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Conversion of *Pinus nigra* Plantations with Natural Regeneration in the Slovenian Karst: The Importance of Intermediate, Gradually Formed Canopy Gaps

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Abstract: Since the mid-19th century, *Pinus nigra* plantations have played a key role in the restoration of degraded European landscapes. Nowadays, these plantations are aging and prone to natural disturbances, insect infestations, and diseases. For their successful gradual conversion, knowledge of optimal gap spatiotemporal dynamics is crucial. We studied herb and natural regeneration patterns along with site factors on 477 subplots within 44 plots distributed over four stand types: closed stand (14% diffuse light), open stand (21%), gap edge (23%), and gap (57%). Despite the abundant *Quercus petraea*, *Q. cerris*, and *Q. pubescens* mast year, no one-year seedlings were recorded, which is likely due to the summer drought. Short seedlings (h < 20 cm) of *Quercus sp.*, *Fraxinus ornus* and *Ostrya carpinifolia* were more successful within closed stands. Short *Quercus* seedlings were positively associated with soil depth and negatively associated with soil nutrients, distance to seed trees, and *Sesleria autumnalis* coverage. Taller *Quercus* seedlings required more light than both of its strongest competitors and were positively related to humid soils and less rocky sites. Ungulate overbrowsing significantly impeded natural regeneration. The results indicate a satisfactory *Quercus* density for conversion and the importance of advanced regeneration, which should be gradually, but persistently, released by progressively widening gaps.

Keywords: gap partitioning; microsite partitioning; topsoil moisture; microrelief; ground vegetation; overbrowsing; conversion; *Pinus nigra*; natural regeneration

1. Introduction

Globally, there are many former forest lands that have been degraded due to clearing, burning, and overgrazing. Afforestation of these areas could improve soil productivity, forest climate and biodiversity, as well as mitigate climate change [1]. Good practices from the past are important for encouraging new forest restoration projects and for learning [2]. Afforestation of the Karst region above the Gulf of Trieste from the mid-19th century represents one of the first successful examples of forest restoration on almost completely barren land exposed to drought and strong winds [3]. Before human colonization, the landscape was overgrown with deciduous forests consisting mainly of oaks (*Quercus petraea* (Matt.) Liebl., *Quercus cerris* L., and *Quercus pubescens* Willd.; hereafter *Quercus*), and, to a lesser extent on more mesophilic sites, *Fagus sylvatica* L. [4].

Due to the degraded sites in the Karst, *Pinus nigra* J.F. Arnold was used for restoration. Although it is not a native species on Karst, it is a specialist on shallow rocky calcareous soils and xerophytic sites. Later, *P. nigra* also subspontaneously expanded. There are about 16,000 ha of *P. nigra* stands alone within the Slovenian Karst region. Nowadays, *P. nigra* plantations across Europe are aging,

prone to fire, and subject to different abiotic disturbances (windthrow, ice storms, droughts), insect infestations, and more recent diseases [5–7]. Native midsuccessional species, such as *Fraxinus ornus* L. and *Ostrya carpinifolia* Scop., are increasingly entering *P. nigra* forest stands, where they form a distinctive layer, while the natural regeneration of *P. nigra* has halted [8]. *Quercus sp.* return very gradually due to the lack of seed trees, degraded forest soils and overbrowsing. Conversion of *P. nigra* plantations is necessary to ensure stable future forests and represents an important, but difficult, task for silviculture [9].

In conifer plantations that are at greater risk of decline, on more degraded forests sites and where there is a lack of seed trees, direct conversion with planting is usually chosen [7]. This is the more demanding and expensive option. Under favorable conditions, the use of gradual conversion based on natural regeneration is the better choice [10,11]. For the latter, one of the key questions involves the optimal spatiotemporal dynamics of the gaps to achieve quality mixed stands with sufficient, mostly light demanding *Quercus* sp., which are robust and valuable tree species vital for the multipurpose functioning of future forests.

Research from the broader European region on planted as well as natural *P. nigra* and *Pinus sylvestris* L. stands in succession indicates the importance of the proximity of *Quercus* seed trees, animal seed dispersal by birds, and successful *Quercus* recruitment in intermediate gaps [12–14]. Several studies of *P. nigra* and *P. sylvestris* stands in succession have stressed the importance of regular thinning for *Quercus* stands, and longer periods of *Quercus* advance regeneration survival under *Pinus* crowns when compared to broadleaved stands [11,13,15]. However, few studies have relied on detailed ground vegetation assessment for indication of site factors supplemented by direct measurements of light climate and soil moisture, both of which are likely to have an important impact on *Quercus* regeneration, especially in the sub-Mediterranean region. The research objectives of this study were to analyze the seedling structure and its dependence on abiotic (e.g., light, soil moisture, relief) and biotic factors (e.g., competition from trees and herbs, presence of seed trees) and to propose guidelines for the transformation of *P. nigra* stands based on natural regeneration.

2. Materials and Methods

2.1. Stand and Site Characteristics

The study was carried out in the Karst region of southwest Slovenia, as seen in Figure 1. The analyzed *P. nigra* plantations are located on flatlands or gentle slopes above an altitude of 235–450 m a.s.l. Carbonate parent material dominates, but there are some small pockets of silicate in the form of chert, flysch, and sands. The soils are eroded and mainly in the form of shallow rendzina [16]. In some places, especially in depressions, deeper brown soils have developed. In addition to soil variability, land degradation has also occurred at different intensities; therefore, the potential natural vegetation is difficult to determine [4]. In more favorable ecological conditions, stands were most likely dominated by sessile oak (*Q. petraea*) (*Seslerio-Quercetum* sensu Braun-Blanque typology), while less favorable sites were dominated by downy oak (*Q. pubescens*), hop hornbeam and flowering ash stands (*Ostryo-Quercetum pubescentis*). *Pinus nigra* stands in Slovene Karst experience severe droughts in summer and higher precipitation than most natural *P. nigra* stands in Europe, which makes them prone to fungal diseases. Therefore, even greater management risks are expected in the future. At present, most stands are two-storied, with 87% *P. nigra* in the overstory and about 10% *F. ornus* and *O. carpinifolia* in the understory. *Quercus* and the noble broadleaves amount to only 3% in the total growing stock. Average growing stock varied from 148–223 m^3 ha^{-1} and increment 3.3–5.1 m^3 ha^{-1} $year^{-1}$. Stands were between 80 and 120 years old, and the upper stand height was about 25 m. The mean annual temperature in the period 2000–2011 was 12.0 °C, and the mean sum of yearly precipitation was 1234 mm, with extensive droughts in summer (Godnje meteorological station, 760 m a.s.l.; [17]). The climate is sub-Mediterranean.
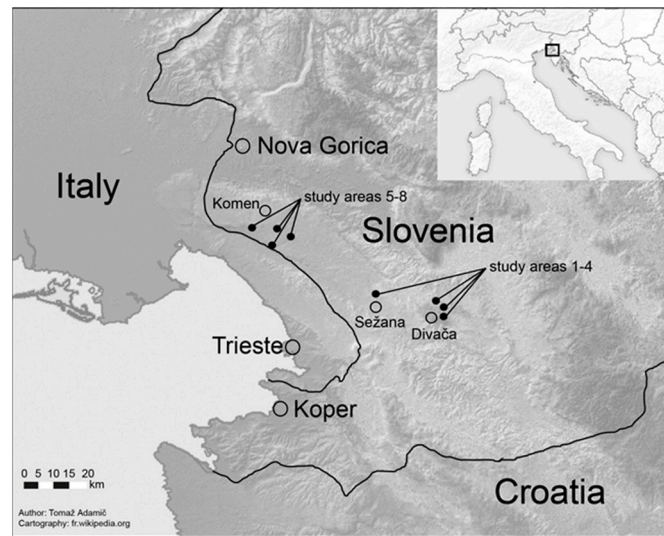
Figure 1. Location of eight study areas where 44 research plots were installed.

2.2. Sampling Design and Recordings

The study object was the entire area of *P. nigra* plantations on comparable sites with mature stands and stands in regeneration, in which there had been no logging in the five years prior to the study. We randomly selected eight locations from the study object and installed 44 plots 25 × 25 m in size, as seen in Figure 2. The plots were randomly selected within four stand types: closed stand, partially open stand, the edge of a canopy gap and the center of a canopy gap. The gaps ranged from 1.2 to 4.4 ha in size. Until recently, mature stands were mostly lightly thinned, and managers only rarely formed gaps deliberately. Thus, it was not possible to select a balanced set of treatments in each location. For each plot, we sampled the main ecological features (relief type, rockiness, slope inclination, and orientation) and typical dendrometric data (e.g., tree species coverage, full inventory of dbh and heights).
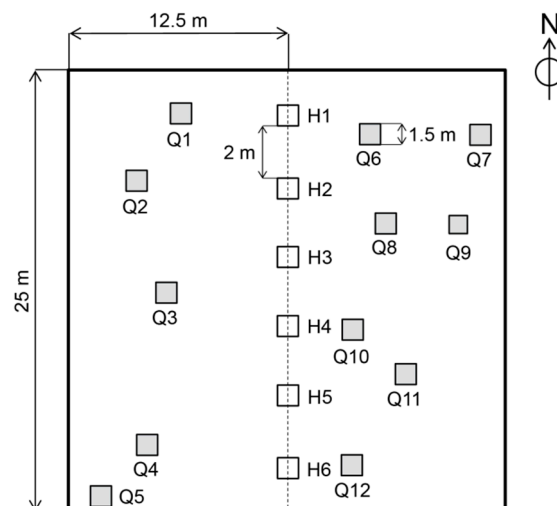

Figure 2. Sketch of plot with arrangement of herb subplots (H1–H6) in white and *Quercus* subplots (Q1–Q12) in grey.

Across the center of each plot, six systematic herb subplots were placed, and two rows of *Quercus* subplots were arranged to the left and right of the central transect, as seen in Figure 2. The first two herb subplots were located 1 m south and north of the plot center. The minimum distance between the two herb or *Quercus* subplots was 2 m. The center of the *Quercus* subplots was defined by the presence of *Quercus* seedlings older than one year. The size of the subplots was 1.5 × 1.5 m. The herb subplots

were installed and recorded on all plots (*N* = 264), while the number of *Quercus* subplots varied from 0 to a maximum of 12 (*N* = 214). On each subplot ground vegetation coverage according to species was estimated visually from above and recorded to the nearest 10% from 10% to 100% and to the nearest 1% from 1% to 10%. Thus, the cumulative cover of herbs and shrubs often exceeded 100%. The same scale was also used for the estimation of coarse woody debris (CWD) and rock coverage (rockiness) on the forest floor. Microrelief (flat, concave, convex), slope inclination and orientation, soil depth, and cumulative depth of the organic horizons (L—litter, F—fermentation horizon and H—humus horizon; hereafter referred to as LFH) were measured. Regeneration density according to species was estimated corresponding to four height classes (one-year old seedlings, seedlings with height <20 cm, seedlings with height ≥20 and <130 cm and seedlings taller than 130 cm). Seedlings were categorized as browsed if the leading shoot was damaged.

On a sample of plots (*n* = 232), relative diffuse light 1.3 m above each subplot was assessed with two point quantum sensors (LI-COR, Inc., Lincoln, NE, USA), one placed above the subplot and the second in a nearby open area. Measurements were taken on overcast days [18]. On the same sample of subplots, topsoil water content (0–10 cm) was measured using time domain reflectometry [19] in September 2012 (moisture1) and October 2012 (moisture2). Each time measurement was taken after a period of dry weather. In 2012, only 400 mm of rainfall fell in the period from May to September, which is 73% of the average in the 2001–2011 vegetation period. At the same time, the average July air temperature at the Bilje meteorological station was 1.6 °C above the long-term average (2001–2011). Measurements of topsoil moisture in 2012 thus indicated topsoil moisture following hot and dry summers [20]. We also sampled features of *Quercus* seed trees and their distance to subplots in a radius of 80 m from each plot.

2.3. Data Analysis

Data were analyzed in R Version 3.6.1 [21]. Seedling density in relation to ecological factors was modeled with a series of generalized mixed-effects models (GLMMs) with negative binomial distribution and a logarithmic link function [22] since the data were overdispersed. All final models were selected following a top-down approach [23]. Different models with all combinations of ecologically meaningful fixed effects (comp. Section 3.4), were built. These models were then compared against simpler nested models based on the ANOVA likelihood ratio test of fits for GLMMs [22]. Research units (i.e., plots) were considered as random factors. For model diagnostics, we inspected confidence intervals of parameters and examined sets of graphical summaries [24]. Light and topsoil moisture measurements were carried out on a sample of subplots (*n* = 215); thus, separate GLMMs for this subsample were carried out.

Mean Landolt indicator values (LIVs for temperature regime, continentality, light quantity, topsoil moisture, soil reaction, nutrient content in the soil, humus content, and soil aeration) were estimated as a weighted average of the Landolt indicator values [25] of all present understory layer species, and their abundances were used as weights [26]. Principal coordinate analysis (PCoA) was used to ordinate subplots based on the 2012 vegetation survey. The distance matrix was calculated by applying the Bray–Curtis distance measure to the square root of the plant species coverage data. Based on inspection of the eigenvalues, we selected only the first and second principal coordinate for presentation. Ecological variables (light and topsoil moisture measurements, distance to beech seed trees, etc.), mean LIVs, and seedling density according to species groups were fitted onto an ordination plot using the vegan package [27]. In identifying the indicator species of each group, we used the Indicator Value Index and its components [28] using the package *indicspecies* [29]. Differences in ecological factors between stand types and subplot types were tested with the nonparametric Kruskal–Wallis and Wilcoxon tests.

3. Results

3.1. Variability of Ecological Factors within and between Stand Types

The median of relative diffuse light amounted to 13.8% below the closed stand and increased through the open stand (20.8%) and gap edge (23.1%) to the gap, at 57.3%, as seen in Figure 3. The lowest variability of light conditions was measured below the closed stand, followed by the gap edge, the open stand and lastly the gap, which exhibited considerably higher variability. The light distribution was followed by the response of the cumulative coverage of herbs and shrubs with the lowest values below the closed stand (55.0%), followed by the open stand (91.3%), the gap edge (100.0%), and the gap (100.1%). The overall topsoil humidity was lower in September compared to October 2012, with medians of 10.0% and 22.4%, respectively. In September, topsoil moisture was higher under the closed stand when compared to the other three stand types, while in October, the differences were smaller, as seen in Figure 3. The LIV for light followed a similar gradient to that of measured diffuse light, with increasing levels from the closed stand to the gap (K–W $p < 0.001$). LIV for continentality (K–W $p < 0.001$) and nutrients (K–W $p = 0.0013$) also indicated increasing values towards the gap. Phytoindication LIV values for soil moisture indicated lower values in the open stand and at the gap edge (K–W $p = 0.0013$).
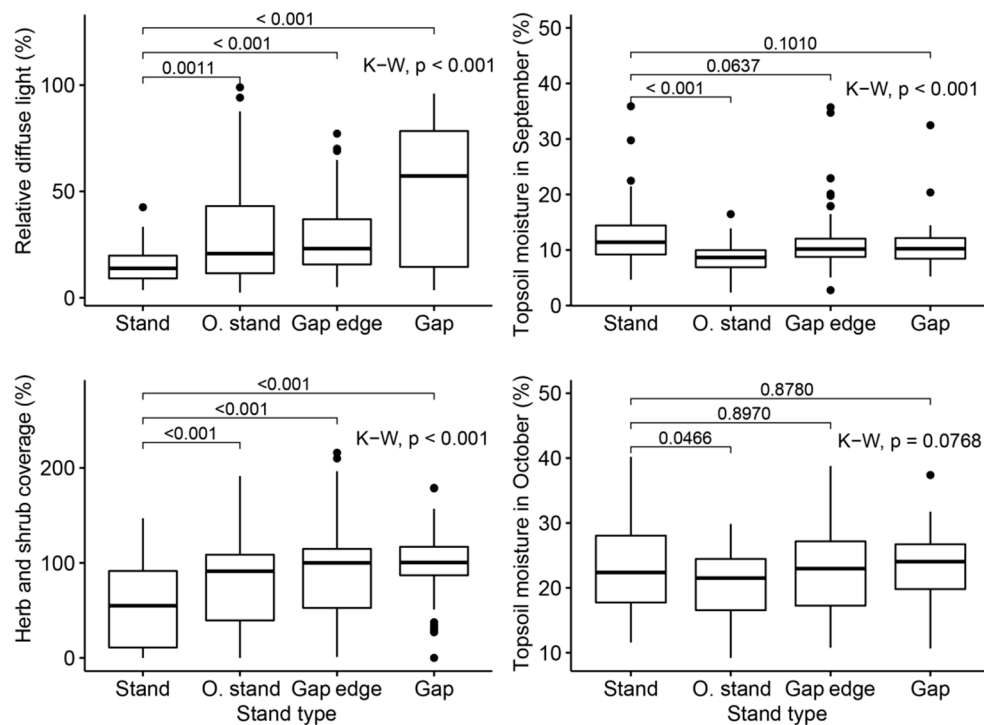

Figure 3. Box and whisker plots of relative diffuse light, topsoil moisture in 2012 and herb and shrub coverage according to stand type. The numbers above the whiskers denote significance levels between stand types. K–W stands for the Kruskal–Wallis test.

3.2. Natural Regeneration

The regeneration density on both herb and *Quercus* subplots was high, at nearly 30,000 trees ha^{-1} on average, as seen in Table 1. Although 2011 was an abundant *Quercus* mast year, we did not record any one-year-old seedlings. In a separate sample outside our plots, we dug out 38 *Quercus* seedlings and found that only 5% were of a vegetative origin. Herb plots give an unbiased assessment of overall regeneration structure, and they indicated domination of *F. ornus* at 73%, followed by *Quercus* at 10%, *O. carpinifolia* at 9%, and *Ulmus glabra* Huds. aggr. at 2%. The noble broadleaves (*Acer pseudoplatanus* L., *Acer obtusatum* Waldst. & Kit ex Willd., *Prunus avium* L., *Tillia cordata* Mill., *T. platyphyllos* Scop.,

Fraxinus excelsior L., and *Sorbus torminalis* (L.) Crantz) and other species amounted to 6%, as seen in Appendix A. From the composition of regeneration according to height class, we can observe a slight decrease in the share of *F. ornus*, a considerable decrease in *Quercus* and noble broadleaves, and an increasing share of *O. carpinifolia*, as seen in Figure 4a. It seems that the average growth conditions do not allow recruitment of the first group of tree species to higher regeneration classes. This is even more evident if we look at the regeneration structure according to tree species, height class, and stand type (Section 3.4).

Table 1. Density of regeneration per hectare according to subplot type, height class, and tree species. Legend: N. Brd.—Noble Broadleaves.

| Height Class	*F. ornus*	*O. carpinif.*	*Quercus*	*Ulmus*	N. Brd.	Other	Sum
Herb Subplots							
h < 20 cm	9616	321	1859	270	710	152	12,928
20 ≤ h < 130 cm	9632	1724	794	253	744	51	13,164
h ≥ 130 cm	1335	422	68	17	51	68	1960
Total	20,583	2467	2721	541	1504	270	28,086
Quercus Subplots							
h < 20 cm	8494	353	4237	166	228	42	13,520
20 ≤ h < 130 cm	6397	1059	6044	332	187	145	14,164
h ≥ 130 cm	748	602	166	0	0	21	1537
Total	15,639	2015	10,447	498	415	208	29,221
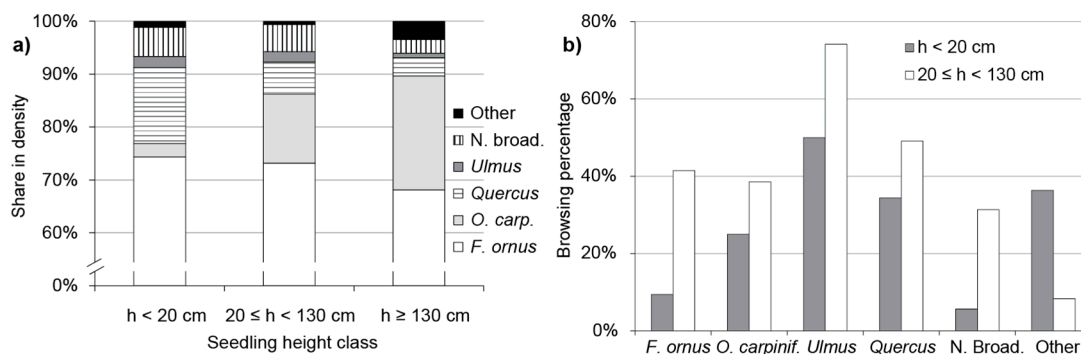
Figure 4. (**a**) Seedling species composition according to height class in the herb subplots. (**b**) Percentage of seedlings with terminal shoot browsed according to tree species and height class.

Within the first (h < 20 cm), second (20 ≤ h < 130 cm) and third regeneration height class (h ≥ 130 cm), the average share of seedlings damaged by ungulates amounted to 16%, 43%, and 26%, respectively. The overall browsing damage rate was 30%. Virtually all tree species were most damaged in the second height class, as seen in Figure 4b. Among the species, *Ulmus* was the most damaged, followed by *Quercus*, *F. ornus* and *O. carpinifolia*.

3.3. Herb Vegetation and Indication of Ecological Factors

We recorded 28 species of trees, 31 species of shrubs, and more than 120 species of herbs, which is by far more than that recorded in similar research in other phytogeographic regions of Slovenia. Ordination of vegetation indicated two main gradients, as seen in Figure 5. The first seems to be influenced by stand type. LFH thickness, CWD, and rockiness increase in the direction of closed stand conditions, while LIV for soil moisture and minimum and average distance to seed trees decrease. However, the centroids of stand types are located close together, indicating that other factors are also important, e.g., geographical distances between the plots. The second gradient, which is independent of the first, indicates changes in LIV for reaction, continentality and light as well as slope and coverage

of *Sesleria autumnalis* Scop. The density of shorter and taller *F. ornus* and *O. carpinifolia* seedlings increases in the direction of closed stand. The seedling density of shorter *Quercus* seedlings was not significantly related to the ordination axes, while taller seedlings seem to be more associated with LIV for light than *O. carpinifolia* or *F. ornus*. The density of species that were significantly related to the ordinal axes was not related to *S. autumnalis* coverage.
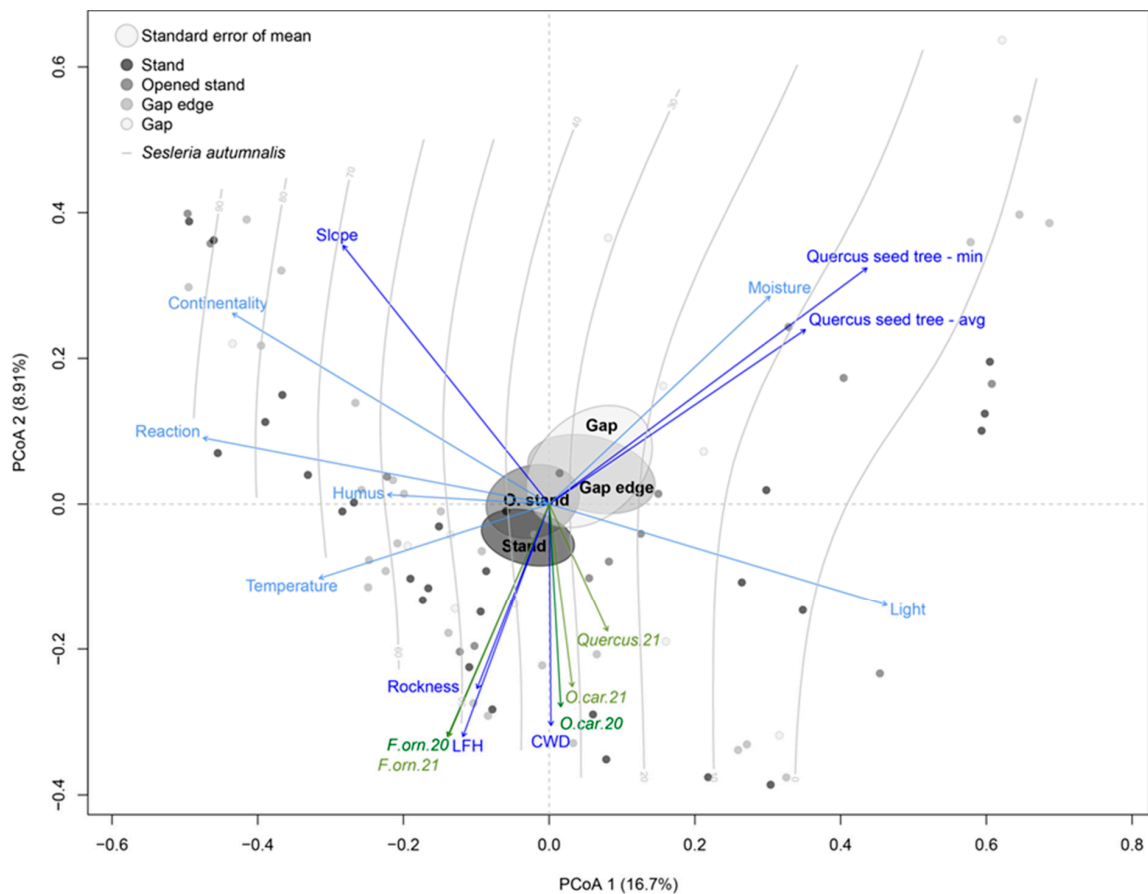

Figure 5. Ordination biplot of a principal coordinate analysis (PCoA) for vascular plant cover in the herb layer (Bray–Curtis distance measure) in 2012. Grey circles represent the location of plots on the first and second axes of the PCoA analysis. The arrows show the direction of the gradient, and the length of the arrows is proportional to the correlation between the variable and the ordination. Only factors with a *p*-value < 0.05 are plotted, with the exception of rockiness (*p* = 0.1). Smaller angles between the arrow and axis represent a higher correlation between the two values. Green arrows represent regeneration density per species and developmental stage, e.g., *F.orn*.20 for *F. ornus* short seedlings. Dark blue arrows represent measured ecological factors, e.g., CWD coverage, LFH thickness, and minimum and average distance to *Quercus* seed trees. Light blue arrows are for Landolt phytoindication values for light, continentality, temperature, reaction, nutrients, and soil moisture.

3.4. Drivers of Regeneration Dynamics

From the differences in ecological factors between the herb and *Quercus* subplots, we can deduce the peculiarities of the microsites where *Quercus* regenerated. Significant differences were found for topsoil moisture in September (*p* = 0.0429), *Rubus sp.* coverage (*p* = 0.0019), rockiness (*p* = 0.0099), and LIV for soil reaction (*p* = 0.0339). The *Quercus* subplots had slightly moister topsoil, were more overgrown by *Rubus* sp., were less rocky and had lower soil reaction. Herb species with the highest specificity (association) with herb subplots were *Corylus avellana* L., *Salvia pratensis* L., and *Euphorbia*

nicaeensis All., while *Rubus ulmifolius* Schott, *Rosa arvensis* Huds. and *Lamium galeobdolon* L. were associated with *Quercus* subplots.

Models for the density of shorter *Quercus* and *F. ornus* seedlings predicted a significant decrease from the closed stand, through the open stand and gap edge, to the gap, as seen in Figure 6 and Table 2. The lowest density of all three main tree species was recorded within the gap. *Quercus* seedlings taller than 20 cm were most frequent in the open stand, followed by the gap edge. They required more light compared to shorter *Quercus* seedlings. *Quercus* competitors, *F. Ornus* and *O. carpinifolia*, indicated similar patterns for taller seedlings. The density decline towards the gap edge and gap center was more pronounced for both competitors, but especially for *O. carpinifolia*, suggesting a slightly higher shade tolerance in both species. These patters were consistent on the herb and *Quercus* subplots.
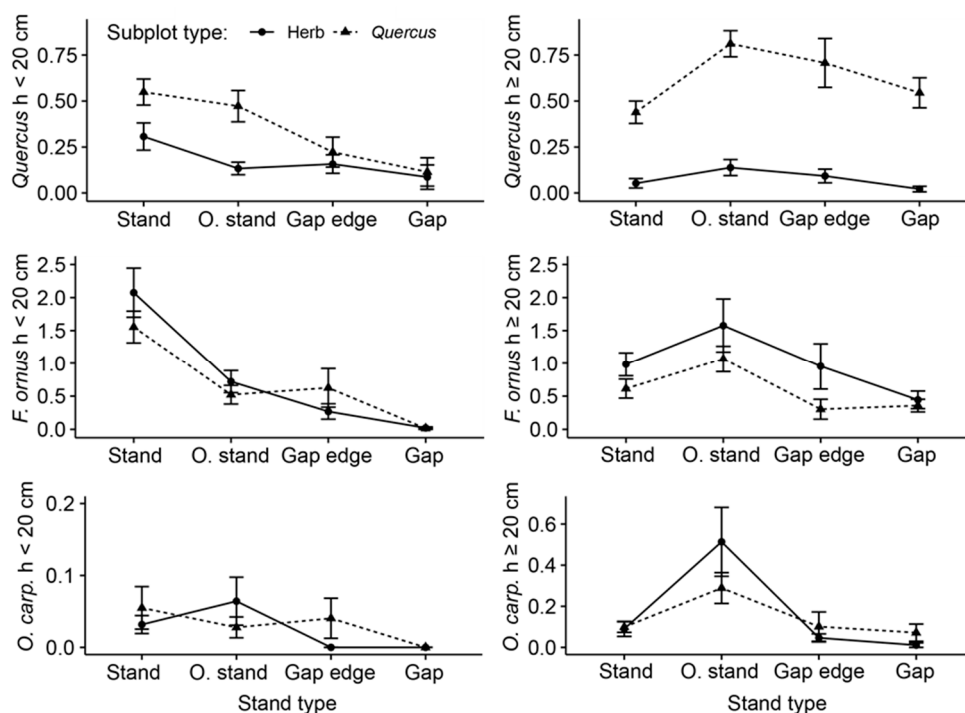

Figure 6. Mean seedling density per m^2 (error bars represent the standard error) according to the main tree species, height class, stand type, and subplot type.

The density of shorter *Quercus* seedlings was additionally positively associated with soil depth and LIV for continentality and negatively associated with LIV for nutrients, coverage of *S. autumnalis* and distance to *Quercus* seed trees, as seen in Table 2. The GLMM model for the subsample with measured diffuse light and topsoil moisture indicated largely the same pattern with a negative association of *Quercus* density with distance to seed trees and diffuse light intensity, with the exception of a positive association with coverage of *F. ornus*. The GLMM model for taller *Quercus* seedlings indicated a positive association with LIV for light, LIV for soil moisture, and distance to *Quercus* seed trees, and a negative association with rockiness. The model for the subsample indicated a negative association with rockiness and coverage of *F. ornus*.

The density of shorter *F. ornus* seedlings was positively associated with soil reaction and negatively associated with LIV for nutrients, continentality and light. The density of taller *F. ornus* seedlings indicated a positive association with LIV for soil reaction, coverage of *S. autumnalis* and LFH and a negative association with LIV for continentality, soil moisture, and flat relief. The *O. carpinifolia* short seedling sample was too small to be modelled. The model for taller *O. carpinifolia* seedlings indicated a negative association between density and LIVs for continentality, light and soil moisture, as well as for rockiness.

Table 2. Results of the generalized mixed-effects model (GLMMs) analysis of natural regeneration density according to tree species predicted by factors (*n* = 477). Research plots were treated as random effects. Labels following factor names denote the factor levels for comparison, while the numbers in brackets within the results denote the standard error (SE).

Variable	*Quercus* < 20 cm	*Quercus* ≥ 20 cm	*F. ornus* < 20 cm	*F. ornus* ≥ 20 cm	*O. carpinif.* ≥ 20 cm
Intercept	−0.78 (1.55)	−5.65 (0.90) ***	12.16 (2.64) ***	9.72 (2.25) ***	15.33 (3.60) ***
Stand type: closed vs. open	−0.26 (0.20)	0.94 (0.16) ***	−0.72 (0.21) ***	0.44 (0.19) *	−0.61 (0.40)
Stand type: closed vs. gap edge	−0.62 (0.28) *	0.57 (0.22) **	−1.30 (0.30) ***	−0.06 (0.27)	−0.89 (0.39) *
Stand type: closed vs. gap centre	−0.17 (0.35) ***	0.13 (0.22)	−3.61 (0.67) ***	−0.004 (0.28)	−1.28 (0.36) ***
Transect: *Quercus* vs. Herb	0.92 (0.17) ***	1.95 (0.16) ***	ns	−0.40 (0.17) *	ns
Soil depth	0.34 (0.12) **	ns	ns	ns	ns
LIV nutrients	−0.83 (0.37) *	ns	−2.32 (0.48) ***	ns	ns
LIV continentality	0.77 (0.35) *	ns	−2.21 (0.42) ***	−2.79 (0.39) ***	−2.23 (0.57) ***
LIV light	ns	0.48 (0.18) **	−0.92 (0.33) **	ns	−1.74 (0.49) ***
LIV moisture	ns	0.74 (0.27) **	ns	−2.09 (0.43) ***	−1.70 (0.69) *
LIV soil reaction	ns	ns	1.39 (0.41) ***	1.30 (0.38) ***	ns
Coverage *S. autumnalis*	−0.29 (0.11) **	ns	ns	0.42 (0.09) ***	ns
Distance to *Quercus* seed trees	−0.12 (0.05) *	0.08 (0.04) *	nt	nt	nt
Rockiness	ns	−0.48 (0.22) *	ns	ns	−1.73 (0.44) ***
LFH	ns	ns	ns	0.09 (0.03) **	ns
Relief: flat vs other	ns	ns	ns	−0.39 (0.20) *	ns
Random effects: a Plot	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (<0.01)	<0.01 (0.09)	<0.01 (<0.01)

[a]: For random effects, variance and standard deviation in parenthesis are given; Levels of significance: * *p* < 0.05, ** *p* < 0.01, *** *p* < 0.001. ns: not significant; nt: not tested.

4. Discussion

In the black pine plantations of the Slovenian Karst, a significant density of *Quercus* (2700 ha^{-1}) and noble broadleaves (1500 ha^{-1}) was found, mostly in form of advance regeneration. Similar *Quercus* seedling densities in *Pinus* plantations have been reported in some studies [12,13]. Higher densities have been reported in studies from Balkan mountains [11] and from Poland [14], while in some other studies the densities were lower, likely due to more extreme sites and higher stand densities [15].

Since 2011 was an abundant mast year for *Quercus* [30], we expected many one-year-old *Quercus* seedlings. However, we did not record any one-year-old seedlings from any of the main tree species in 2012, which is probably due to the dry spring and summer of that year. The period from May to September in the research area had less precipitation than the 1971–2000 average [20]. This finding is consistent with the results of other authors who conclude that tree regeneration in Mediterranean forests is restrained by drought and therefore canopy provides a significant nurse effect for seedlings [31,32].

Quercus establishment was better within closed stands, on deeper silicate soils, with less *S. autumnalis* coverage and in proximity of seed trees. The importance of soil depth, ground vegetation competition and seed trees for *Quercus* establishment has been emphasized in several studies [11,13,33]. In addition to stronger seed rain under forest stands and less competition from ground vegetation, small rodents and birds, especially jays (*Garrulus glandarius* L.), are also important factors as vectors for acorns. It appears that they prefer forest stands rather than gaps [13,15].

Taller *Quercus* seedlings were more abundant in open stands and at gap edges, on more humid soils and on less rocky sites. Due to the deep root system of *Quercus*, competition with the grass *S. autumnalis* did not represent a major hindrance to already established *Quercus* seedlings. Many other researchers have stressed the relative abundance of *Quercus* advance regeneration in stands and problems with establishment in gap centers [11–15,33].

It seems that taller *Quercus* seedlings are more light demanding than competing *F. ornus* and *O. carpinifolia*; they may also better tolerate the influence of the continental climate within gaps (i.e., low relative air humidity, large daily and annual variation in temperature), especially *Q. cerris* and *Q. pubescens* [25]. However, due to the low *Quercus* density, it seems that gaps in this study were too large and were not made gradually following established *Quercus* advance regeneration. In the sub-Mediterranean region, special care is needed when regenerating stands, as gaps can also be problematic due to summer droughts [32]. Unlike other studies of topsoil moisture distribution within gaps [34,35], measurements in this study indicated that seedlings in gaps were more exposed to drought during summer months compared to closed stand (comp. [36]), despite the absence of interception by crowns and water consumption by tree roots.

An important difference between *Quercus* and its two main competitors is that it thrives better on deeper and more acidic soils. While the proportion of *Quercus* declined with height class, the proportion of *F. ornus* was more stable and *O. carpinifolia* increased in number. The latter is probably partly due to its higher shade tolerance and lower mortality, and partly also due to the successional development of stands and improved soil conditions. The ratio of *Quercus* to competing tree species is strongly in favor of the latter; therefore, tending and mixture regulation in favor of *Quercus* is needed [12].

In addition to soil conditions, overbrowsing by ungulates represents another factor that is not directly influenced by silviculture. Browsing of regeneration by ungulates exceeded the recommendations for sustainable natural regeneration [37], and in particular hampered the development of *Quercus*. The association of *Quercus* subplots with thorny species (*Rosa* sp., *Rubus* sp.) may also indicate an escape strategy for this species [38]. Thus, successful recruitment of seedlings would require a significant decrease in game density.

5. Conclusions

This study did not cover all gap sizes. The task of future research is to consider a larger range of gap sizes, which will be available with the further development of gradual conversion. The guidelines

presented are therefore largely based on past *Quercus* regeneration studies [12,39–41] and observations and should be followed with some caution. Contrary to the common opinion that *Quercus* seedling potential is low in *P. nigra* plantations, this study indicated that gradual conversion by means of natural regeneration is feasible. This is especially true for less degraded sites with deeper, silicate soils. *Quercus* establishment is successful under closed stands (e.g., 15–20% of diffuse light). Regular thinning of *P. nigra* stands is important to favor stability and facilitate recruitment of advanced regeneration. Later, with the development of *Quercus,* small gaps (e.g., 20–30% of diffuse light) should be created and progressively expanded. Since *Quercus* seedlings can survive up to 25 years below *P. nigra* canopies, the interventions can be gradual. Low advance regeneration density and overbrowsing require strict protection of seedlings from harvesting and browsing damage as well as regulation of tree competitors. If tree commercial quality is a concern, following the thicket phase, the gap size should reach at least 0.5 ha due to the heliotropic growth of *Quercus*. It seems likely that at current game densities active gradual transformation of *P. nigra* plantations is not possible. Therefore, in order to promote stable mixed future forests, in addition to the described silvicultural methods, it is also necessary to regulate ungulate populations.

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Appendix A

List of sampled tree species and shrubs on vegetation subplots. Frequency represents the proportion of subplots where a species was present; regeneration means overall regeneration structure.

Trees	Frequency %	Regeneration %	Shrubs	Frequency %
Fraxinus ornus	70	73	*Hedera helix*	39
Quercus sp.		10	*Clematis vitalba*	35
Quercus pubescens	20		*Ligustrum vulgare*	30
Quercus cerris	11		*Rubus hirtus*	25
Quercus petraea	3		*Cornus mas*	21
Quercus rubra	1		*Prunus spinosa*	19
Ostrya carpinifolia	37	9	*Crataegus monogyna*	15
Ulmus glabra aggr.		2	*Prunus mahaleb*	14
Ulmus glabra	2		*Frangula rupestris*	11
Ulmus minor	5		*Rubus ulmifolius*	10
			Corylus avellana	6
Noble Broadleaves			*Cotinus coggygria*	6
Acer pseudoplatanus	5	3	*Lonicera xylosteum*	6
Fraxinus excelsior	4	2	*Lonicera etrusca*	5
Tilia sp.		<1	*Rosa* sp.	4
Tilia platyphyllos	2		*Berberis vulgaris*	2
Tilia cordata	1		*Rhamnus cathartica*	2
Prunus avium	1	<1	*Euonymus verrucosus*	2
Sorbus torminalis	2	<1	*Rosa canina*	2
			Cornus sanguinea	2
Other tree species			*Euonymus europaeus*	2
Robinia pseudoacacia	3	<1	*Rubus* sp.	2
Sorbus aria	2	1	*Viburnum lantana*	2
Abies alba	2	<1	*Rubus fruticosus* aggr.	1
Acer campestre	2	<1	*Frangula alnus*	1
Castanea sativa	<1	<1	*Rosa arvensis*	<1
Juglans regia	<1	<1	*Rosa gallica*	<1
Malus sylvestris	<1	<1	*Rubus bungeana*	<1
Pyrus pyraster	<1	<1	*Rhamnus saxatilis*	<1
Sorbus aucuparia	<1	<1	*Rosa guleana*	<1
Acer monspessulanum	<1	<1	*Rubus caesius*	<1
Celtis australis	<1	<1	*Rubus idaeus*	<1
Pinus nigra	<1	<1		

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