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The Strong Position of Silver Fir (*Abies alba* Mill.) in Fertile Variants of Beech and Oak-Hornbeam Forests in the Light of Studies Conducted in the Sudetes

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Abstract: Silver fir is one of the longest living and tallest trees in Europe, it has major commercial importance and may be found in various communities predominantly connected with lower mountainous locations in Central Europe. One of the northernmost ranges in the region is the Sudetes. Currently, the once numerous fir is greatly dispersed, with just several specimens to be found together at one site on average. This drastic reduction in the number of specimens is mainly attributable to intensive forest management, based on the artificial cultivation of fir, conducted in the 19th and 20th centuries, and high industrial air pollution (mainly in the 20th c.). Because practically no firs have been cultivated for the last 200 years, the remaining sites of the species that are remnants of its bigger populations should be regarded as natural. This paper compares fir locations with areas of potential natural vegetation. The obtained results indicate that firs may grow in various types of habitats, with the preferred one being fertile beech woods and richer variants of oak-hornbeam forests. In our opinion, the presented findings are of great importance for the knowledge of the ecology of the species in question and for providing appropriate forest management.

Keywords: ecology; silviculture; phytosociology; habitat preferences

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1. Introduction

The European silver fir (*Abies alba* Mill.) is a large tree (the tallest fir specimens in the Black Forest were even 68 m high) found in Central, Southern and Eastern Europe. The tree is regarded as an important species from the perspective of ecology, forest functioning and maintenance of forest biodiversity. Because of the tree's dimensions, very big numbers of specimens in forest stands, wood with good mechanical properties, and the fact that it is also used for paper production, it is a commercially important species. In its natural condition, it grows in mountainous and sub-mountainous areas and in France and Poland—also in lowlands [1–5].

Silver fir prefers areas with higher humidity and evenly distributed rainfall at the level of 700 to 1800 mm (with exceptions). Usually, such areas are located at an altitude of 500–2000 m above sea level. In favorable conditions (cool and wet habitats) it lives for up to 600 years. In places where firs are concentrated, summer temperatures range from 14 to 19 degrees [1,3,4,6,7]

Silver fir grows on various types of fresh soils and in a wide pH range. The tree avoids very compact and wet soils. At higher altitudes, it forms poor and mixed tree stands with Norway spruce (*Picea abies* (L.) H.Karst), Scots pine (*Pinus sylvestris* L.) and, above all, Common beech (*Fagus sylvayica* L.). At lower altitudes it also occurs in oak-hornbeam forests. It is classified as a shade-tolerant species and the younger generations under the canopy of the main stand often create a so-called 'seedling bank' [1–7].

Silver firs are said not to be resistant to late frosts, fires and industrial air pollution, especially SO_2 [3,4,6].

Firs growing in different parts of the present natural range come from different glacial refuges: the Iberian, Balkan and Apennine peninsulas. This fact has a significant impact on their current genetic diversity [8,9].

For various reasons, in many areas silver fir is now on the decline [3,6,10]. In recent years, especially in dendrochronological studies, an improvement in the condition and growth of firs has generally been noted [4,10]. However, the future of this tree, considering, the climatic changes, is not clearly defined. Some studies suggest an increase of its importance in forest resources [11,12], while others predict a regress and a decline in numbers [13,14]. According to Korpel (Jaworski) [3], forests with dominant fir have a development cycle of 400 years. The tree has been subject to numerous studies, including [15–19]. Just one periodical, called 'Sylwan', has printed over 40 publications during the last ten years.

The main goal of our research was to answer the question: is there a relationship between a potential natural community developing in specific habitat conditions and the number of potentially natural fir localities?

This article aims to present data that may shed some more light on the position of fir in potential, natural vegetation arrangements (ecosystem types) and provide some new arguments in the discussion about the habitat requirements of the species.

'Potential natural vegetation' (PNV) is understood as a hypothetical state of vegetation described by means of phytosociological units of vegetation (communities) that might be achieved by natural primary or secondary succession if anthropogenic influences were eliminated and the plants typical of a given region might make full use of the possibilities created by varied habitats [20].

Potential natural vegetation is determined based on a survey of actual vegetation communities as well as direct and indirect analysis of an abiotic habitat [21].

Knowledge of vegetation diversity in connection with environmental diversity provided the grounds for developing applied phytosociology [22]. The best-known uses of phytosociology are in forestry, where it is used to assess the transformations of the natural environment caused by human activities, e.g., in defining indicator (phytoindicative) properties of communities [23]. The determination of potential natural vegetation is the easiest way to establish the productive capability of a habitat. This constitutes the basis for silvicultural planning and operations [22,23]. Poland was one of the first countries to develop a map of potential natural vegetation—at a scale of 1:300,000 [21]. A map of potential vegetation for Europe, together with a description of the main vegetation formations was presented by Bohn et al. [24].

The study described here complements the findings of the work done in the years 1998–2006 as part of two research projects (grants) that were to form the basis for a program to restitute fir in the Polish part of the Sudetes [25]. The Sudetes are a mountain range about 300 km long, situated in south-western Poland and northern Czechia [26] (more information is provided in the Section 2 below). The program to restitute fir in the Sudetes, which was launched in 1999, aims to raise fir's share in forests up to 18%. In order to achieve the aim, a number of preservative seed plantations were set up to provide afforestation material at a later stage [27,28].

The studies referred to above assessed the resources of fir in terms of its genetic diversity (isoenzyme studies) [29], the total number of sites and specimens [30], occurrence in various habitat conditions [31], growth rate, crown development and damage in various conditions [32,33], growth during the last decades (dendrochronological studies) [10], natural regeneration [34,35], soil properties at sites where it occurs [36,37], the degree of development of symbiosis with mycorrhizal fungi [25], and the impact of present and future human management on the species [25]. It was found, for instance, that *Abies alba* used to be common in the Sudetes at an altitude of 350–800 MASL. Firs grow here satisfactorily at sites with different exposure, representing a broad spectrum of vegetation communities and forest habitat types [30,31]. The Sudeten fir woods, significantly reduced (by 70%–80%) as a result of intensive forest management in the 19th c. and the first half of the 20th c. (promoting spruce monocultures) e.g., [25,38–40], in the years 1960–1990 were subject to the strong pressure of industrial pollution, especially SO_2, whose average concentration in many locations exceeded 60 $\mu g/m^3$, and periodically even 190 $\mu g/m^3$ e.g., [25,38,39,41]. These conditions, in combination with commercial activities that failed to account for fir's specific requirements, led to a situation in which its share in the forest composition was markedly lower than the initial 1% level [25]. The principal factor that hinders the restoration and spreading of the tree in the Sudetes is currently a very significant scattering of its specimens, which makes the exchange of its genetic material difficult (large, hardly airborne pollen grains). When the pollution level dropped, a surprisingly intensive fir revitalization was observed, which usually took place according to the following pattern: development of a regenerative crown on the trunk—regeneration of the trunk thickness growth—regeneration of the primary crown in the upper part of the tree (mainly development of lateral shoots)—increased blooming and cone crops. It turns out that silver fir, regarded as very sensitive to changes in the environment, is able to live in unfavorable conditions for a long time, with a reduced crown and minimum growth, only to greatly increase its growth once the conditions improve. During a period unfavorable to growth for instance, because of a sudden canopy disruption, many trees rebuild their crown from a broad one to a narrower and more compact one, and so become more resistant to industrial pollution [25]. Isoenzyme analyses have shown that there are genetic differences between firs from the Sudetes and the Carpathians, and most of the firs in the Sudetes are native populations (as opposed to, for instance, spruce). The differences were confirmed by later studies [9,42].

The data regarding the locations of the firs used in this paper also come from the period in which the studies referred to above were conducted. As already mentioned, from the early 19th c. the Sudetes were subject to intensive forest management promoting solid spruce stands. Until the 1970s, firs were practically not planted there. The period following WWII, was connected with strong industrial pollution and the belief that in such conditions firs, sensitive to this type of pollution, [3,4,6] would have no chance to survive. Consequently, it was assumed [25,27–29] that the fir locations surveyed as part of the studies done in the years 2000–2001, and so before the implementation of the restitution program, were largely remains of the natural sites that had existed there before the introduction of intensive forest management practices. In our opinion, this means that the location data we have are well suited for comparison with potential natural vegetation. The artificial cultivation of a species, which we do in Europe in the case of a majority of commercially important trees, may distort their original distribution and habitat preferences, which is probably the reason for the lack of studies similar to ours.

2. Materials and Methods

There are not many papers assessing habitat preferences of the silver fir based on the distribution of its localities. This was one of the reasons why we decided to compare data regarding the locations of fir sites in the region of the Sudetes [25] in which this tree is most abundant with the map of the potential natural vegetation of the area [21]. The available data refer to the locations of firs aged 50 years or over in the area covered by the study at the turn of the present century, i.e., before the launch of the current fir restitution program. As it follows from the earlier papers, the sites of such firs should mainly originate from natural sowing and usually have natural character. This results from the fact that during the period in which the localities were formed, there were practically no artificial fir planting attempts (as opposed to spruce).

The Sudetes—a mountain range in south-western Poland and northern Czechia with the highest summit Śnieżką being 1603 MASL. The mountains are located in Non-Alpine Central Europe and are the highest part of the Bohemian Massif [26]. Direct studies covered an area situated in three forest districts of State Forest National Forests Holding: Baro

Śląskie, Bystrzyca and Międzylesie (Figure 1), which amount to a total of 34,968 ha of forests. These forests surround the Kłodzko Valley, which is located in the central part of the Sudetes. The area is varied in terms of habitats. It has practically all types of forest communities occurring in the Sudetes. Selected information regarding the studied area is presented in Table 1. The study used data regarding the locations of 843 localities.

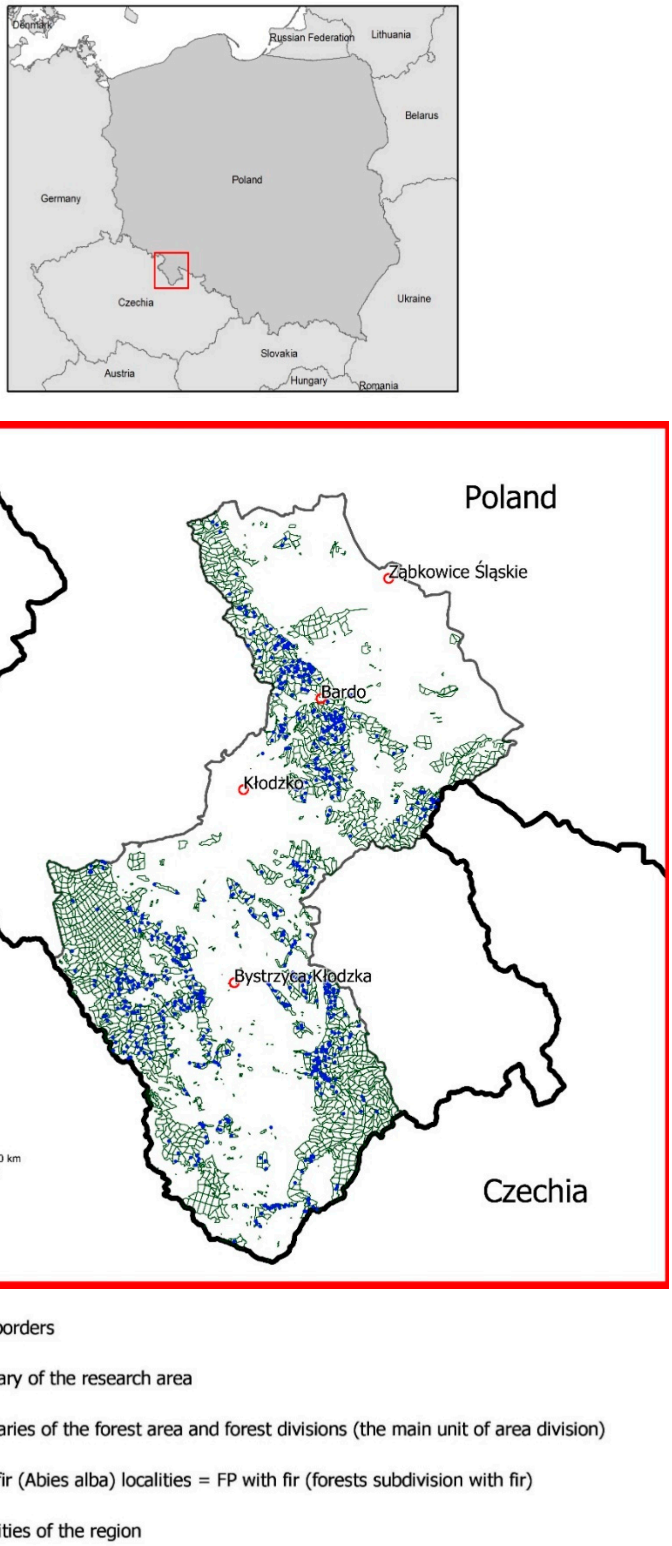

Figure 1. Location of the study area.

Table 1. Characteristics of the study area. The values were calculated on the basis of data from the publications of Zielony, Kliczkowska [26] and Kondracki [43].

Area	Forest Area	Forest Area	Average Annual Temperature	Vegetation Period	Average Annual Rainfall (mm)	Elevation
(km^2)	(km^2)	(%)	(°C)	(days)		m.a.s.l
1052	340.968	32	7.0	170–210	750–1000	350–1424

When assigning fir localities to areas in which particular vegetation communities (formations) might be present, we used the raster versions of the map sheets of Poland's potential natural vegetation [44] marked as D1D2 [45] and digital maps of the forested areas managed by the State Forests National Forest Holding (LP): geometric layers (LP's organizational units, branches and basic forest management units) and data of appraisal descriptions of forest stands as data from the Forest Database, made available by the Bureau for Forest Management and Geodesy [46]. The data were processed using the following computer software: MS Excel 2010 and QGIS version 2.12.3-Lyon (license: GNU GPL) with Georeferencer version 3.1.9 (plug-in integrated with QGIS)—Open Source Geospatial Foundation (OSGeo) project (Chicago, USA). This enabled a spatial reference to be assigned to a bitmap image (map D1D2). The raster map was georeferenced by means of the control point reference method, using a few dozen characteristic points located along the country's border. In order to verify the earlier map calibration, spatial references were re-assigned to the bitmap. For this, the nodal points of the ATPOL (Atlas of Poland) were used [47], and the grid on the map D1D1 was calibrated according to the ATPOL grid points in the Shapefile (SHP) format developed by Piotr Kobierski [48]. The next calibration did not affect the earlier findings.

The combination of the calibrated raster map of Poland's potential vegetation [45] with LP's numerical maps [46] enabled us to determine the number of fir localities occurring within individual communities of potential natural vegetation. The European silver fir locality (FL) were identified by assigning them to a specific forest plot (FP) ('subdivision'), i.e., the smallest unit of the area division of Polish forests, separated on the basis of specific forest stand characteristics. The units were described in more detail, for instance, in the publication by Napierała-Filipiak et al. [49]. The definition of this unit is practically the same as the definition of forest stand that given in Nyland's [50] handbook ('A forest stand is a contiguous community of trees sufficiently uniform in composition, structure, age, size, class, distribution, spatial arrangement, site quality, condition, or location to distinguish it from adjacent communities'). The total areas occupied in the examined forests by individual types of natural vegetation were also established. This was done by summing up the areas of all FPs in the analyzed area that are situated within the zones corresponding to individual communities of potential natural vegetation.

Approximate data on the share of fir in the stand came from the description of the 'subdivision' (FP) in which they grew [46,49].

As soil properties and topography are taken into account both when distinguishing areas of potential natural vegetation and forest plots (FPs) in our research, the latter (FPs) rarely are situated in areas belonging to different PNV units. However, if such a situation occurred, a detailed description of the FP was analyzed in terms of the location of firs and, on this basis, they were assigned to specific PNV units. Due to the lack of data on fir distribution, several FPs were excluded from the analysis.

The Supplementary Materials contain a Table S1 with a list of all FL (FP with fir) used in this study. The data in the table makes it possible to locate a specific FP on the forest map [45,46].

Differences in the distributions of the analyzed features were tested using the chi-square test of goodness of fit and independence. The significance level was set at $p = 0.05$. For the analyses, the application Statistica version 8.0 (StatSoft Polska Inc., Tulsa, OK, USA) was used [51].

3. Results

Table 2 shows the numbers of localities assigned to the specific plant communities identified on the potential natural vegetation map [21], as well as the areas of the communities in the forested areas of the examined zone, and the numbers of fir sites per area unit of a given community. The total areas of some communities are not big, and there are only several sites within them. The data may be more significant when compared with findings of other studies, but within this context, they should be regarded as not very accurate.

Table 2. Number (N) of fir localities (FL) (in the area covered by the study) within individual areas of potential natural vegetation (PNV, their (PNV) surface area (S) and the number of fir localities (FL) per unit of surface area (N/S).

Numerical Designation and Name of the Plant Community on the Map of Potential Natural Vegetation	Description of the Plant Community [20,21,23,24,52]	N [FL]	S [ha]	N/S [FL/ha]
02—Salici-Populetum	Lowland willow-poplar floodplain forest; regularly flooded—(dynamic complex of Salici-Populetum, Salicetum triandro-viminalis etc.) developed on sandy alluvial soils over larger rivers within the range of annual inundations	0	97.59	0.00
03—Ficario-Ulmetum typicum	Lowland ash-elm floodplain forest; occasionally flooded developed mainly in the valleys of large rivers. on the highest situated floodplain terraces and very fertile typical fine-grained alluvial soils	3	163.26	0.02
04—Ficario-Ulmetum chrysospl.	Lowland eutrophic forb-rich elm-oak forests on the ground-water soils out of floodplains associated with wet depressions, valleys of small watercourses, lakes, ravines and black turf soils	5	229.89	0.02
06—Alnetum incanae	Submontane/montane grey alder floodplain forest developed on highly fertile mountain alluvial soils with a thickness of several dozen centimeters on rocky ground, made of pebbles deposited by water	0	187.49	0.00
07—Carici remotae-Fraxinetum	Submontane forb-rich ash forests along streams and little rivers developing on the lowest alluvial terraces of small streams, with wet soil due to the constant seeping of water near the spreading springs.	7	636.40	0.01
10—Galio-Carpinetum, Sil./Gr.-Pol., poor [2]	Middle European lowland oak-hornbeam forest; Silesia/Great-Poland-vicariant, mesotrophic ("poor") communities developed on moderately fertile habitats in the lowlands and highlands; soils formed on boulders light clays and sands of glacial accumulation, as well as on river sands of accumulation terraces; brown leached soils, brown podzolic and grey-brown podzolic soils	3	84.34	0.04
11—Galio-Carpinetum, Sil./Gr.-Pol., rich [1]	Middle European lowland oak-hornbeam forest; Silesia/Great-Poland-vicariant, eutrophic ("rich") communities developed on fertile fresh and moderately moist habitats in lowlands and highlands; soils formed on boulders clays and clay sands; typical, fluvic and gleyic brown soils, black turf soil	52	1001.42	0.05
12—Galio Carpinetum submont poor [2]	Middle European submontane oak-hornbeam forest; Silesia/Great-Poland-vicariant, mesotrophic ("poor") communities developed on moderately fertile habitats in the foothills; soils formed on boulders light clays and sands of glacial accumulation, as well as on river sands of accumulation terraces; brown leached soils, brown podzolic and grey-brown podzolic soils	52	3370.97	0.02

Table 2. *Cont.*

Numerical Designation and Name of the Plant Community on the Map of Potential Natural Vegetation	Description of the Plant Community [20,21,23,24,52]	N [FL]	S [ha]	N/S [FL/ha]
13—Galio Carpinetum submont rich [1]	Middle European submontane oak-hornbeam forest; Silesia/Great-Poland-vicariant, eutrophic ("rich") communities developed on fertile fresh and moderately moist habitats in the foothills; soils formed on boulders clays and clay sands; typical, fluvic and gleyic brown soils, black turf soil	124	3330.88	0.04
28—Aceri Tilietum	Submontane maple-lime forest on the rocky slopes developed on acidic brown soils in the upper and middle parts of the slopes, typical and diluvial brown soils in the lower parts, and black soils and brown marshes at the bottom of valleys.	0	8.31	0.00
30—Dentario enneaphyllidis-Fagetum submontane [3]	Submontane forb-rich sudetian beech forest developed on medium-deep and deep brown soils.	54	750.1	0.07
31—Dentario enneaphyllidis-Fagetum montane [3]	Montane forb-rich sudetian beech forest developed on neutral or near-neutral medium-deep and deep brown mountain soils, with mild humus (mull)	106	3561.71	0.04
36—Cephalanthero-Fagenion [3]	Calciphilous and subthermophilous beech forests with many orchid species in undergrowth developed on calcareous, often superficial, soils, usually of steep slopes, of the medio-European and Atlantic domains of Western Europe and of central and northern Central Europe	32	269.93	0.11
38—Luzulo luzuloidis-Fagetum [4]	montane/submontane acidophilous beech forest with graminoids and/or dwarf-shrubs in undergrowth developed on brown, acidic and podzolic soils, sometimes brown podzolic soils, with a base of crystalline, metamorphic rocks	330	18,441.21	0.02
39—Acerenion pseudoplatani	Montane sycamore forest with tall forbs in undergrowth developed on fertile soils which undergo strong slope denudation	5	165.07	0.03
45—Calamagrostio-Quercetum	Middle-European lowland acidophilous oak forest developed on grey-brown podzolic soils, brown podzolic soils, brown leached soils and stagnant-gleyic soils	0	193.73	0.00
46—Luzulo luzuloidis-Quercetum	Submontane Middle-European acidophilous oak forests occur on nutrient-poor different acidic soils.	64	2428.72	0.02
57—Abieti-Piceetum montanum	Lower-montane spruce- (rarely fir-spruce- forests, developed on leached brown soils, grey-brown podzolic soils and typical podzolic soils.	13	541.89	0.02
58_Calamagrostio villosae-Piceetum	Sudetian higher-montane spruce forest occurs mainly on acidic podzols, but also on gleyic soils or on rankers over talus slopes.	1	1389.09	0.00

[1] In Table 3, this plant community is included in the group: 'Eutrophic ('rich') oak-hornbeam forests'. [2] In Table 3, this plant community is included in the group: 'Mesotrophic ('poor') oak-hornbeam forests'. [3] In Table 3, this plant community is included in group 'Eutrophic ('rich') beech forests'. [4] In Table 3, this community forms group 'Acidophilus ('poor') beech forests'.

Table 3 and Figures 1–4 present collective data for the main group of communities, i.e., oak-hornbeam forests, divided into eutrophic ('rich') and mesotrophic ('poor') ones, as well as eutrophic ('rich') and acidophilus ("poor") beech forests. The data are provided as totals and by localities with different shares of fir in forest stands. The listing shows a higher number of fir localities per area unit of a given community is characteristic of areas of potential natural vegetation that develop in richer, more fertile habitats.

Table 3. The number (N) of fir localities (FL) (total and broken down into a different share in the stand) within the four most important groups (S > 3000 ha) of natural vegetation in the area covered by the study. Table 3 does not include the plant communities in Table 2 that generally have not many fir localities (FL) and the area of which is less than 3000 thousand ha.

				N [FL] with Different Share in the Stand		
Name of a Group of Plant Communities	**N [FL]**	**S [ha]**	**N/S [FL/ha]**	**Up to 10%**	**11%–49%**	**50% or More**
Eutrophic ('rich') oak-hornbeam forests	178	4332.30	0.04	109	56	13
Mesotrophic ('poor') oak-hornbeam forests	55	3455.31	0.02	43	10	2
Eutrophic ('rich') beech forests	192	4581.77	0.04	124	53	15
Acidophilus ('poor') beech forests	330	18,441.20	0.02	229	82	19

Individual groups of communities include data on the following communities listed in Table 1 and marked with numbers: eutrophic ('rich') oak-hornbeam forests—communities Nos. 11, 13; mesotrophic ('poor') oak-hornbeam forests—communities Nos. 10, 12; eutrophic ('rich') beech forests—communities Nos. 30, 31, 36; acidophilus ('poor') beech forests—communities No. 38.

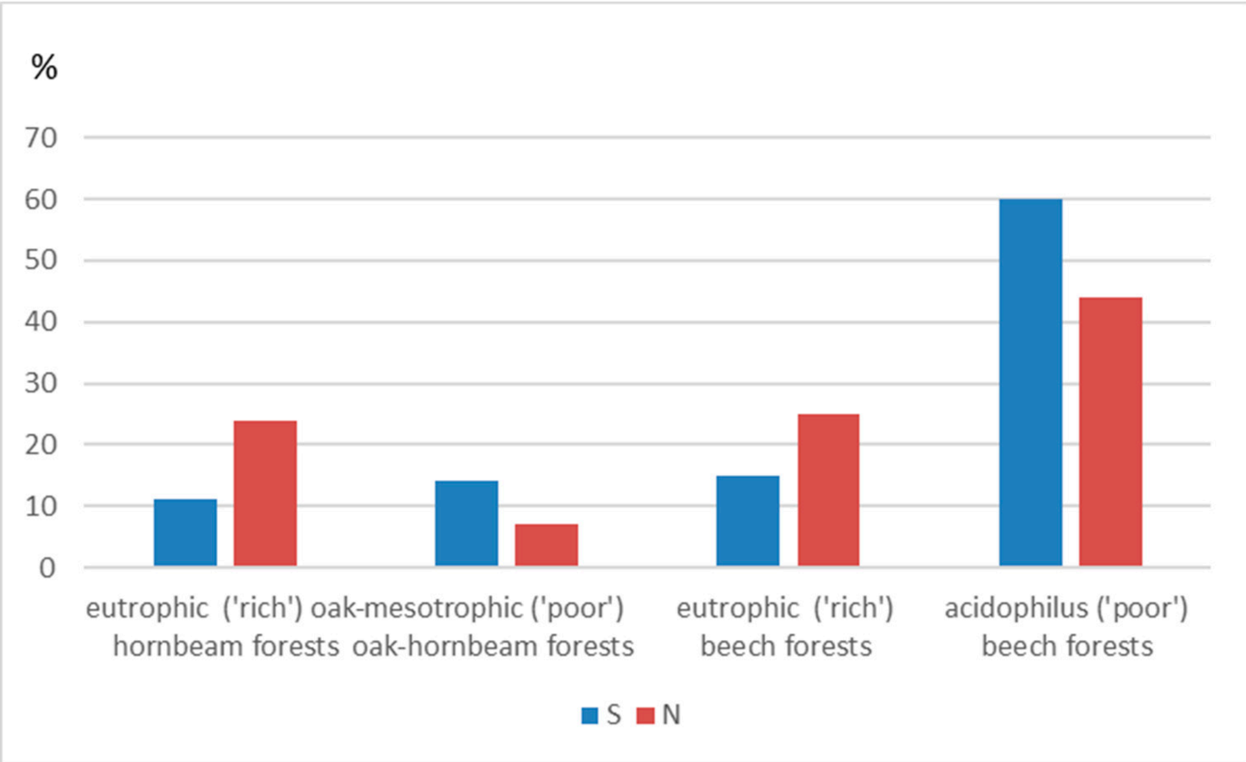

Figure 2. Comparison of the percentage distributions of the surface area (S) most important groups of potential natural vegetation (in the area covered by the study) and the percentage distributions of the total fir localities numbers (N).

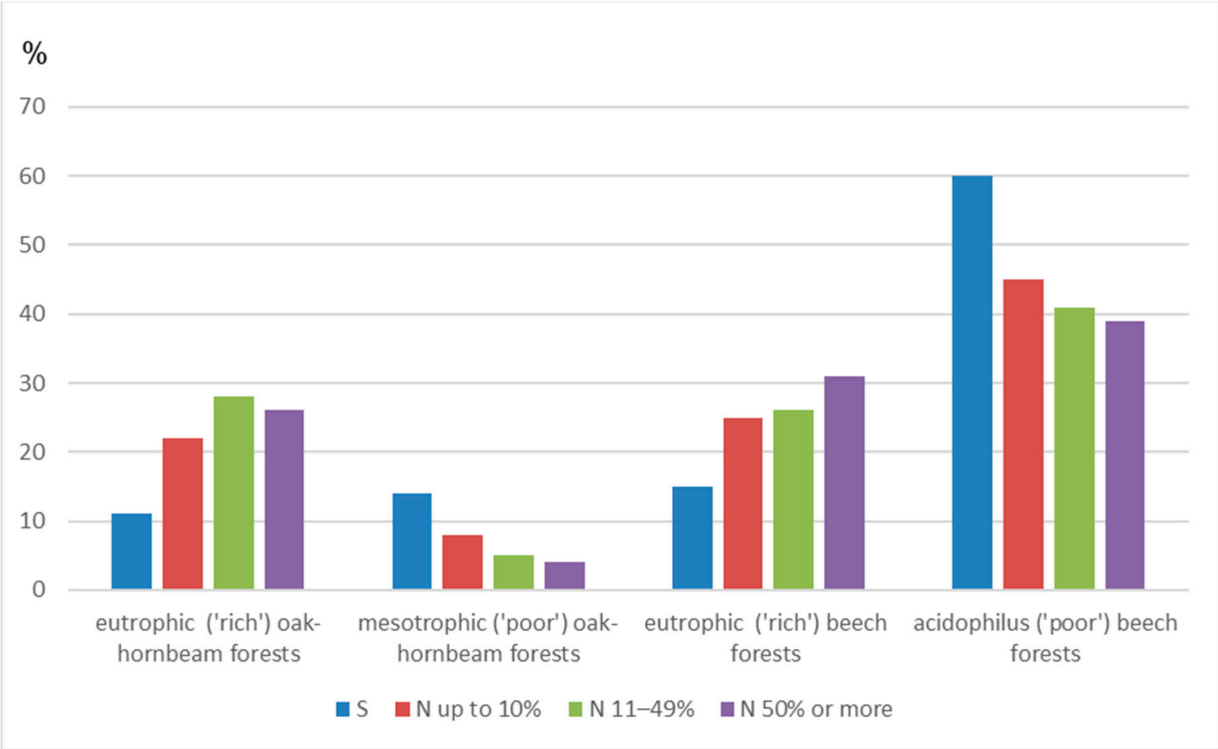

Figure 3. Comparison of the percentage distributions of the surface area (S) most important groups of potential natural vegetation (in the area covered by the study) and the percentage distributions of the fir localities numbers broken down into a different share in the stand (N).

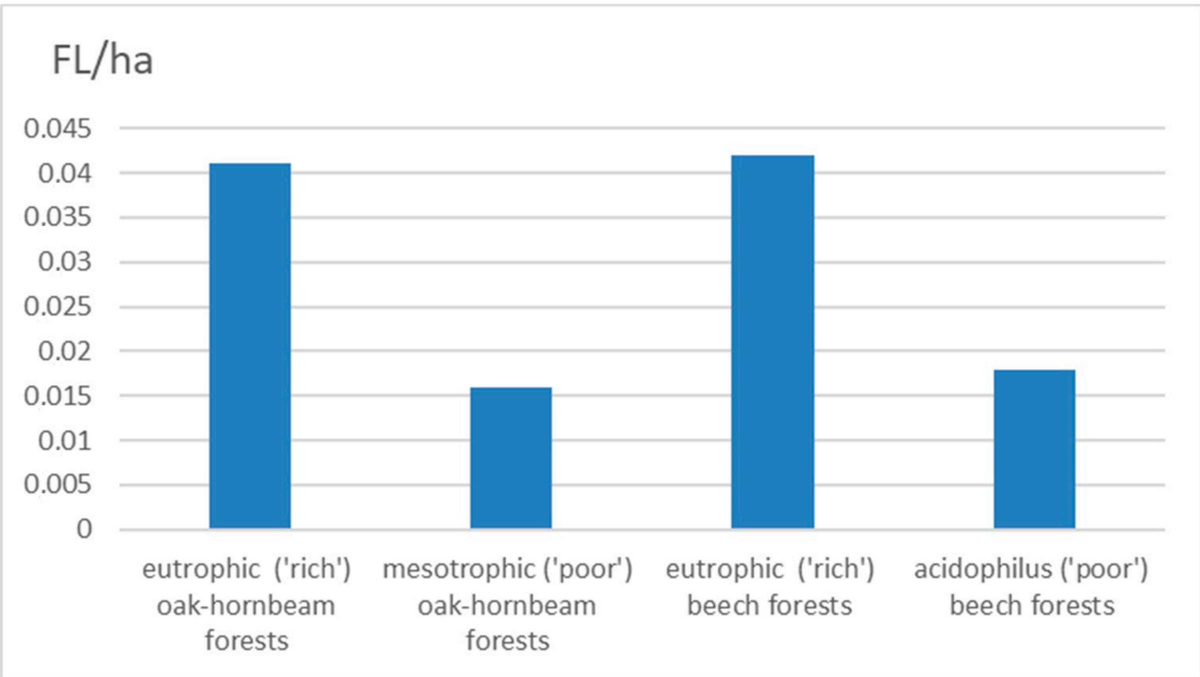

Figure 4. Number of fir localities (FL) per unit surface area of the most important groups of potential natural vegetation in the area covered by the study.

A comparison of the distribution of the surface areas of individual communities and the distribution of the numbers of localities within them proves that they are not correlated. The respective distributions differ statistically—Table 4. Localities (FLs) with a greater share of fir, more often, those with a low share can be found in PNV connected with more fertile habitats. However, at the significance level of $p = 0.05$, the respective data distributions did not differ statistically.

Table 4. Chi-square test results were conducted in order to verify the significance of the differences between the percentage distributions of the surface area of the most important groups of potential natural vegetation (in the area covered by the study) and the number (N) of fir localities (total and broken down into a different share in the stand). Three degrees of freedom.

	N Up to 10%	N 11%–49%	N 50% or More	N Total	S
N up to 10%		1.618	2.738	0.165	6.894
N 11%–49%			0.674	0.767	**13.442**
N 50% or more				1.842	**16.886**
N total					**8.482**
S					

Values in bold indicate statistically significant differences ($p < 0.05$).

4. Discussion

When compared to typical phytosociological studies, we have tried to quantify the differences between individual communities in terms of their usefulness for growing firs.

The earlier phytosociological studies of selected fir sites in the Sudetes and a review of the phytosociological literature regarding the region [31] indicate that *A. alba* has a broad ecological scale, is a component of many forest communities, and that it is found most frequently at potential sites of acidophilic beech forests, whose vegetation is now strongly transformed because of spruce planting. Typical, mainly acidophilic beech forests take second place (in respect of frequent occurrence). Oak-hornbeam forest takes the third position. This agrees with the findings of our study.

The fact that we recorded the highest share of fir in the fertile beech communities in the Sudetes goes against the opinion that the species plays a minor role in Sudeten fertile beech forests [53]. On the other hand, however, Carpathian fertile beech forests are regarded as the optimum place for fir growth, and according to Zarzycki [53], fertile Carpathian beech forests may even be regarded as the center of the occurrence of *A. alba*. Its role in individual subunits of this area and in its various parts may differ [53]. On the other hand, phytosociological units whose names originate from 'fir' (e.g., *Abietetum polonicum*) occur on soils with slightly poorer fertility, and in studies devoted to natural regeneration of fir, habitats with mesotrophic soils are assessed particularly well [20,23,53]. In Jaworski's research [3], fir seedlings survived better in mesotrophic than in eutrophic habitats. According to this author, the pathogenic fungus *Cylindrocarpon destructans* (Zinss) Scholten was to be responsible for the greater mortality of seedlings in fertile habitats.

Both the very variable share of fir in fertile beech sites and the locally recorded problems with its natural regeneration may be linked to the view that suggests the existence of a natural crop rotation involving fir and beech [1–7]. As Vrška's et al. [54] research suggests, the historically recorded changes in the shares of beech and fir in fertile lower-montane forests in large areas of the Carpathians are principally attributable to changes in forest management. However, this does not mean that periodical changes in the shares of beech and fir that occur locally in relatively small areas are not natural in character [3,55–60]. If the natural crop rotation referred to above is a common phenomenon, this means that the operating cycle of fertile lower-montane forests may be more complex than we thought and longer than 300–400 years. The fact that studies are conducted at various phases of the cycle, which is additionally modified by various human activities, may account for apparently divergent findings.

The results of our studies indicate a strong position of fir in fertile beech habitats also in the Sudetes, i.e., in a region whose firs, just like the Alpine ones, are closely connected to the Apennine glacial refugium than those in the Carpathians [9]. Consequently, the strong position of fir in eutrophic lower-montane forests and submontane oak-hornbeam forests seems to have a universal character.

A relatively small share in the Sudetes of eutrophic beech communities may indicate that in this region, the original resources of fir may have been relatively smaller than those in the Carpathians. This has been suggested by, for instance, Barzdajn et al. [27]. The historical data show, however, that the percentage was definitely not lower than 20% [25,27,61].

In our opinion, determining the frequency of natural fir localities (FL) within areas of potential plant communities that develop under certain habitats under natural conditions is of great importance to the ecological characteristics of the species, including its potential role in the composition of fertile submontane and lower montane forests. Before conducting the study, when analyzing the literature data, we expected smaller differences and that they would mainly occur between beech and hornbeam forests, while the fertility of the habitat turned out to be the main differentiating factor. Unlike most other members of the *Pinace* family, which naturally occur in poorer habitats, *Abies alba* successfully competes with angiosperm deciduous trees in fertile habitats under stable climatic conditions (no severe frosts and prolonged droughts).

That this is the case—we have known for a long time. But the particular strength of this competition, as suggested by our results, is a novelty. Our research, like any other in this field, is contributory in nature. Its results shift the main center of the natural occurrence of silver fir towards fertile habitats. To us, it is interesting and important.

5. Conclusions

The results of our research bring new information to the discussion concerning the habitat preferences of silver fir. They indicate the habitats of the fertile foothill forests (oak-hornbeam forests) and particularly the lower sub-mountain forests (beech forests) as potential main centers of fir occurrence in Central Europe. In the case of the Sudetes, this is new information, and in the case of other parts of the natural range, confirmation of some previous studies, but our results indicate that fir favors such habitats particularly strongly.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12091203/s1, Table S1: 'The strong position of silver fir (*Abies alba* Mill.) in fertile variants of beech and oak-hornbeam forests in the light of studies conducted in the Sudetes', supplementary materials: *Abies alba* localities (FL).

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