



RESEARCH ARTICLE

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Secondary forest succession in Silver birch (*Betula pendula* Roth) and Scots pine (*Pinus sylvestris* L.) southern limits in Europe, in a site of Natura 2000 network – an ecogeographical approach

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Abstract

Aim of study: To investigate the secondary forest succession in the study area and the pathways of its spread and the existing environmental, autecological factors and possible inter-specific competition relationships.

Area of study: The study area is a Site of Natura 2000 network in northern Greece dominated by two pioneer forest species, *Betula pendula* and *Pinus sylvestris*. Study area is the southern limit of Silver birch in Europe and genotypes of these forests may be important due to the anticipated global increase of temperature and the forthcoming climate change.

Material and methods: The main forest types studied were: pure forests of *B. pendula* and *P. sylvestris* and mixed forests of these two main species. To study the expansion of forests in the area, a spatial analysis was performed based on geographical data. To detect forest changes, the rate thereof and their specific spatial distribution and preferences, a statistical analysis was performed.

Main results: Approximately 60% of the studied area in 1945 was transformed from grasslands/barelands to forests. The composition of new forests was found to be different from the old ones. The rate of forest establishment in the first years was lower than in the latter years. All factors examined played an important role to the expansion of forest except slope.

Research highlights: Distance from the old stands played the most determining role to new forest structure and composition. Inter-specific competition results to the formation of pure stands, as indicated by the older stands.

Keywords: secondary forest succession; *Betula pendula*; GIS; spatial analysis; forest species competition; forest species distribution.

Authors' contributions: NO and PG conceived the idea and the structure of the article. In particular, NO contributed to the collection and interpretation of the data and made drafts of the manuscript, and PG supervised the work and coordinated the research project.

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Introduction

Silver birch (*Betula pendula* Roth) is a cold-tolerant and fast-growing tree species, distributed across Europe, from the Mediterranean to central Siberia (Beck *et al.*, 2016). It is a light-demanding species that can grow rapidly even on poor soils, while its winged fruits are very efficiently distributed by wind and its roots are easily associated with a large number of ectomycorrhizal fungi. These combined characteristics make birch trees thrive as pioneers during early stages of secondary vegetation succession (Beck *et al.*, 2016). Silver birch is mostly abundant in the boreal zone of northern Europe, where it can co-dominate or dominate in late-successional vegetation. In southern Europe,

it is confined to mountainous areas, as it does not tolerate prolonged summer drought. Thus, the southernmost distribution limits appear to be determined by summer drought.

In Greece it commonly appears in sparse individuals and it forms compact stands only in the western Rhodope Mountain, close to the Greek-Bulgarian borders. *B. pendula* in Greece is considered to have colonized the area after the Last Glacial Maximum (LGM), as the population in Greece has similarities with the population of Central Europe (Maliouchenko *et al.*, 2007). The Balkan peninsula functioned as a *refugium* for many flora and fauna species after LGM, and then there was a postglacial expansion back to northern Europe (Hewitt, 2000). Conversely, the southern population in

western Europe differs from the central ones. This population consists of a low-latitude limit of the species (rear edge) range, which is also the case in Italy and Spain. These rear edge populations are highly important for the species' genetic diversity. Their ecological features, dynamics and conservation requirements differ from those of the other parts of their range, and common conservation practices may not have the desired effect to their maintenance (Hampe & Petit, 2005). Very little is known about the amount and organization of genetic variation in the southern marginal areas (Vakkari, 2009). Recent data from the local Forest Service show that the area occupied by the species has greatly changed during the last decades. However, there is no available knowledge about changes in species distribution, which probably result in species habitat limitation.

Scots pine (*Pinus sylvestris* L.) is a pioneer species also, light-demanding, with great tolerance to drought and poor-nutrient soils (Gaudio *et al.*, 2011). Scots pine is also popular in the area forming pure or mixed stands with Silver birch. For both species the study area is the southern-eastern limit of their expansion in Europe. For this reason, studies in this area are very important, as both species may address the evolutionary adaptation problem due to climatic change (Kuparinen *et al.*, 2010). Species adaptability to climate conditions is facilitated by genetic diversity (Hamrick, 2004) and gene flow (Aitken *et al.*, 2008). Thus, this region constitutes a conservation area for genes that have adapted to climate change and may contribute to better adaptability of the species in the future, enabling them to endure more prolonged summers in Europe.

Silver birch and Scots pine have rapidly colonized large abandoned areas during the last decades, which gives rise to the question of how and at which sites they dominate. Other important scientific questions could be: How rapid is the process that has taken place? Which factors affect the colonization paths? Is there any interaction between the rates of two species expansion?

Following the above-mentioned questions, the aim of this study is to investigate the land cover changes in the study area, focusing on the area of birch geographical distribution and deepening and widening the knowledge of birch spreading, so as to enhance the conservation of the species in its southern-eastern distribution in Europe. The specific objectives of the study were: i) to detect, quantify, measure and map birch forest changes using airborne data; ii) to spatially identify site preferences of birch forest in correlation with environmental factors at a local scale; and iii) to detect the significance of each environmental or autecological (distance from parental clusters) factor to the species distribution in the area.

Materials and methods

Description of the study area and history

The study area is public land, located in northern Greece at the Greek–Bulgarian borders and it extends to an area of 6934.51 ha (Fig. S1 [suppl.]). This site is of great importance for biodiversity conservation as it belongs to Natura 2000 network (site code: GR1140002), according to the Habitats Directive 92/43/EEC. The vegetation of the area is dominated by the tree species: *Pinus sylvestris* L., *Betula pendula* Roth and oaks (*Quercus frainetto* Ten, *Q. petraea* (Matt.) Liebl.), which form pure and mixed stands. Other tree species present are: *Picea abies* (L.) H.Karst., *Fagus sylvatica* L. and *Pinus nigra* Aiton (the last one is found in small reforested areas). Pure or mixed stands of Scots pine and Silver birch cover about 80% of the area (approximate 5600 ha). Many rare and endangered species of fauna (listed in the Standard Data Form of the site) and flora (Eleftheriadou, 1990) of the region are directly dependent on the intra-forest environment of the region. The importance of these rare species has been recognized as they are included in lists II and / or IV of the Habitats Directive 92/43/EEC or in List I of Directive 79/409/EEC rare birds.

The area is also part of the European Green Belt (EGB). The EGB, running 12,500 km throughout Europe along the former Iron Curtain is the Europe's backbone of an ecological network, and a living monument and global symbol for transboundary cooperation in nature conservation and sustainable development (Schindler *et al.*, 2011). The heterogeneity and the intense dynamics of the studied area can allow a wide range of factors affecting forest dynamics (Teixeira *et al.*, 2009).

The history of the site and the use of the land have historically played an important role in the vegetation formation of the area. Before 1922, there were some small settlements nearby, inhabited by nomads. As evidence, a traditional settlement is visible at aerial photographs taken in 1945. Extensive meadows and sparse remnants of forest stands existed at that time in the area (Zagas, 1990; Oikonomakis & Ganatsas, 2012). After 1946, the nomads abandoned the region and almost the entire Central Rhodope was designated as a Forbidden Zone. Thus, the existing scattered parental forest stands gradually colonized the whole area. After 1960, the forests were put under the management of Forest Service.

Methods applied to detect land cover changes, data processing and analysis

Remote Sensing (RS) accompanied by Geographic Information Systems (GIS) was used to investigate land

cover changes, which is considered an inexpensive and practical solution and produces easily land cover maps and solves various environmental problems (Fassnacht *et al.*, 2006). Given the above statement, the following geographical data were used to analyze the land cover changes in forest cover and the expansion of the different forest types in the area:

- Aerial orthoimages of year 1945 and recent (2009) RGB aerial orthoimages of 0.5 m spatial resolution provided by the Greek cadastral service.
- Orthophotomaps of the year 1975 (forest vegetation maps) from the Hellenic Forestry Service.
- Forest maps produced by the local Forest Service for the preparation of forest management plans with field measurements, which are updated along with the forest management plans every 10 years. The scale used was 1:20000. These analog maps were corrected using the high resolution Orthophotographs of the Greek cadastral service and a digital up-to-date forest cover map was produced.
- Digital Elevation Model (DEM) (labelled as ASTER 30, downloaded from <https://search.earthdata.nasa.gov/search>, in 30 m spatial resolution) used to create class maps of aspect, slope and elevation of the area.
- Historical climate data (19 bioclimatic variables) were downloaded from the world climatic data website: <http://www.worldclim.org> (accessed in 25-3-2020). These variables are used often in ecological niche modeling (Hijmans *et al.*, 2005; O'Donnell & Ignizio, 2012; Fick & Hijmans, 2017).
- Auxiliary data such as: CORINE 2000 (<http://geodata.gov.gr/dataset/corine-2000>), Natura 2000 outlines (<https://www.eea.europa.eu/data-and-maps/data/natura-11/natura-2000-spatial-data/natura-2000-shapefile-1>), Google maps (<https://www.google.gr/maps>) and ground observations of the area.

All raster and vector dataset projected into the Hellenic Geodetic Reference System (HGRS '87).

Initially, landcover maps for each time period were created from the available orthoimages. Detailed photointerpretation (minimum mapping unit: 0.1 ha) was conducted to classify forest cover using basic principles (Lillesand *et al.*, 2015). As a result, a three-class cover map was created, categorized as: Forest1 – sparse forests - canopy cover 10-40%, Forest2 – dense forests – canopy cover 40-100%, Grasslands (non-forested areas)

Forest types were distinguished using the latest available forest maps of the Forest Service. The dataset was

corrected by any convenient way including photointerpretation and in-situ observations as well as other auxiliary data, such as Land Use/Land Cover (LULC) maps of CORINE 2000 dataset and google maps. The final vegetation cover maps included the following categories: 1) forests dominated by Silver birch, 2) forests dominated by Scots pine. The more interesting categories with the greatest expansion were 3) mixed birch-pine forest dominated by Silver birch, 4) mixed pine-birch forest, 5) grasslands – barelands.

A spatial analysis was performed in order to estimate land cover changes and their forest type distribution. The spatial and quantitative distribution of birch and other species was investigated in the newly established forests in the later periods (after 1945). In the area of newly established forests, each factor's (elevation, slope, aspect, bioclimatic variables, distance from parental clusters) spatial output was examined separately within the spatial database created with the appropriate GIS analysis, such as spatial overlay, reclassification, spatial query functions with either vector or raster layers (Oikonomakis & Ganatsas, 2012).

To facilitate statistical analysis, a random network of points was used with the limit being at least 50 meters apart. Following application of that limit, the number of random points was limited to about 2300 points, which were finally used. All the environmental and autecological factors were calculated for each point, and, thus, a random network of points (n=2267) with all the information (forest type, elevation, aspect, slope, bioclimatic variables, distance from parental clusters from the pre-existing forest in 1945) for statistical analysis was created. The Generalized Linear Model (GLM) (Guisan *et al.*, 2002) was applied, in order to model the available data and to estimate the impact of each factor on the patterns of birch and pine forest changes. The data were separated in two time periods (1945-1975 and 1975-2009) and two GLMs were, thus, applied, to enable comparison of results between the first and the second period of forest expansion. The dependent variable is by nature categorical, the aspect variable was converted to categorical and the other variables were used as continuous.

Bioclimatic variables were tested for collinearity and correlations. Strong correlations among them can result in over-fitting of models in species distribution modelling (Pradhan, 2016). The variables were tested through multiple regression models and Variance Inflation Factors (VIF) were calculated. The cutoff value >10 was selected as in other studies (Shekede *et al.* 2018; Dong *et al.* 2020; Ncube *et al.* 2020). As a result, only two of them were selected: Mean Temperature of Driest Quarter (3-month interval) - BIO9; Precipitation of Driest Quarter (BIO17). These two variables delimit the temperature and drought tolerances of forests species.

Boxplots were used as a data exploration method for further insight on spatial distribution of forest species. The InterQuartile Range (IQR, $Q1 - Q3$), which represents 50% of the distribution was used as a robust scale measure (Tarr et al., 2012) to better understand the distribution of forest species in relation with each factor. All the variables were also converted to categorical ones, so as to cross-tabulate them with forest formation variables and to estimate differentiations from expected values, performing the chi-square χ^2 test.

The following categories were selected: 1) Dependent variable: 1: pure birch forest, 2: mixed birch-pine, 3: mixed pine-birch and 4: pure pine forests, 2) Aspect: North, NE, East, SE, South, SW, West, NW, 3) Slope: <10, 10-20, 20-30, 30-40, 40-50, $\geq 60\%$, 4) Elevation: <800, 800-900, 900-1000, 1100-1200, 1200-1300, 1300-1400, 1400-1500, ≥ 1500 m., 5) Distance from parent clusters: <100, 100-200, 200-300, 300-500, 500-800, ≥ 800 , 6) BIO9: equal intervals of 1°C (temperature) were created and 7) BIO17: equal intervals of 3mm (rainfall) were created. SPSS statistical package was used for the statistical analysis.

Results

Tree colonization pattern in the non-forest areas

During the studied 64-year period, the forest expanded dramatically, occupying the existing non-forest areas.

This resulted in almost all the area being covered by forests. Specifically, in 1945, the non-forest area was extended to 61.7% of the total studied area, and the forests covered only 38.3%. In 2009, after the gradual colonization of forest species, the area was found to be covered by forest by 97.8%, while only a very low percentage (2.23%) thereof remained as forest openings (Table 1). These very few areas that remained uncovered by forests are either remote areas (grasslands) or rocky areas which do not favor tree establishment. Photointerpretation of the available images showed that some areas have not been reached yet and remain as forest openings, as the direction of the expansion indicates. Rocky areas are also photo-interpreted in small areas. Forest species colonized almost all the existing non-forested areas (grasslands), which were found to cover 3,993.0 ha or 59.5% of the total area (Table 1). The area covered by forests and typical landcover examples of the three years 1945, 1975 and 2009 are displayed geographically and exemplified in Fig. 1.

The rate of forest expansion was lower during the first period (1945-1975), and significantly higher during the next period, 1975-2009. In 1975, the grasslands diminished to a percentage 37.13% of the total area. Specifically, the annual rate of this forest expansion was 55.06 ha/year in the first post-war period, and 68.86 ha/year during the second period (Table 1). An analysis of the expansion rates and behavior for each of the dominant forest species revealed that:

Birch increased (almost doubled) its occupied area during the studied period. In 1945, the species covered

Table 1. Land cover area in studied years, land cover changes and annual rates of change

Land cover in distinct years									
Land cover classes*	1945		1975		2009				
	Area (ha)	(%)	Area (ha)	(%)	Area (ha)	(%)			
Grasslands	4142,61	61,75	2490,79	37,13	149,59	2,23			
Forest1	1012,15	15,09	2114,48	31,52	645,11	9,62			
Forest2	1554,14	23,17	2103,63	31,36	5914,20	88,15			
Total	6708,90	100,00	6708,90	100,00	6708,90	100,00			
Changes in land cover. Examined years 1945, 1975, 2009									
Land cover classes*	Change 1945-1975			Change 1975-2009			Total change 1945-2009		
	Area (ha)	Area (%)	ha/ year	Area (ha)	Area (%)	ha/ year	Area (ha)	(%)	ha/ year
Grasslands	-1651,82	-24,62	-55,06	-2341,20	-34,90	-68,86	-3993,02	-59,52	-62,39
Forest1	1102,33	16,43	36,74	-1469,37	-21,90	-43,22	-367,04	-5,47	-5,74
Forest2	549,49	8,19	18,32	3810,57	56,80	112,08	4360,06	64,99	68,13

* Land cover classes:

- Forest1 – sparse forests - canopy cover 10-40%
- Forest2 – dense forests – canopy cover 40-100%
- Grasslands (non-forested areas)

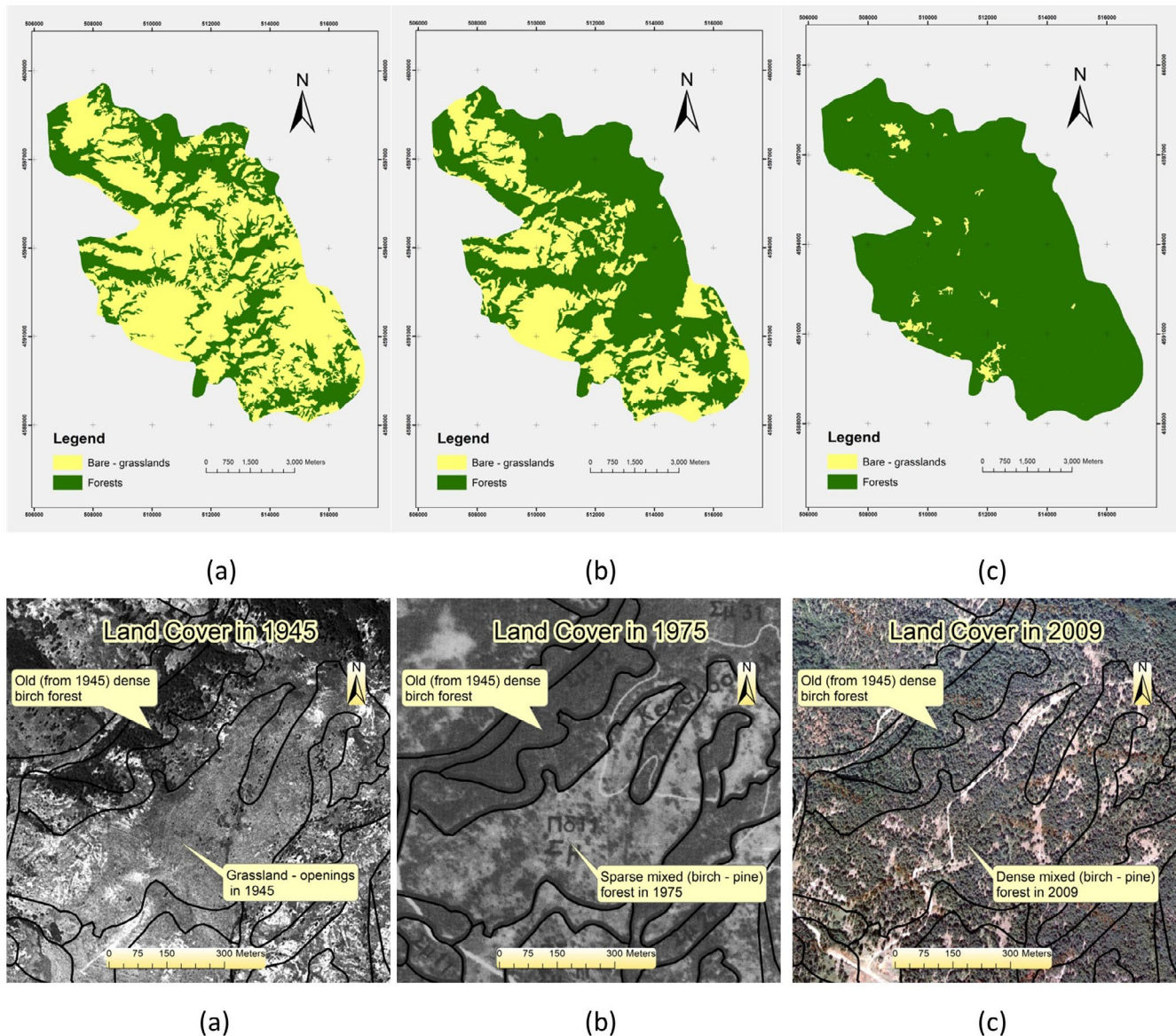


Figure 1. a) Land cover maps of the examined years and examples of landcover in each year. b) Examples of forest colonization in grasslands-barelands. Delineation in the examples is of the year 1975 and shows a typical mixed pine-birch forest installation in grassland

an area of 616.8 ha (mean altitude: 1124 m, mean BIO9: 14.04°C, mean BIO17: 113.32 mm, main aspects: North-NW-West slopes), and by gradual colonization of the open non-forest land, increased by another 536.4 ha (mean altitude: 1064 m, mean BIO9: 14.10°C, mean BIO17: 114.44 mm, main aspects colonized: South – South-West slopes) reaching to a total area of 1153.2 ha pure birch forests in 2009 (Table 2, Fig. 1). Simultaneously, the mixed stands dominated by birch almost tripled, from 299.0 ha (mean altitude: 1141 m, mean BIO9: 13.97°C, mean BIO17: 114.31 mm, main aspects: NW-West slopes) to 824.5 ha (mean altitude: 1175 m, mean BIO9: 13.92°C, mean BIO17: 113.97 mm, main aspects: South-SW slopes) and eventually covered 1123.5 ha in the study area. A similar trend was also observed for Scots pine. *P. sylvestris* colonized another part of the bare land, resulting in the whole

area being covered by forests. Similarly to birch, the mixed stands dominated by *P. sylvestris* increased considerably, from 406.6 ha (mean altitude: 1334 m, mean BIO9: 13.56°C, mean BIO17: 115.73 mm, almost equal aspect slopes) to 1076.7 ha (mean altitude: 1211 m, mean BIO9: 13.79°C, mean BIO17: 115.34 mm, main aspects: SE-South-SW slopes).

These species trends and the combination thereof resulted in the formation of much more mixed stands than pure stands of both dominant tree species, leading to a coexistence of the two pioneer forest species *B. pendula* and *P. sylvestris*, in the greatest part of the afforested area.

As a consequence, mixed forests (especially the type: *P. sylvestris*– *B. pendula*) are the most abundant among the newly established forests, covering a large part of the newly forested area (1901.1 ha - 46.74%), while pure

Table 2. Land cover area in studied years, land cover changes and annual rates of change

FOREST TYPES	1975-2009	1945-1975	1945	1975-2009 (%)	1945-1975 (%)	1945 (%)
	Area (Ha)	Area (Ha)	Area (Ha)			
<i>Betula pendula</i>	263.57	272.82	616.79	12.14	13.98	23.85
<i>B. pendula</i> - <i>P. sylvestris</i> (mixed)	497.30	327.16	299.03	22.90	16.76	11.57
<i>P. sylvestris</i> - <i>B. pendula</i> (mixed)	517.66	559.01	406.58	23.84	28.64	15.73
<i>Pinus sylvestris</i>	202.88	503.82	502.70	9.34	25.81	19.44
Grasslands - barelands	217.86	0.00	0.00	10.03	0.00	0.00
Other forest types	472.28	288.94	760.53	21.75	14.80	29.41
TOTAL	2171.53	1951.74	2585.62	100.00	100.00	100.00

forests (especially *B. pendula* forests) can primarily be found at the old forest areas (1119.4 ha – 43.29% total pure forests). The distribution of forest cover in the time periods examined is shown geographically in Fig. 2 a) and Fig. 2 b). Fig. 2 c) also shows the percentages of the occupied area in three time periods. The percentage of the landcover is greater for *P. sylvestris* in new forests. Especially in the first period of expansion, pure and mixed *P. sylvestris* forests cover a large area (54.45% of the area forested in the period 1945-1975) which indicates that it has been spreading faster than *B. pendula* in pure or mixed formations. In the second period of expansion (1975-2009), the percentages for pure pine or birch forests are significantly lower than those for mixed forests.

Factors affecting the expansion of forest species

The statistical analysis revealed significant differences in some of the environmental parameters between the areas colonized by birch and the areas colonized by Scots pine, probably due to differences in their niche requirements, or due to environmental barriers (e.g. distance from forest edges).

Environmental drivers

Especially, during the first post-war period (1945-1975), birch was found to colonize lower altitudes (Q1:1159 - Q3:1282 m) compared to *P. sylvestris*, which was found to colonize higher altitudes (Q1:1262 - Q3:1416 m). In the second period of expansion, both species would spread to lower altitudes (Fig. 3). Also, birch was found to show preference to North-NW-West slopes, compared to *P. sylvestris*, which showed preference to south faced

slopes. (Fig. 4). GLM models, which were implemented separately for the two time periods of forest expansion (1945-1975 and 1975-2009), showed that all environmental factors played an important role, except slope and BIO9 (Table 3), probably due to the fact that they overlapped with the other factors. According to Wald chi-square statistic, the greatest influence among the environmental factors comes from the elevation. Elevation inevitably correlates with bioclimatic variables because at higher altitudes the temperature is lower and rainfall is greater.

According to the distribution frequencies of the sample, in general (for the whole period 1945-2009) birch was found to colonize lower altitudes (Q1:1063 m, Q3:1253 m), compared to *P. sylvestris*, which was found to be established in higher altitudes (Q1:1219 m, Q3:1398 m) (Fig. S2 [suppl.]). Elevation and bioclimatic variables also diverged significantly from the expected values (Table 4) of possible species distribution (expected values), which entails that they are major factors with important influence to the final species geographical distribution.

The aspect in study area is distributed unevenly (Fig. S3 [suppl.]). The forested area in 1945 is dominated by North-NW-West aspect slopes. On the contrary, newly shaped forests are dominated by SW-South-SE aspect slopes. For this reason, new forests had to colonize southern slopes for the largest part. The geographical distribution analysis focused on the preference of species to certain aspect slopes, applying a chi-test to compare observed values with expected values.

A GIS analysis in combination with a statistical analysis (χ^2 test) showed that pure *B. pendula* forests showed preference to Northern aspects (mainly West-NW-North) (Fig. 4), while mixed forests with *B. pendula* as dominant species do not deviate from expected values in terms of their distribution (Fig. S4 [suppl.]). Conversely, *P. sylvestris* pure forests show preference to southern

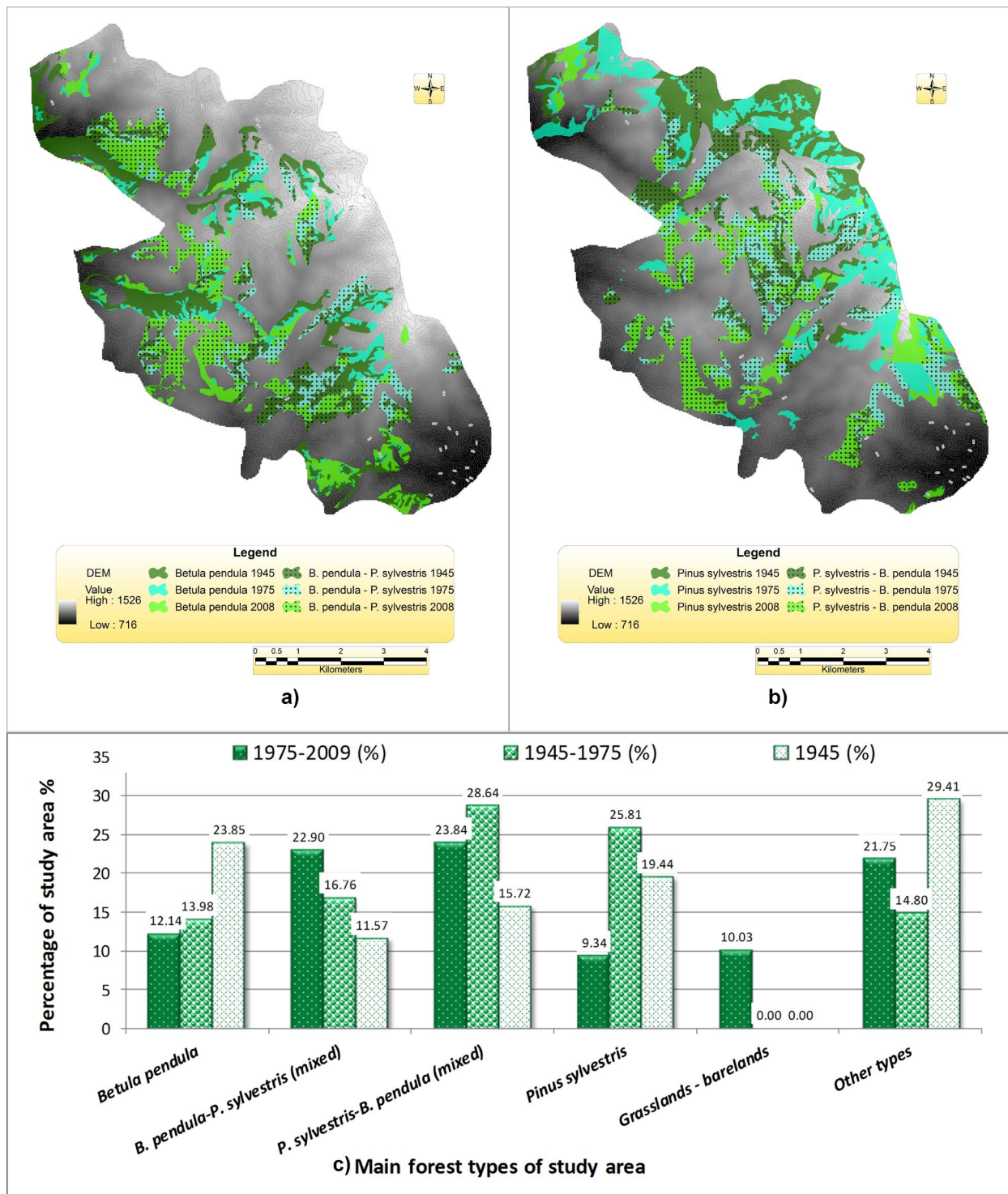


Figure 2. Space-time composition of spread of the examined forest species – a) Silver birch, b) Scots pine and mixtures of them. c) Percentages of landcover of the main forest species of the area.

aspects (mainly SW-South), and mixed forests (*P. sylvestris*-*B. pendula*) preferred East, NE and SE aspects (Fig. S4 [suppl.]). In the second period of expansion, *P. sylvestris* forests still preferred North and South aspects, but the differences are not so obvious, as the χ^2 test values are lower (Table 4). Interestingly, the remained bare lands and grasslands differ in their environmental

parameters, compared to the areas occupied by forests, being more abundant in S and SW aspects (Fig. S4 [suppl.]). This suggests that S and SW aspects were the least preferable (or less feasible) areas for colonization of tree species.

Generally, all new forest types were distributed in lower altitudes because it is easier for them to expand

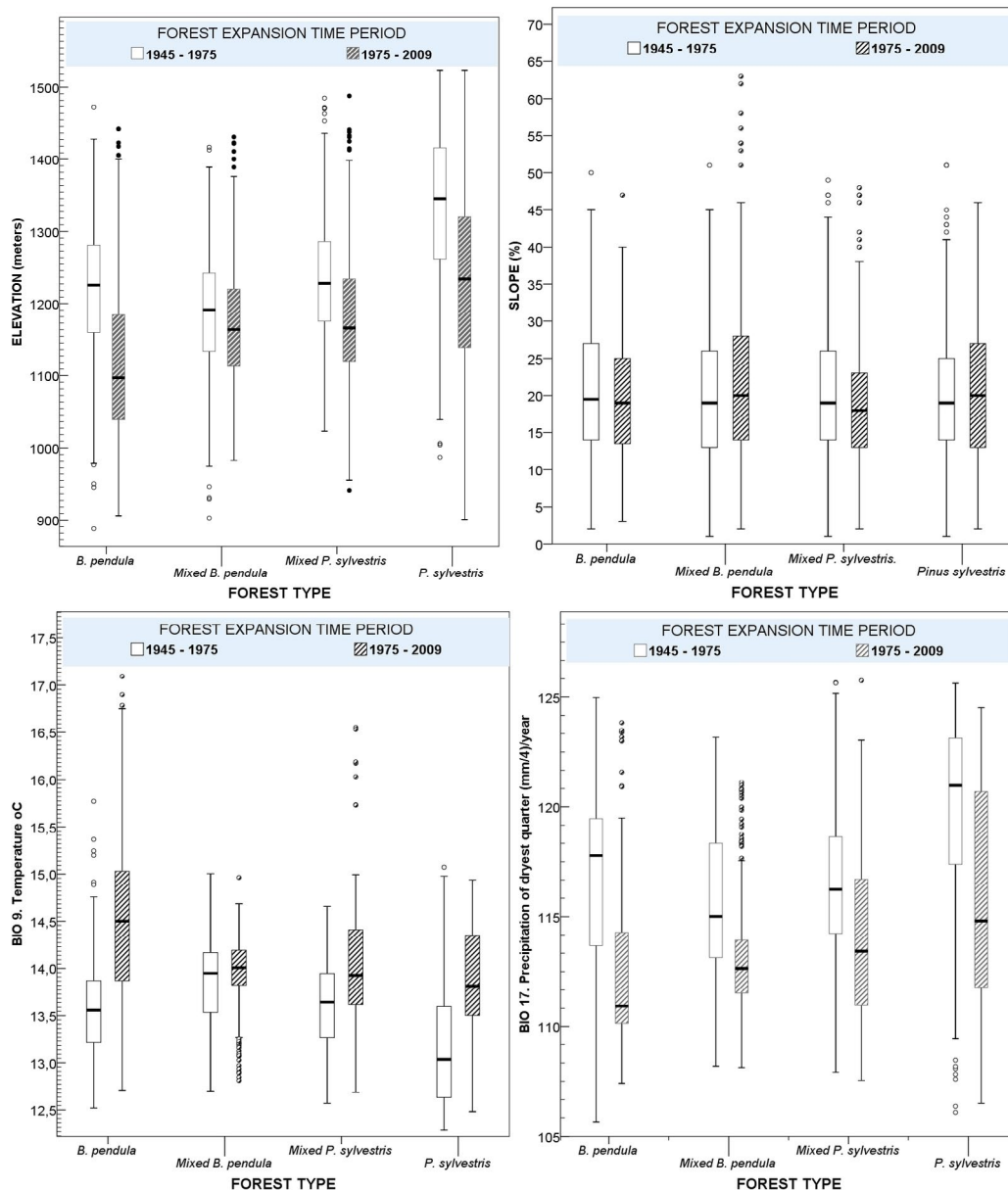


Figure 3. Boxplots showing the expansion of main forest types in relation to slope, elevation and bioclimatic factors over two periods of forest expansion.

downhills. As a consequence, new forests colonized drier and hotter sites as shown in the climatic variable boxplots (Fig. 3). The direction followed by all forest types was from colder and rainier sites to hotter and drier sites. This is shown in Fig. 3 gradually from mature forests (<1945) to later-established forests (1945-1975) and finally to younger forests (1975-2009). The chi-test revealed higher values than expected for *B. pendula* in lower temperatures and lower rainfalls (BIO9: 13-14°C, BIO17<113mm) in the first period of species colonization (1945-1975). It also revealed higher temperatures and lower rainfalls than expected (BIO9: 15-17°C, BIO17<113mm) for the second period of birch colonization (1975-2009). On the contrary, the χ^2 revealed higher values than expected for *P. sylvestris*, in the col-

dest and wettest areas of its expansion, in both periods of its colonization (for period 1945-1975: BIO9<13°C, BIO17>119mm and for period 1975-2009: BIO9<14°C, BIO17>119mm).

Finally, slope inclination does not seem to play an important role in the manner of expansion of the examined tree species, as the two species and their mixed forest types demonstrate a similar behavior, especially in the first period of forest expansion. Generally, slope is the environmental factor with the lowest and least significant χ^2 test values (Table 4). Generally, goodness of fit for GLMs shows that in the second period of expansion (1975-2009) the model fitted better, since the AIC value for the second model is lower (2539.9) than in the first period (2830.6).

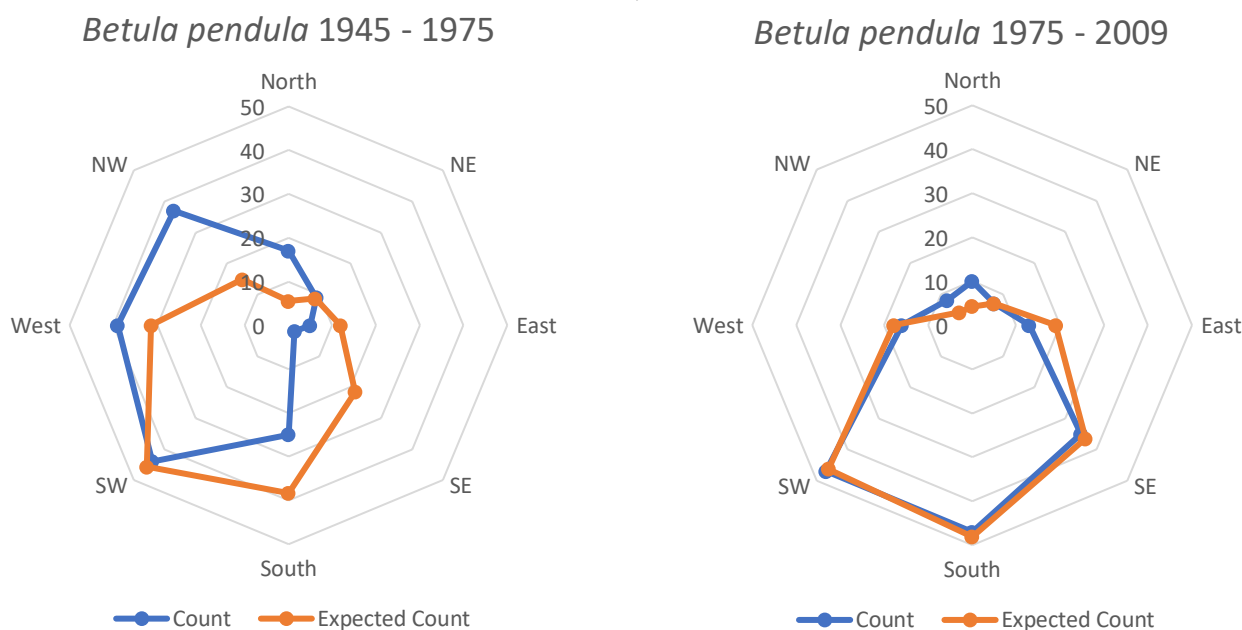


Figure 4. Graphs showing the distribution of points of two main species pure forests in relation to the expected values of χ^2 test.

Distances from parent clusters as an autecological factor

The analysis of geographical data showed that the expansion of pure birch forests was greatly affected by the distance from old parental stands. Generally, areas that were mostly colonized by birch forests are definitely those of close distance (<100 m) from the parent clusters, for both periods (Q1: 33 m – Q3: 99 m for period 1945-1975 and Q1: 49 m – Q3: 107 m for period 1975-2009), while more distant areas were found to be less abundant in trees (Fig. 5). Consequently, in the case of birch forests, the distance from pre-existing (in 1945) birch forests plays the most important role for species expansion, especially as regards the formation of pure birch stands. By contrast, although distance from old pine stands played the most important role in the *P. sylvestris* expansion, it did not exert much influence - as in birch - on the expansion of pure and mixed forests of *P. sylvestris* (Table 3). Therefore, *P. sylvestris* in this study area can colonize more distant zones (Q1: 50 m – Q3: 201 m for period 1945-1975 and Q1: 55 m – Q3: 162 m for period 1975-2009). Consequently, there is a strong relation to distance from near pre-existing (in 1945) birch forests, which is stronger than that of pine.

Discussion

B. pendula is a pioneer and photophilous tree species (Rebele 1992; Suominen K. et. al 2003) which colonizes bare lands (Kinnaired, 1974). The same characteristics also appear at the species *P. sylvestris* (Gaudio

et al., 2011; Durrant et al., 2016). *B. pendula* competes with *P. sylvestris* in space occupation in the existed non-forested areas, as revealed by the results. This competitive process resulted in the co-existence of the two pioneer forest species in the same area, and the formation of mixed forests. The high open space colonization capacity is attributed to the autecological behavior of the two species. Therefore, according to the results, there was a remarkable forest expansion in the study area, which was greater in the second period of the expansion studied (1975-2009).

The forested area in the period 1945-2009 was predominated by southern slopes (Fig. S3 [suppl.]). As a consequence, the secondary ecological succession occurred mainly in warmer and drier soils. In Northern Europe, *B. pendula* prefers similar sites to *P. sylvestris*, i.e. dry soils with low solute concentration (Hynynen et al., 2009). Therefore, both species easily expanded in those areas, which adequately fulfilled their niche requirements. However, at late successional stages, the upper story controls competitive interactions between pine and birch, and birch decreases its presence and forms more compact stands, because pine is less sensitive to the competition of the upper story than birch (Paluch & Bartkiewicz, 2004). This explains why older forests in the study area are occupied by pure forests to a greater extent. Scots pine in this study colonized bare areas faster than Silver birch. This can be explained by its niche requirements and its initially higher-altitude position, which enables it to spread fast downhill. Also, Scots pine often produces large quantities of seeds, which are small and lightweight and are easily dispersed by wind over relatively long distances. The reproductive cycle of the species starts early, from

Table 3. Tests of Model Effects for variables in GLM models for main forest formations against environmental and autecological factors. Df=degree of freedom

Time period of forest expansion		Type III		
		Wald χ^2	Df	p- value
<i>Examined period 1945 – 1975</i>	(Intercept)	3.610	1	0.057
	Aspect	47,794	8	0,000
	Elevation	56,477	1	0,000
	Slope	0,218	1	0,641
	BIO9	0,271	1	0,603
	BIO17	35,434	1	0,000
	PIN_DIST_45*	61.725	1	0.000
	BET_DIST_45*	148.234	1	0.000
	PIN_BET_DIST_45*	2,915	1	0,088
	BET_PIN_DIST_45*	43,025	1	0,000
<i>Examined period 1975 – 2009</i>	(Intercept)	0,690	1	0,406
	Aspect	7,848	7	0,346
	Elevation	18,158	1	0,000
	Slope	3,452	1	0,063
	BIO9	0,068	1	0,795
	BIO17	1,879	1	0,170
	PIN_DIST_75*	95,681	1	0,000
	BET_DIST_75*	111,523	1	0,000
	PIN_BET_DIST_75*	20,290	1	0,000
	BET_PIN_DIST_75*	17,058	1	0,000

Dependent Variable:

FOREST_CAT = Forest categories (1=*B. pendula* pure, 2=*B. pendula* mixed, 3= *P. sylvestris* mixed, 4=*P. sylvestris* pure)

* explanation of variables

PIN_DIST_45 = Distance from *P. sylvestris* forest existing in 1945,
 BET_DIST_45 = Distance from *B. pendula* forest existing in 1945,
 PIN_BET_DIST_45 = Distance from mixed *P. sylvestris* - *B. pendula* forest existing in 1945,
 BET_PIN_DIST_45 = Distance from mixed *B. pendula* - *P. sylvestris* forest existing in 1945,
 PIN_DIST_75 = Distance from *P. sylvestris* forest existing in 1975,
 BET_DIST_75 = Distance from *B. pendula* forest existing in 1975,
 PIN_BET_DIST_75 = Distance from mixed *P. sylvestris* - *B. pendula* forest existing in 1975,
 BET_PIN_DIST_75 = Distance from mixed *B. pendula* - *P. sylvestris* forest existing in 1975

the 30th year in close stands, and much earlier, from the 7th to 10th year for individuals grown in free space in the studied area, which allows the species to quickly colonize non-forested areas (Zagas, 1990).

Combined geographical and statistical analysis showed that elevation is the most important environmental driver which triggers the differentiation of the two spe-

cies in terms of colonization. Scots pine trees expanded to higher altitudes (Q1:1219 m, Q3:1398 m) than Silver birch (Q1:1063 m, Q3:1253 m). However, the mixtures of the two species make the establishment more complicated, especially due to the fact that both species have an obvious tendency to spread in lower altitudes, which are easier to colonize. GLM's higher Wald chi-square

Table 4. χ^2 test values for established forests after 1945. Observed vs. Expected values for pure and mixed *B. pendula* and *P. sylvestris* forests. N=degrees of freedom.

		Forest expansion period	
		1945-1975 (N=1198)	1975-2009 (N=1069)
		Pearson χ^2	Pearson χ^2
Aspect	Value	170.742	115.323
	Df	24	21
	p-value	0.00	0.00
Slope	Value	8.90	39.54
	Df	15	18
	p-value	0.88	0.00
Elevation	Value	353.375	234.317
	Df	21	18
	p-value	0.00	0.00
BIO9	Value	267.057	257.939
	Df	12	18
	p-value	0.00	0.00
BIO17	Value	302.780	319.331
	Df	21	21
	p-value	0.00	0.00
Distance from pure birch forest	Value	582.358	476.651
	Df	15	15
	p-value	0.00	0.00
Distance from pure pine forest	Value	596.703	543.354
	Df	15	15
	p-value	0.00	0.00
Distance from mixed birch-pine forest	Value	707.631	549.166
	Df	15	15
	p-value	0.00	0.00
Distance from mixed pine-birch forest	Value	461.367	448.581
	Df	15	15
	p-value	0.00	0.00

BIO9 and BIO17 are explained in methodology

values and χ^2 test showed that elevation is the most important environmental factor because it influences the distribution of the final species, as it differs from the expected distribution.

The GIS analysis showed that pure Silver birch forests showed a preference to N, NW and W aspects, while pure Scots pine forests preferred S and SW aspects (Fig. 4) following the distribution of barelands-grasslands. *P. sylvestris* probably meets the competence of *B. pendula* in northern slopes and has greater adaptability to southern slopes which are drier and hotter than northern slopes

(Kinnaid, 1974; Kutiel & Lavee, 1999; Sternberg & Shoshany, 2001).

The χ^2 of bioclimatic variables revealed that Scots pine forests in colder and wetter locations are more abundant than expected. Silver birch did not show clear patterns of preferences, except for the first period of its expansion, in which it showed preference to colder areas. This suggests that it was easier for Scots pine to distribute in better climatic condition sites because of the advantage of the initial higher altitudes of their parental clusters. This contributed to a large concentration of pines in more

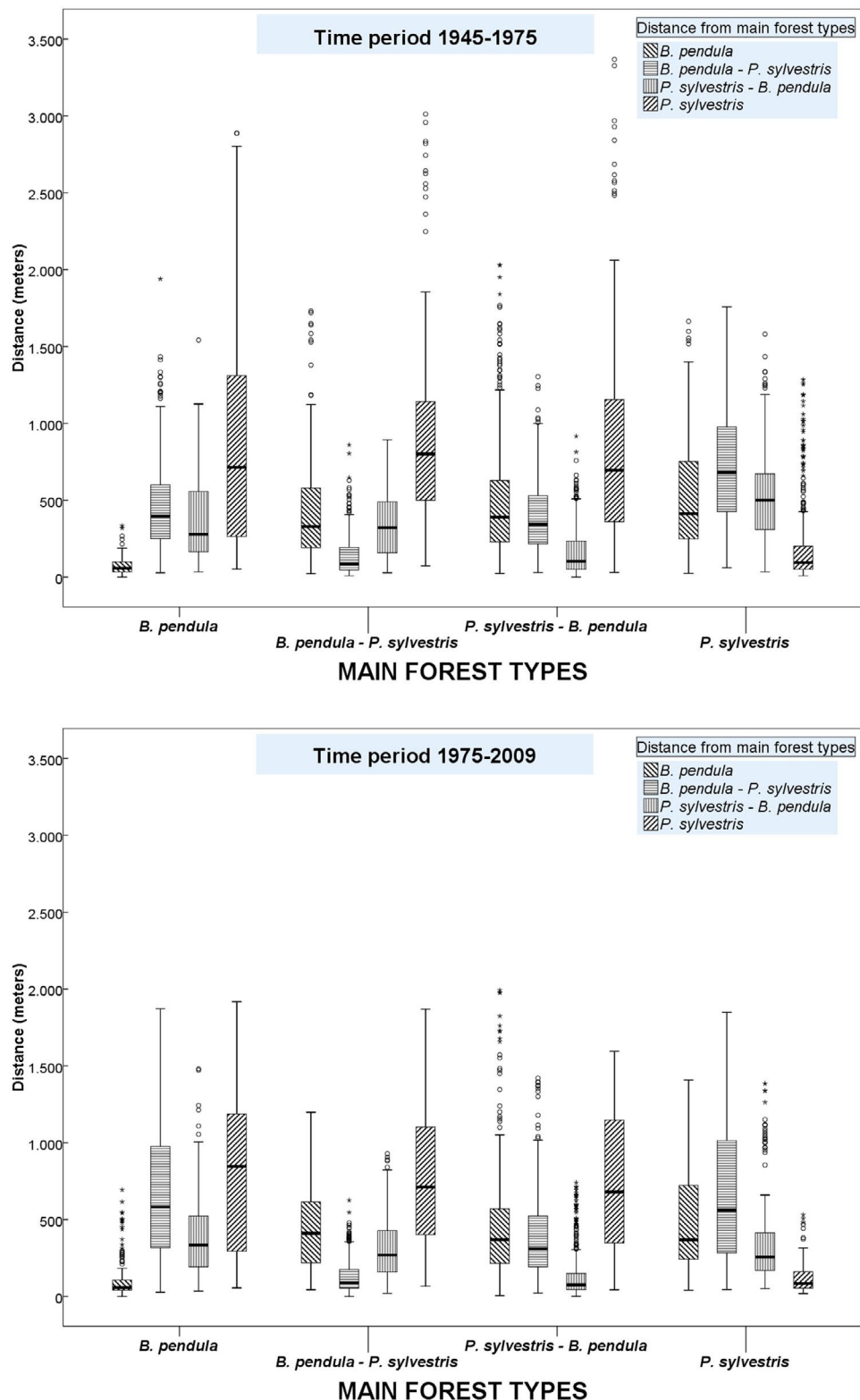


Figure 5. Boxplots of main forest types, showing the distribution of main forest types in relation to distance from parental clusters for two periods of forest expansion.

climatically preferable sites. In contrast, this was probably not feasible for Silver birch, which did not have the opportunity to distribute in wetter and colder sites. Therefore, this indicates that Silver birch is probably located in more unfavorable sites compared to Scots pine.

Slope inclination proved to play a less important role in the expansion of the examined forest species. An older site condition study (Kinnaird, 1974) with findings about the colonization conditions of Silver birch has also showed that slope did not affect their seedlings and

saplings growth. The study also suggested that there was a low preference of southern slopes, which is consistent with the present study findings. Finally, the study verifies that gaps in woodland and bare soils had the highest densities of seedlings that survived and developed better at these sites, which somehow explains the rapid expansion of birch in the present study area.

The geographical analysis of the spread of the two main species of the area showed that *P. sylvestris* expansion is faster than *B. pendula*'s expansion. The rate of expansion depends on the seed and pollen dispersal distances and the mortality of the seedlings. Kuparinen *et al.* (2010) suggests that the maturation age is 13 years for *B. pendula* and 20 years for *P. sylvestris*, and that birch performs better than pine in seed and pollen distance dispersal. If this is the normal condition of the two species expansion, birch should have established better in the study area. Nevertheless, Scots pine occupied more non-forested space and faster than Silver birch in this area. One possible explanation is that Scots pine individuals start their reproductive cycle very early in open space. Another possible explanation is that the mortality of birch seedlings may be higher than that of pine, due to lack of water, and drought. Besides, Scots pine is more resistant to drought and poor-nutrient soils (Gaudio *et al.*, 2011). These characteristics give an advantage to *P. sylvestris* over *B. pendula* in hotter and drier conditions, and, thus, it can expand better during summer periods or prolonged summers. Another advantage of *P. sylvestris* in the area is that its parental clusters are located at a higher altitude, which allows easier spreading at downhill and faster and more distant colonization. Finally, it was proved that the expansion of Silver birch is more dependent on distance to parental clusters than the expansion of Scots pine.

The newly-formed forests differ from the pre-existing (in 1945) forests, which were mainly pure forests of the two main species. Species interspecific competition is probably the main reason why at a later successional stage the two species tend to form pure (non-mixed) forests. According to the bibliography, the two pioneer tree species tend to form pure stands as the time passes from their early life until they become mature stands. Valkonen & Ruuska (2003) showed that as the number of birches increases in mixed stands, there is a negative effect on the diameter growth and the maximum branch diameter in pine, while the height of *P. sylvestris* is not affected. The latter means that pines compete with birch for the upper story and suffer an impact in growth. Paluch & Bartkiewicz (2004) make reference to the tendency of young pines to concentrate around the old ones; this was attributed to pine elimination by birches in gaps, which were more rapidly growing and strongly competing for water. This is the possible explanation for the extended areas of pure Silver birch forests in old forests of the area. It is also reported that there is a negative influence of young

and old pines on birches, probably because of the worse light conditions, which explains the successive isolation of the two species. Other studies have concluded that *B. pendula* is able to modify its crown architecture and alter its strategy to compete with different neighbors (Lintunen & Kaitaniemi, 2010). *B. pendula* and *P. sylvestris*, as early-successional species, respond to shade with an increase in stem height and changes to biomass, and *B. pendula* fiercely competes with conifer species such as *P. sylvestris*, especially in fertile humus soils (Dehlin *et al.*, 2004).

Management implications and conclusions

The dramatic changes observed in vegetation can be characterized as positive for the enhancement of natural ecosystems and biodiversity conservation. However, the area is under the management of the Forest Service, and is exploited for wood production, while maintaining the principles of sustainability and improving soil productivity. Management should also include provision for the conservation of biodiversity except for wood production by protecting flora and fauna species. This can be achieved by the implementation of management plans, friendly to the ecosystem and based on selective logging and natural forest regeneration, as well as actions to improve the habitats of important species.

Conservation of the Silver birch population in this area is of critical importance, as this area forms the southernmost limit of birch, and the disturbance occurred in a vast area in which the forest was rapidly re-established in the past few years. Thus, with the expected temperature rise (Meehl *et al.*, 2007), the transplantation of these birch genotypes (which are more resilient to prolonged summer drought) to higher latitude forests could contribute to the improvement of northern birch forests (Hoegh-Guldberg *et al.*, 2008; Marris, 2009). More adapted genotypes to climatic conditions could support and accelerate the evolutionary process. Kuparinen *et al.* (2010) estimated that the genotypic growth period length of both species will lag more than 50%, according to predictions for the next 100 years of climate change. The results of the present study showed that there is an increase in the mixtures of the two main species in newly established forests and a good adaptability of *B. pendula* in hot and dry locations. However, this is not the desirable outcome due to the fact that it is more likely that the vigorous growth of pines will tend to progressively eliminate the admixed birches (Mason & Connolly, 2016).

Due to the fact that this study area is the rear edge of expansion of the two studied forest species and it is the only region in Greece with a compact birch forest, forest management should, among other purposes, to maintain pure and mixed *B. pendula* forests, since the only pure birch forest in Greece exists in the area, so as to conserve

the genetic diversity of the southern birch forest in Europe due to the upcoming global temperature increase. This can be achieved by maintaining blocks of Silver birch scattered within Scots pine areas, which will be large enough to resist interspecific competition, especially in the closest-to-birch niche requirements (e.g. better soils – northern aspects). The strengthening of birch sites will also serve as a future seed source that will contribute to the long-term conservation of the species in the area and the possible future colonization of other areas in the wider region; to control any possible invasion of shade-tolerant, late-successional species, such as *P. abies* and *F. sylvatica* (Seppä *et al.*, 2009; Björkman, 1999) that exist in the wider region, which will compete intensively with birch, and will prevail over this species stands; to maintain the existing gaps and open areas near birch forests, so that they will be able to colonize them. In summary, the changes in birch forest observed in the study area dynamically occurred in sites abandoned by human activities. The most common forest types installed in the last seven decades were mixed stands dominated by *B. pendula* and *P. sylvestris* (pure and mixed - sometimes predominant *P. sylvestris* and sometimes *B. pendula*). The observed changes were found to be associated with environmental factors – niche requirements such as land altitude, aspect and bioclimatic factors. Distance from the existing forest boundary, especially distance from birch parent stands, appears to play the most important role, and has a significant and lasting influence on the dynamics of birch forest development, affecting the manner and the time of this species colonization in specific areas. Therefore, for the application of effective forest management and conservation of biodiversity, especially for the birch population, which is unique in Greece, the observed changes in birch population and the drivers affecting should be taken into account. Management objectives must be set in accordance with the site-specific characteristics and the forest dynamics, and they should not take into consideration only wood production, but also biodiversity conservation, and especially the important birch population. Having regard to the future climate changes, threats for the species may increase, since birch does not tolerate prolonged drought and hot summers. Also, it is not certain that it will be able to compete with Scots pine in the future, and it may have to compete with invasive and shade-tolerant species which exist in the area, such as *P. abies* and *F. sylvatica*. However, the maintenance of *B. pendula* should set high priority to improve stand stability to drought, heat, storms and secondary factors with silvicultural measures. Future research in this rear edge population of *B. pendula* should set targets due to adaptive forest management that will combine: 1) species suitability tests and modelling activities at an international scale, 2) priority mapping of adaptation strategies at a national to regional scale and 3) implementation at a local scale. (Bolte *et al.*, 2009).

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