cartometric, meaning they contain some distortions in angles and distances. A second order polynomial function was used for map transformation, as it usually helps to reduce map inaccuracy. The root mean square error (RMSE) of the georeferenced map from 1915 was 31.22 m, and of the map from 1935 was 24.77 m. The local georeferencing procedure can additionally improve the cartometricity of the source maps [58]. Its purpose is to georeference not the whole sheet, but individual fragments independently. In this instance, the same 20-point calibration procedure was repeated, but only for smaller parts of map sheets in the vicinity of the research site. Total RMSEs remained similar (32.92 m for the map from 1915, and 24.12 m for the 1935 dataset), but the visual alignment of the content of the maps improved. Both datasets contained many permanent dirt roads and their junctions, located inside the study site. They served successfully as control points. In addition, some old borders of the surveyed forests stayed stable. Both dirt roads and some old forest edges could still be recognized on recent orthophotomaps. For these reasons, we considered that the cartometricity of the old datasets was sufficient to prepare the map of forest continuity for the study site.

**Table 1.** Cartographic materials used for preparation of forest continuity rank (“zero” value was assigned if forest was not present in the most recent dataset, with higher ranks assigned when forest cover was present in earlier datasets, starting from the youngest).

No of Dataset	Dataset Scale	Actuality	Type of Dataset	Source of Dataset	Forest Continuity Rank Value
1	1:100,000	1915	topographic map	[39]	5
2	1:100,000	1935	topographic map	[40]	4
3	1:10,000	1982	topographic map	[41]	3
4	1:5000	2001	orthophotomap	[42]	2
5	1:5000	2014	orthophotomap	[42]	1

Forest cover was digitized separately for each dataset. Then the vector forest data were geoprocessed with the intersect, difference and union GIS tools to produce one map of forest continuity rank (Figure 1). If forest cover was lacking in the “older” dataset, the rank of the “younger” value was assigned regardless of the presence of forest on even older maps. Temporary deforestation was rarely observed in the study site and was not recorded at any of the studied plots, so it was not taken into the account as a possible additional variable. Thus, the rank value assigned for each sample plot was the number of datasets with the presence of forest cover, starting from the most recent one (Table 1). If forest cover was not observed in the dataset from 2014 (corresponding to recently abandoned fields sparsely covered with young trees), the “zero” rank value was assigned. The average minimum sampling-point distance to the closest boundary of the forest continuity patches was 61.60 m and in case of boundaries derived from georeferenced material 97.72 m respectively.

A high resolution (1 m grid cell with 0.15 m mean height error) Digital Elevation Model (DEM) was used [51] to calculate the Topographic Position Index (TPI). This index is defined as the difference between the elevation at a cell and the average elevation of cells within a predetermined radius [59]. Values greater than zero indicate locations higher than average (e.g., ridges). Negative values of TPI show lower elevation locations (e.g., valleys). Values close to zero indicate flat areas and constant slopes. Calculation of TPI at the fine scale (100 m radius) is considered appropriate for ecological research [59]. TPI can correlate with the ecological characteristics of the site [60]. Three TPIs were calculated at 25 m, 50 m and 100 m radii, respectively. Ground water level was calculated on the basis of DEM and a hydrogeological site map [61]. The assessment of forest continuity and TPI were conducted with QGIS 3 and SAGA 2 software [62,63].

The maximum <0.1 mm % fraction was calculated separately for each soil profile. Soil disturbance rank (Table 2) was assigned to each plot, corresponding to soil denudation levels described for Brunic Arenosols from Central Europe [18,64].

**Table 2.** The ordinal scale of soil disturbance; descriptions are based on [18,64] criteria for Reference Soil Groups, principal and supplementary qualifiers based on WBR (2015) [47] and Kabata et al. (2019) [56].

Soil Disturbance Rank	Description of the Disturbance Level Detected in the Soil Profile	Differentiating Criteria	Reference Soil Group, Principal and Supplementary Qualifiers
1	no soil disturbance detected	surface soil horizon present; brunic qualifier present; ploughing layer absent	Brunic Arenosol
2	ploughing disturbance detected; soil profile erosion absent or small (Bv horizon present)	surface soil horizon present; brunic qualifier present; ploughing layer present	Aric Brunic Arenosol
3	ploughing disturbance detected; soil profile erosion strong (degradation of Bv horizon)	surface soil horizon present; brunic qualifier absent; ploughing layer present	Aric Haplic Arenosol
4	ploughing disturbance detected; soil profile erosion very strong (degradation of Bv horizon), including the strong erosion of surface (A) soil horizon (<10 cm); in addition, traces of old dune processes (phytogenic hillocks) often present	only remnants of surface soil horizon and/or ploughing layer present; brunic qualifier absent	Protic Arenosol (incl. Aric Protic Arenosol)

#### 2.4.2. Data Analysis

The environmental variables used in this study were of two types: Scale variables, included pH; conductivity and organic matter content in the soil at a 10 cm depth; organic horizon thickness, mass percent <0.1 mm fraction in the profile; TPIs at 25 m, 50 m and 100 m radii; and slope and ground water level. Rank and nominal variables were soil disturbance, forest continuity and traditional management (Table S2 in Supplementary materials). All of these scale, rank and nominal variables were assessed using Spearman's rank correlation prior to analysis (Table S3 in Supplementary materials). Conductivity and TPI at 50 m radius were excluded from further analysis due to high collinearity (Spearman's  $r > 0.7$ ). Their simple effects (the variation explained by single variables without covariables) were lower than for other colinear variables (Table S4 in Supplementary Materials). Non-scale variables were treated as factors (aggregations of nominal or categorical variables). Canonical Correspondence Analysis (CCA) was performed. Whole vegetation dataset was used. A square root vegetation data transformation and downweighting of rare species were applied. A forward selection procedure was applied to all variables not excluded in order to identify those that were significant. Selection was stopped at  $p$ -value = 0.05 and the final CCA model was determined (Figure 2). The significance of variable effects and species–environment relations were checked with a Monte Carlo test (9999 permutations). The false discovery rate method was used for probability adjustment. Differences in the values of significant environmental variables between vegetation types were checked by non-parametric Kruskal–Wallis and Mann–Whitney *post-hoc* tests (Figure 3). A set of Generalized Additive Models (GAM) was calculated, together with response curves for *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl., for soil organic matter content (Figure 4), according to recommended procedures [65]. CCA ordination and GAM analyses were performed in CANOCO 5 software [66]. A pairwise correlation analysis of environmental variables was conducted in PAST 4 software [67].

Vegetation data were classified using Ward's method, after square root transformation (Figure S1 in Supplementary Materials). The average cover (Barkman's Total Cover Value, TCV) and Phi (Pearson's  $\phi$ ) coefficients (as a measure of species fidelity) were calculated for each of the groups of plots identified. The significance of species Phi coefficients was checked with Fisher's exact test, according to Chytrý et al. (2002) [68]. The groups obtained were assigned to associations on the basis of cover and fidelity of the dominant and diagnostic species according to regional literature [38,69–71]. Ward's analysis was conducted using PAST 4 software [67]. The average cover and Phi coefficients, together with Fisher's tests, were calculated in JUICE 7 software [72,73]. The EU Natura 2000 habitat types were identified according to the Interpretation Manual (2013) [36] and regional literature [37,44].

### 3. Results

The results of CCA indicated significant effects of environmental variables relating to soil properties, forest continuity and soil disturbance on vegetation composition (Table 3, Figure 2). The most important variable affecting vegetation composition was thickness of the soil organic horizon.

For five groups of relevés distinguished in Wards analysis (Figure S1 in Supplementary Materials), the main diagnostic and dominant species are given in Table 4. The first group (PG) represents abandoned farmlands, gradually replaced with Scots pine with dominance by species connected to psammophilous grassland (e.g., *Cladonia uncialis* (L.) Weber ex F.H. Wigg. or *Polytrichum piliferum* Hedw.) in the herb layer. They belong to the *Corynephorion canescentis* Klika 1931 alliance and meet the criteria for non-forest EU habitat type no 2330. The second group (CPF) is the *Cladonia*-Scots pine forest *Cladonio-Pinetum* Juraszek 1928, meeting the criteria of the 91T0 EU habitat type 91T0. It is distinguished by the codominance of lichens on the forest floor and the presence of diagnostic lichen species (e.g., *Cladonia gracilis* (L.) Willd. or *C. rangiferina* (L.) Weber ex F.H. Wigg.). The third group (PF) meets the criteria for *Vaccinio myrtilli-Pinetum sylvestris* Juraszek 1928, a highly common pine forest type in Central Europe. The fourth group (OPF) reflects mixed oak–pine stands

and corresponds to *Quercus-Pinetum* (W. Mat. 1981) J. Mat. 1988. It is a transitional community between oak and pine forest types. The fifth group (AOF) represents the *Calamagrostis arundinaceae-Quercetum petraeae* Hartm. 1934 Scam. et Pass. 1959 acidophilous oak forest association, and thus, the EU Natura 2000 9190 habitat type. It can be distinguished especially by the dominance of *Quercus petraea* in the overstory and the presence of *Carex pilulifera* L., *Hieracium lachenalii* C. C. Gmel., and *H. murorum* L. in the herb layer as diagnostic species.

**Table 3.** Environmental variables chosen during the forward selection procedure of CCA (variable types: general—scale, factor—nominal or categorical, *p*-values with 9999 Monte Carlo permutations, false discovery rate method used for *p*-value adjustment).

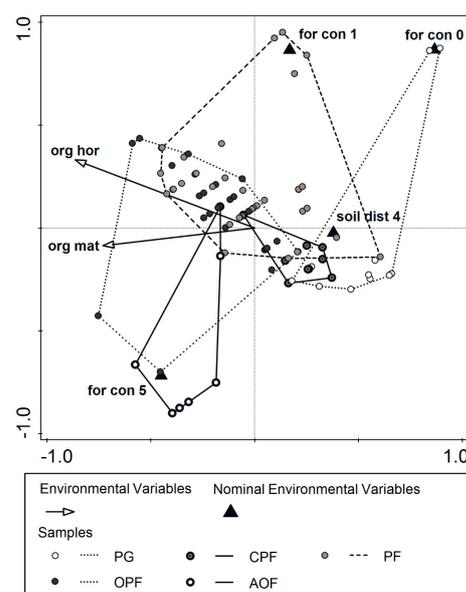
Full Name	Short Name	Variable Type	Explains %	Contribution %	Pseudo-F	<i>p</i> -Value	<i>p</i> (Adjusted)
organic horizon thickness [mm]	org hor	general	12.3	25.3	12.3	0.0001	0.0003
forest continuity factor. for con 5	for con 5	factor	8.4	17.2	9.2	0.0001	0.0003
forest continuity factor. for con 0	for con 0	factor	6.1	12.5	7.1	0.0003	0.0012
forest continuity factor. for con 1	for con 1	factor	5.9	12.1	7.4	0.0001	0.0006
soil disturbance factor. soil dist 4	soil dist 4	factor	2.6	5.4	3.4	0.0001	0.0005
organic matter content in soil at 10 cm depth [%]	org mat	general	1.4	2.8	1.8	0.0113	0.0387

**Table 4.** Average percentage cover (Barkman's TCV) and fidelity (upper index—Phi coefficient given if Fisher's test  $p < 0.05$ ) of species for the groups of plots distinguished by Ward's method (main diagnostic and dominant species presented; A—stand, B/C—in undergrowth): PG—psammophilous grassland, CPF—*Cladonia*-Scots pine forest, PF—pine forest, OPF—oak-pine mixed forest, AOF—acidophilous oak forest.

Group of Plots	PG	CPF	PF	OPF	AOF
Number of samples	13	9	35	26	7
<i>Quercus petraea</i> (Matt.) Liebl. agg A	0.038	0.389	0.057	11.827 <sup>42.6</sup>	68.714 <sup>54.2</sup>
<i>Quercus petraea</i> agg B/C	2.481	1.323	2.603	26.154	5.214
<i>Pinus sylvestris</i> L. A	6.692	17.333	46.286 <sup>22.8</sup>	27.346 <sup>22.8</sup>	3.857
<i>Juniperus communis</i> L. B/C	2.17	0.578	0.563	1.413	0.943
<i>Betula pendula</i> Roth A	2.669	19.778 <sup>53.7</sup>	0.271	2.027	1.714
<i>Pinus sylvestris</i> B/C	14.154 <sup>26.2</sup>	2.157	1.298	0.783	0.006
<i>Convallaria majalis</i> L.	0	0	0	0.008	4.357 <sup>78.8</sup>
<i>Hieracium lachenalia</i> C. C. Gmel.	0.001	0	0.006	0.008	0.257 <sup>78</sup>
<i>Calamagrostis arundinacea</i> (L.) Roth	0	0	0	0.008	0.171 <sup>57.6</sup>
<i>Polytrichastrum formosum</i> (Hedw.) GL Smith	0	0.022	0.007	0.016	0.559 <sup>59.9</sup>
<i>Siuro-hypnum oedipodium</i> (Mitt.) Ignatov & Huttuman	0.246	0.001	3.167	0.126	0.174 <sup>39.6</sup>
<i>Hieracium murorum</i> L.	0	0	0	0	0.003 <sup>49.2</sup>
<i>Carex pilulifera</i> L.	0	0.023	0.017	0.197 <sup>14.5</sup>	1.457 <sup>56.8</sup>
<i>Pteridium aquilinum</i> (L.) Kuhn	0	0	0.006	0.497 <sup>12</sup>	3.957 <sup>61.9</sup>
<i>Vaccinium myrtillus</i> L.	0.015	0.056	0.661	4.708 <sup>16.5</sup>	14.571 <sup>39.1</sup>

Table 4. Cont.

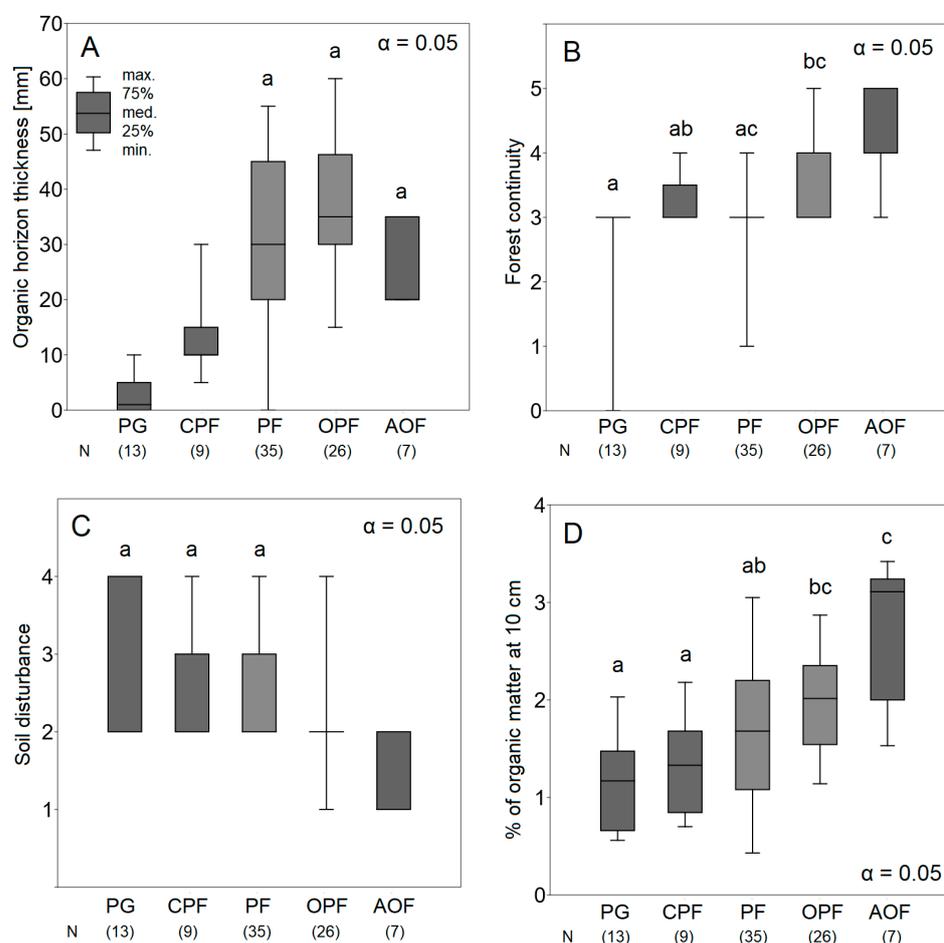
Group of Plots	PG	CPF	PF	OPF	AOF
<i>Melampyrum pratense</i> L.	0.247	0.512	0.712	1.697 <sup>21.4</sup>	1.373
<i>Calluna vulgaris</i> (L.) Hull	0	0.022	0	0.37 <sup>22.6</sup>	0.071
<i>Pleurozium schreberi</i> (Brid.) Mitt	2.24	11.212	55.392 <sup>17.2</sup>	52.731	7.7
<i>Hieracium pilosella</i> L.	2.169	0.412	0.133	0.021	0
<i>Vaccinium vitis-idaea</i> L.	0	0	0.001	0.354	0.001
<i>Dicranum polysetum</i> Swartz	3.185	8.8	8.581	7.008	0.93
<i>Dicranum scoparium</i> Hedw.	4.493	14.446	6.306	3.134	0.09
<i>Leucobryum glaucum</i> (Hedw.) Ångstr.	0	0.056	0.006	0	0.029
<i>Deschampsia flexuosa</i> (L.) Trin	0	0	0	0.008	0
<i>Cladonia rangiferina</i> (L.) Weber ex F.H.Wigg.	0	8.667 <sup>39.9</sup>	0.101	0.008	0
<i>Cladonia furcata</i> (Huds.) Schrad.	0.017	0.179 <sup>34.4</sup>	0.662	0.249	0
<i>Festuca ovina</i> L.	0.463	3.137 <sup>28.2</sup>	0.051	0.832	3.429
<i>Cladonia gracilis</i> (L.) Willd.	0.586 <sup>26.3</sup>	3.467 <sup>57.3</sup>	0.304	0.058	0
<i>Cladonia arbuscula</i> ssp. <i>mitis</i>	19.001 <sup>31.1</sup>	33.389 <sup>54.3</sup>	0.831	1.335	0
<i>Cladonia uncialis</i> (L.) Weber ex F.H. Wigg.	4.962 <sup>37.9</sup>	0.867 <sup>50.1</sup>	0.132	0.008	0
<i>Cladonia phyllophora</i> Ehrh. ex Hoffm.	0.956 <sup>37.6</sup>	0.137 <sup>34.9</sup>	0.108	0	0
<i>Corynephorus canescens</i> (L.) P.Beauv.	1.132 <sup>57.9</sup>	0.103 <sup>31.3</sup>	0.129	0	0
<i>Cephaloziella divaricata</i> (Sm.) Schiffn.	0.032 <sup>34.4</sup>	0	0.001	0	0
<i>Cetraria aculeata</i> (Schreb.) Fr.	0.941 <sup>70.5</sup>	0	0.006	0	0
<i>Cladonia cervicornis</i> (Ach.) Flot.	0.523 <sup>56.4</sup>	0	0.001	0	0
<i>Cladonia macilenta</i> Hoffm.	0.804 <sup>41.9</sup>	0.003	0.02	0.011	0
<i>Polytrichum piliferum</i> Hedw.	6.208 <sup>54.7</sup>	0.08	0.715	0	0
<i>Stereocaulon condensatum</i> Hoffm.	0.569 <sup>61.1</sup>	0	0	0	0



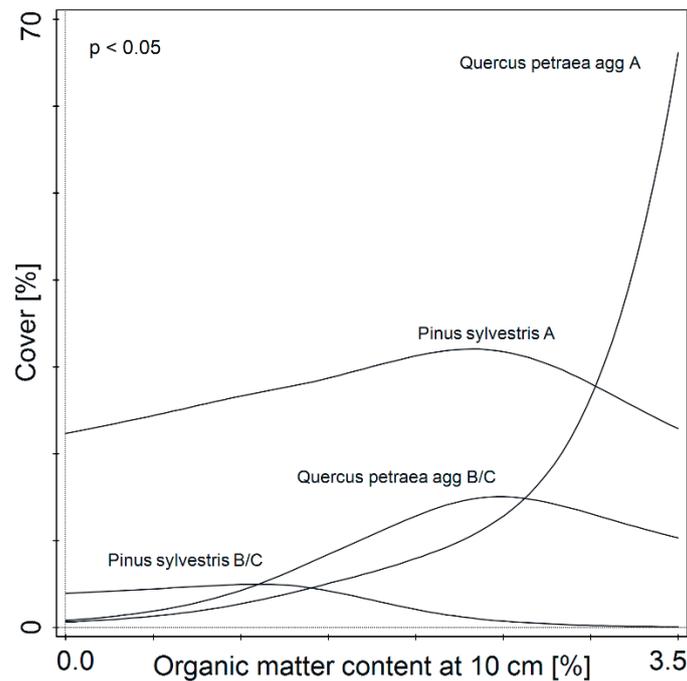
**Figure 2.** CCA plot of samples and significant environmental variables (vegetation types: PG—psammophilous grassland, CPF—*Cladonia*-Scots pine forest, PF—pine forest, OPF—oak-pine mixed forest, AOF—acidophilous oak forest; names of environmental variables are as in Table 3).

The organic horizon was thinnest in psammophilous grasslands (PG). Medium values of this variable were a feature of *Cladonia*-Scots pine forests (CPF) and acidophilous oak forests (AOF), and the highest values occurred within pine forests (PF) and oak–pine forests (OPF) (Figure 3A). All of the habitats but AOF had lower forest continuity (Figure 3B). Additionally, some differed between themselves. Early successional habitats (PG, CPF, and PF) were characterized by higher soil disturbance ranks than late-successional ones (OPF and AOF), however AOF suffered the least soil disturbance (Figure 3C). Soil organic matter content was lower in PG, CPF, and PF habitat types. Higher values of soil organic matter were associated with OPF and AOF communities (Figure 3D).

Models of the response of *Pinus sylvestris* L. and *Quercus petraea* (Matt.) Liebl. to percent organic matter content in soil were significant ( $p < 0.05$ ) (Figure 4). Medium values of organic matter in soil were connected with a higher abundance of Scots pine. Higher values were associated with a greater abundance of sessile oak. Both species were less abundant in soils with the lowest organic matter content.



**Figure 3.** Variation in main environmental variables between vegetation types (PG—psammophilous grasslands on abandoned fields 2330, CPF—*Cladonia*-pine forest 91T0, PF—pine forest, OPF—oak-pine mixed forest, AOF—acidophilous oak forest 9190): (A) organic layer thickness, (B) forest continuity rank, (C) soil disturbance rank, (D) organic matter content in soil at 10 cm, (Kruskal–Wallis and Mann–Whitney *post hoc*, Holm–Bonferroni sequential correction used for  $p$ -value adjustment, lowercase letters—homogenous groups at  $\alpha = 0.05$ ).



**Figure 4.** The relationship between soil organic matter content and percentage cover of *Pinus sylvestris* and *Quercus petraea* agg in tree stands (A) and undergrowth (B/C) (*Pinus sylvestris*: A  $R^2 = 0.034$ , B/C  $R^2 = 0.184$ ; *Quercus petraea* agg: A  $R^2 = 0.269$ , B/C  $R^2 = 0.194$ ;  $N = 90$ , in all cases  $p < 0.05$ ).

#### 4. Discussion

##### 4.1. Predictive Variables

The diverse geological properties within the study site may be a key factor in explaining vegetation pattern [6,7]. For this reason, the study was conducted within an area of homogenous substrate of loose-sand deposits of fluvioglacial origin [46]. The maximum mass % of a <math>< 0.1</math> mm fraction in the soil profile was used to confirm the minor impact of bedrock. This is a highly stable characteristic that influences soils' biophysical properties. Fine-textured soils are usually much more fertile [74] and this could impact the results obtained. The other important drivers of vegetation differentiation are the slope, position in the landscape (expressed as TPIs) and ground water level [10,59,60]. However, in this study, these environmental variables did not contribute to the final CCA model, indicating that local topography did not significantly impact vegetation at this study site. Moisture can also influence vegetation patterns [7], but here, ground water table was not a significant factor, due to the very deep water table which occurs at an average depth of 20.6 m.

Significant variables obtained in the CCA model were directly related to soil conditions, forest continuity and soil disturbance.

##### 4.2. From Psammophilous Grasslands, through Cladonia-Scots Pine Forest, to Acidophilous Oak Forest—Uniquely Diverse Vegetation within Initially Homogenous Psammophilous Conditions

The studied vegetation can be considered uniquely diverse in terms of the number of habitat types. The CCA indicated their possible chronosequence, starting from abandoned fields with plant communities belonging to *Corynephorion canescentis* Klika 1931 alliance (Natura 2000 code: 2330), followed by *Cladonio-Pinetum* Juraszek 1928 pine forest (Natura 2000 code: 91T0), and *Vaccinio myrtilli-Pinetum* Juraszek 1928 pine forest (also known by the name *Leucobryo-Pinetum* W. Mat 1962 in Poland) W. Mat et J. Mat 1973), succeeded by the mixed oak–pine forest *Quercus-Pinetum* (W. Mat. 1981) J. Mat. 1988 and finishing with *Calamagrostio arundinaceae-Quercetum petraeae* Hartm. 1934 Scam. et Pass. 1959 acidophilous oak forest (Natura 2000 code: 9190). Parts of this sequence have already been described by other authors as successional seres. The abandonment of agriculture on low-productivity, sandy soils usually leads to the formation of psammophilous grasslands within the first few

years after the cessation of tillage, e.g., [75]. Then, the first shrub and tree species appear and gradually change the non-forest communities into oligotrophic pine forests, with a forest floor dominated by lichens or mosses. This stage can last ca. 40–70 years [25,75]. The *Cladonia*-rich pine forests are nowadays considered transitional communities, and only persist in the lichen-abundant form for between ca. 22–36 years [32]. The successional sere is usually finished at the point of mesic pine forest, which is often considered a climax forest formation within such sites, developing after ca. 60–70 years of succession [25,75,76]. On the other hand, spontaneous oak encroachment into pine stands on sandy soils has been observed [43,77,78] and acidophilous oak forest has become more common in the Central European landscape [38,39]. This could potentially prolong the possible trajectory of succession on an oligotrophic, sandy substrate. It is highly probable that the documented vegetation diversity belongs to the same sere. It would be a much longer sere, compared to others reported in research on forest succession in Europe. They tend to be much shorter and usually include one or two forest communities, often compared with some pre-forest vegetation, i.e., [23,26,39,76].

#### 4.3. Historic Soil Disturbance by Tillage Explains the Present Diversity of Vegetation

Brunic Arenosols (commonly called rusty soils in Poland) are formed from sands and can be distinguished by a thick Bv (sideric) horizon of diagnostic value [79]. Forests are known for their soil-protecting role [80], which is manifested in this study by the lowest level of soil disturbance in mature oak stands (AOF), characterized by high forest continuity. Agricultural soil disturbance is caused mainly by tillage. Plowing results in erosion by exposure of the soil surface to wind and water, e.g., [17,18,64,80]. The results of this process were observed within the study site. They were manifested firstly by the presence of a plough layer and secondly through increasing denudation of the soil Bv horizon. In such cases, Brunic Arenosols lose their diagnostic Bv horizon and are named Haplic Arenosols (typical) or Protic Arenosols (initial) in the case of close to complete soil profile destruction. Soil truncation of Brunic Arenosols can easily reach 40–50 cm [18]. Such a high level of denudation is probable within the study site. Denudation was also indirectly identified in the field by the presence of common juniper (*Juniperus communis* L.) on phytogenic hillocks, often observed in the vicinity of plots characterized by the highest levels of soil degradation. This type of formation results from wind erosion [52].

Time since agricultural land abandonment is an important factor influencing forest species composition [81]. In this study, the AOF (and partially OPF) vegetation were characterized by higher forest continuity. Lower continuity was a feature of PG and pine forests. The significance of this time-related variable in the final CCA model indicates the succession process occurring within the study site. The regeneration of forest is slower within more oligotrophic habitats [25,81]. This may be the reason for CPF tendency to slower regeneration than PF.

Agricultural use of sandy forest soils leads to decreased organic carbon and soil organic matter [15,82]. Moreover, soil organic matter accumulation is a good predictor of successional changes [83]. One of the characteristic features of early successional habitats, such as psammophilous grasslands and *Cladonia*-Scots pine forest, is low organic matter content in soil [8,84]. Pine forests are characterized by only slightly higher organic matter content [8], with the highest soil organic matter in oak forests [9], a result confirmed in this study. Despite this, a high negative correlation between soil disturbance rank and organic matter content suggests that the level of initial habitat impoverishment by tillage can be of the same importance as the increase in organic matter content observed during succession [83]. Soil fertility is an important driver of community assembly during forest succession [85]. Thus succession within initially more organic matter-rich sandy soils is faster than within soils characterized by lower organic matter content [25]. Such a process likely occurred in this study. This can also explain the higher cover of oak in undergrowth within more organic matter-rich plots, in spite of the fact, that colonization by oak could have begun together with pine during the transition from the non-forest habitats [86].

Soil pH had no explanatory power in the CCA model and soil conductivity was collinear. However, their correlations with organic matter content are also interpretable. The pH of the upper soil horizons of arable fields is higher than that of forest stands [15], most likely because of the high acidity of pine needles. In spite of its importance for nutrients cycling in topsoil [87], the decay of coniferous litterfall can decrease soil pH under trees [88] and accelerate podzolization process [89]. In the present study, the increase in soil conductivity was changing with vegetation. This was most likely connected with rising concentrations of H<sup>+</sup> ions caused by the increasing presence of organic acids in oligotrophic and humus-enriched soils, as soil conductivity was positively correlated with organic matter concentration at 10 cm and negatively with soil pH at 10 cm. Such a relationship can be observed within early successional habitats affected by the accumulation of strongly acidic litter [90]. However, the organic matter concentration at 10 cm had better explanatory power in CCA. This supports its use as a variable connected with successional changes, as proposed by Walker et al. [83].

Litter accumulation influences species composition [90]. A low amount of litter is particularly suitable for *Cladonia* species and can be observed in psammophilous grasslands and *Cladonia*-rich pine forests [84,91]. A thicker layer of organic matter is characteristic of other pine and acidophilous oak forests [8,9]. The growing thickness of the organic horizon is connected to coniferous litter accumulation over time. The disintegration of pine needle litter is much slower than oak leaves [92] and results in thinner layers of organic matter under oak trees. This explains the finding of slightly lower values of organic horizon thickness observed in AOF.

Previous tillage-connected soil disturbance resulted in soil truncation and degradation of soil profiles within the study site. This was demonstrated by the decrease in organic matter content (but also by raised pH and decreased conductivity of soils). The abandonment of agricultural cultivation enabled secondary succession. However, it occurred especially on close to initial post-agricultural soil conditions. This favored the development of *Cladonia*-rich non-forest and then forest habitat types, both protected as Natura 2000 habitats (2330, 91T0). Mid-successional communities were of lower conservation value. A gradual replacement of pine by oak is observed in the undergrowth and increasingly in tree stands on the research site. Such changes were also documented in other studies, e.g., [26,78], but the process was usually less well advanced. The spontaneous replacement of pine by oak in undisturbed habitats tends to be slow because both species are long-lived [78]. The complete replacement of pine by oak in the study site was observed in the older oak stands with undisturbed soil. It was also evident in some post-agricultural plots. We think that this process was enhanced by traditional management of private forest land, where there was better establishment of oak within patches with less degraded soils, however management type did not contribute to the final CCA model. Traditional management is still practiced in some private forests in Poland, usually involving the gradual harvesting of older pine, leading to a reduction in light concurrency [93]. This enhances oak development [94]. Young oak in the understory tend to be omitted during harvesting and gradually reach the tree layer. After pine replacement by oak, vegetation reaches the late-successional stage acidophilous oak-forest, the other Natura 2000 habitat type (9190). The results indicate that the temporary coexistence of four unique types of forest communities (including two Natura 2000 forest habitat types) is possible within one homogenous geological substrate.

This study provides information that may be used to determine the potential natural vegetation (PNV) of the study site. The concept was introduced by Tüxen in 1956 [95] and, despite some misunderstanding and thus criticism, it has been used widely as a valuable decision-support tool for land management and ecological restoration [96]. The interpretation by Somodi et al. (2021) [97] of Tüxen's original PNV definition (as well as subsequent and related definitions) was used to interpret the results of this study. As the concept leaves some discretion in its interpretation, a rough and clear division into pine and oak forest was adopted. The PNV is focused on the actual habitat conditions of the

analyzed areas and incorporates anthropogenic impacts on soil. Nowadays, impoverished soils are mainly regenerated with coniferous trees. The abundance of oak was much lower within habitats characterized by low soil organic matter content. Thus the current PNV of the study site consists of both pine (in habitats with soil-disturbance) and oak forests (in less impoverished soils or undisturbed habitats). The potentially restorable vegetation (PRV), in the sense of Somodi et al. (2021) [97], corresponds with the reconstructed natural vegetation as conceptualized by Moravec (1998) [98], in which the entire study site would be acidophilous oak forest. It can be concluded, that due to human impact on soil, the actual PNV differs from PRV.

#### 4.4. Implications for Forest Management and Conservation

##### 4.4.1. Implications for Nature Conservation

Agricultural deforestation was once a common practice in Eurasia [12]. Nowadays, land abandonment is the most frequent driver of landscape change across Europe [21]. In Poland, the share of post-agricultural lands in State Forests is at least 22.1% [24]. Land abandonment leads not only to ecological succession, but also to changes in forest disturbance [30]. As a result, many human disturbance-related ecosystems, including some early successional and disturbance-related forests, became increasingly threatened. Their conservation requires anthropogenic disturbance, e.g., [91,99–102], even drastic soil disturbance in the case of initial, psammophilous habitats [84,103]. Importantly, in this study, the occurrence of *Cladonia*-Scots pine forest was dependent on prior agricultural use and soil impoverishment. As a transitional and short-lived forest type [32,33,37], it requires active conservation in order to persist while maintaining its inherent biodiversity. Litter-raking and single-tree cutting are usually thought to be potential traditional forms of *Cladonia*-Scots pine forest management [37,91,104]. Our results suggest that strong soil disturbance is a possible method of maintaining this habitat-type, however it is difficult to implement in afforested landscapes and in light of general trends in nature protection strategies within European Union [105]. Moreover, secondary succession within the close-to-initial sandy conditions is a slow process, e.g., [25,26,75]. Due to this, ploughing cannot be used for short-term habitat conservation. Litter-raking and deadwood removal appear to be more appropriate strategies, as thinner litter layer is characteristic of *Cladonia*-rich forests [45,91]. Additionally, litter-raking is known to decrease soil fertility [106,107]. It is worth mentioning, that *Cladonia*-rich pine forest communities are vanishing, not only from the Central European landscape, but also in Scandinavia, where they are an important food source for reindeer, i.e., [108,109].

In contrast, acidophilous oak forest can function successfully both with and without human assistance [40]. It is a late-successional community on an oligotrophic, sandy substrate [44]. This habitat type tends to be expanding in Central Europe [38,39]. Both passive protection and sustainable forest management can ensure its effective conservation [44].

The potential co-occurrence of two completely different, legally protected EU forest Natura 2000 habitat types has implications for conservation planning. In some cases, this may result in the need to reassess management decisions, since planning to protect one type may lead to the exclusion of the other.

##### 4.4.2. Implications to Forest Management

Conservation of *Cladonia*-Scots pine forests faces difficulties due to insufficient knowledge, and the rapid reduction in the area covered by this community. Overall, well-proven conservation methods are lacking, but some traditional procedures that reduce canopy closure are likely appropriate. The introduction of any understory is discouraged [37]. Large-scale clearcutting is also sometimes proposed [104]. The results of this study favor increased soil disturbance as a possible long-term habitat management tool. However, such a practice is becoming less acceptable in modern forestry, which is instead focused on the replacement of pine stands by mixed pine–oak and pure oak stands [41,110]. Given that

*Cladonia*-Scots pine forest can occur both on Brunic Arenosols and Haplic Arenosols [8], litter raking seems a possible method to promote *Cladonia*-Scots pine forest habitat conservation.

Due to their low agricultural suitability, Brunic Arenosols were mostly abandoned and then afforested in the 20th century. Nowadays, they occupy 65.8% of all post-agricultural lands in Polish State Forests, and are predominantly covered by pine forests [24]. Intact Brunic Arenosols are suitable for forestry and enable the cultivation of broadleaved forests, e.g., pedunculate and sessile oaks [111]. When these soils are degraded by podzolization, they are more appropriate for Scots pine [112]. In our study, plots with slightly degraded Brunic Arenosols were intensively colonized by oak, whereas sites with a strongly denudated soil profile were dominated by pine. Thus, we conclude that slightly degraded post-agricultural sandy soils can support oak forest. Sites with intermediate levels of disturbance tend to be more suitable for pine plantations, and forest patches characterized by the highest levels of soil profile degradation should be the focus of *Cladonia*-Scots pine forest conservation.

## 5. Conclusions

- Past soil disturbance resulting from tillage is the main factor enhancing the diversity of forest communities in the oligotrophic fluvio-glacial site.
- The presence of two protected forest EU Natura 2000 habitat types, which need different management methods, may require choosing, whether to protect transitional and anthropogenic *Cladonia*-Scots pine forest (code 91T0) or late-successional acidophilous oak forest (code: 9190). Management decisions will be more concerned with the fate of lichen-rich pine forests.
- It may be necessary to reassess management plans and conservation decisions when considering forests on oligotrophic-sandy substrates.
- Post-agricultural Brunic Arenosols that are lightly degraded appear to promote oak establishment, while medium soil disturbance favors pine plantations.
- Near complete soil-profile denudation can be used as an indicator of potential sites for *Cladonia*-Scots pine forest conservation.
- The potential natural vegetation of the study site differs from potentially restorable vegetation: the PNV of pine forest is still pine forests, the PNV of oak–pine forest and acidophilous oak forest is acidophilous oak forest, and the PRV of the entire study site is acidophilous oak forest.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13020198/s1>, Table S1: vegetation data; Table S2: environmental data; Table S3: Spearman's rank correlations of the explanatory variables; Table S4: environmental variables used in forward selection procedure of CCA; Figure S1: dendrogram of Ward's analysis.

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