Role of environmental filtering and seed source availability in natural regeneration processes following large-scale disturbances in mountain forests

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Abstract

The relative importance of environmental factors and species pool in natural regeneration processes is still intensively disputed. Is environmental filtering especially important for species with higher requirements for temperature and soil fertility? Is the seed source limitation especially pronounced among tree species with lower dispersal abilities? Trees, seedlings and saplings measurements were conducted in 600 plots of 0.05 ha distributed in a regular grid in the Tatra Mountains (elevation range 817–1797 m a.s.l.). Boosted regression trees were used to analyse the relationships between the numbers of young trees, factors acting as environmental filters and the potential seed source availability. The most important factor affecting the distribution of young trees of most species was elevation; bedrock type was the second most important factor for *Acer pseudoplatanus*, while potential solar radiation was important for *Sorbus aucuparia*. The relationship between the presence of mature trees and abundance of young ones was strong in *Fagus sylvatica*, moderately strong in *A. pseudoplatanus*, and weak in *Picea abies*, *Abies alba* and *S. aucuparia*. The role of environmental factors in shaping the abundance of young trees varies strongly among species, while the seed source availability is very important for large-seeded trees.

Keywords Dispersal limitations · Environmental filtering · Forest dynamics · Large-scale disturbances · Natural regeneration · Seed source availability

Introduction

The relative roles of environmental factors and the presence of already established individuals in vegetation dynamics have been a matter of discussion in several recent papers (Burton et al. 2011). The environmental factors act as filters, determining the possibility of a given species to become established and survive in certain habitats (Franklin et al. 2013; Kraft et al. 2015). The broader meaning of

the environmental filtering includes the indirect effects of environmental factors upon the growth, survival and reproduction of plants, affecting their relative competitive abilities (Cadotte and Tucker 2017). Among the factors acting as environmental filters in woody plants are temperature, light intensity, soil moisture and availability of nutrients. As in many cases, it is not feasible to measure these factors directly, elevation is commonly used as a proxy for temperature and humidity in the mountains, while bedrock and soil types as proxies for soil water and nutrient availability.

In forest communities, the performance of plants growing on the forest floor is strongly affected by the tree canopy. Mature trees directly reduce the availability of light to the shorter plants, but they are also strong competitors for water and nutrients (Canham et al. 1996). However, after an intense disturbance and high mortality among mature trees, resources are released. By the time they are taken by the understory plants, they are available for the young trees. Therefore, the environmental filtering effects in the case of young trees should be clearly visible (Laliberté et al. 2014).

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The mature trees are potential sources of propagules and make the establishment of young plants of a given species more likely (Yang et al. 2016; Han et al. 2018). Several studies based upon seed trapping showed that regeneration processes are delayed because of the scarcity of seeds (McEuen and Curran 2004; Cai et al. 2018). However, as it is not feasible to conduct seed trapping at the landscape scale, the presence of mature trees is considered a potential seed source for a given species (Sheffer et al. 2013; Willis et al. 2016). The importance of potential seed sources for the regeneration dynamics in forest communities has been documented by numerous authors (Dovčiak et al. 2003; Donato et al. 2009; Tepley et al. 2017).

The other important factor is history; the role of historical filters has been elucidated by several authors, mainly in the context of long-term processes like speciation or species migrations following deglaciations (Bonada et al. 2005). However, historical legacies can also be important in shorter time periods, measured in decades or centuries and reflect various kinds of human impact (Murphy et al. 2015). Certain types of human management promote some species at the expense of the others; as a result, some species are absent in places where the environmental conditions are conducive for their growth, while the other species are numerous in places where they could have been eliminated by superior competitors. However, once the superior competitors have been marginalized by human management, the weaker species can thrive in places that without human intervention would be taken by other species. That can also affect the local seed source availability, giving the species once promoted by human management an advantage that could persist long after human management has ceased.

The spontaneous regeneration of forest stands is a good example of a situation where all these mechanisms (environmental filtering, seed source availability and historical factors) play important roles (Wild et al. 2014; Szwagrzyk et al. 2018). The relative importance of these mechanisms depends on the ecological context and can be difficult to separate (Brown et al. 2015). The diversity of habitat types is usually strongly associated with the spatial scale, making niche-based and stochastic effects difficult to disentangle (Chase and Myers 2011). Therefore, environmental filtering can be easier to detect in strongly heterogeneous landscapes, where the environmental factors vary strongly along relatively short distances, which are within the dispersal ranges of the local tree species (Gratzer and Waagepetersen 2018). Mountain ranges are good places to conduct such analysis. They provide a wide range of environmental conditions, climates, bedrock types and soils, and usually harbour tree species with very different ecological characteristics. This would allow the forest composition to vary a lot according to the local combination of environmental factors.

Seed source availability can be crucial in environments dominated by a single species, where admixtures are unevenly distributed, and their propagules are available only in certain places (de Andrés et al. 2014). Under such circumstances, the chances of becoming established for the less abundant species strongly depend on the presence of some mature individuals in close proximity (Cremer et al. 2012).

As forest communities are dominated by long-living trees, the effects of changes in environmental factors can be strongly delayed. However, large intense disturbances may set back the system and start new dynamics or succession processes (Frelich 2002). They kill many mature trees and increase the availability of resources, especially light, for the new generation of trees, including pioneer species (Turner 2010). Nowadays, with recurring windstorms and bark beetle outbreaks (Mezei et al. 2016; Potterf et al. 2019), the forests of the Tatra Mountains are in a state of transition. The mortality of *Picea abies* (L.) H. Karst. mature individuals was high (Sproull et al. 2017), the forest canopy is more open, and the natural regeneration processes are very intense (Bodziarczyk et al. 2019).

In case of the Tatra Mountains, there is also another important mechanism; the species composition of the forest stands has been profoundly changed over centuries of management, including mining, grazing and logging (Gazda et al. 2018). During reforestation of the cleared areas, one species—*P. abies*—has been favoured over the other native trees. Therefore, in many places, where the environmental conditions are conducive for other tree species, we find pure *P. abies* stands as a legacy of the long management history. Tree species that were strongly affected in a negative way were European beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.). Beech was strongly exploited during the period of iron ore mining and iron production in the nineteenth century. Sycamore maple has been preferably used for production of furniture and tools by the local inhabitants and was very strongly reduced due to selective human pressure (Gazda et al. 2018). In case of silver fir (*Abies alba* Mill.), the effects were less pronounced, as this species was used for timber in the same way as the more numerous spruce. Rowan (*Sorbus aucuparia* L.), a small tree with a low quality of wood, was probably the least affected one by the direct human influence. However, planting of dense spruce stands in the late nineteenth and early twentieth centuries could adversely affect this species in an indirect way.

The question, to what extent the regeneration processes are shaped by the environmental constraints, and to what extent by seed source availability, is the main aspect of this work. As already mentioned, both the environmental filtering and seed source availability have been modified by the historical factors, mostly associated with the past human management. Therefore, looking at the environmental context of forest regeneration, we have historical filtering

working alongside with environmental filtering. Joint effects of these two mechanisms upon five tree species under study are shown in Table 1.

We could expect that species with higher requirements for temperature and soil fertility should be more affected by environmental filtering. According to the results of earlier works (Piękoś-Mirkowa and Mirek 1996), the occurrence of these species in the Tatra Mountains is constrained to certain elevation zones or to certain bedrock types. We expected strong effects of environmental filtering in *A. alba*, where the effects of environmental factors are not masked by historical filters. In *F. sylvatica* and *A. pseudoplatanus*, environmental filters can be modulated by historical filters and therefore produce less apparent results. In the case of *S. aucuparia*, the historical factors probably outweigh the weak environmental constraints. In the case of *P. abies*, the environmental effects are weak and not masked by historical factors. That would lead us to the hypothesis 1:

The role of environmental filtering is most apparent in *A. alba*, less so in *F. sylvatica* and *A. pseudoplatanus*, where the effects of environmental filtering are offset by historical factors, and it is of least importance in *P. abies* and *S. aucuparia*.

Historical factors strongly modified the seed source availability. As *P. abies* has been promoted all over the Tatra Mountains, there is ample seed source of this species in all locations. Because species like *F. sylvatica* or *A. pseudoplatanus* have been reduced by human management, their seed sources are absent in many places conducive for the establishment and growth of these species. Therefore, the actual seed source availability can differ strongly from what could have been produced by the long-lasting processes of environmental filtering. These effects can be especially pronounced in species with short dispersal distances.

Our second hypothesis was as follows:

Seed source availability strongly affects the occurrence of young trees of species that are characterized by lower dispersal abilities, like *F. sylvatica*, but they do not play a large role in the distribution of young individuals of species with higher dispersal abilities: *P. abies*, *A. alba* and *S. aucuparia*.

Material and methods

Study area

The Tatra National Park (latitude 49° 10' 42.36" to 49° 20' 21.01" N, longitude 19° 45' 29.78" to 20° 7' 55.49" E) encompasses the Polish part of the Tatra Mountains, the highest range of the Carpathians, covering the area of 210 square kilometers, ranging in elevation from 816 to 2500 m. The northern and central parts of this area are built of sedimentary rocks, mainly limestone and dolomite, on which various types of Rendzic Leptosols have developed. The southern part is made up of gneisses, granodiorites and granites, covered with Podzols (Skiba 2002; Piotrowska et al. 2015).

The climate of the forest belts of the Tatra Mountains ranges from average temperature + 5 °C, average precipitation—approx. 1100 mm in the foothills (900 m a.s.l.), to + 1 °C and about 1700 mm in the uppermost forest limits (1550–1700 m a.s.l.) (Ustrnul et al. 2015; Żmudzka et al. 2015). The lowest areas are occupied by the Carpathian *Fagus–Abies–Picea* forest, transformed into artificial *P. abies* stands over significant areas. In the slightly nutrient poorer habitats, *A. alba* forests have developed. The upper montane zone is the domain of *P. abies* forests. The entire Tatra range is now protected by national parks—Slovak (TANAP) and Polish (TNP). In the Polish Tatra National Park, more than half of the forest area is strictly protected, and the rest is subject to active management.

The average volume of live trees in the forests of the TNP is about 253 m³/ha, and there is a huge variation (from 0 to almost 1000 m³/ha) among plots (Bodziarczyk et al. 2019). The dominant species is *P. abies*, followed by *A. alba* and *F. sylvatica*; *S. aucuparia* is quite abundant on the basis of tree number (Table 2), but its share expressed in units of basal area is below 1%. The share of *P. abies* calculated on the basis of basal area (BA) ranges from 81% below 1200 m a.s.l. to 98% between 1200 and 1400 m a.s.l. As a result of recent windstorms and bark beetle outbreaks, the mortality of trees, especially of *P. abies*, has been very high (Sproull et al. 2017). This contributed to a large accumulation of dead trees, both snags and downed logs. The average volume of dead trees is 176 m³/ha, almost two-thirds of the living trees volume. The share of *P. abies* in the volume of dead trees was about 97%.

Table 1 Expected effects of environmental and historical filters upon the analyzed tree species

Filter	Species				
	<i>F. sylvatica</i>	<i>A. pseudoplatanus</i>	<i>A. alba</i>	<i>S. aucuparia</i>	<i>P. abies</i>
Historical	Strong	Strong	Moderate	Moderate	Weak
Environmental	Strong	Strong	Strong	Weak	Weak

Table 2 Characteristics of forest stands in Tatra National Park

Species	Average tree density (ind./ha)	Share in % by number	Basal area (m ² /ha)			
			Average	SD	Minimum	Maximum
<i>Picea abies</i>	567	84.6	23.60	20.28	0	101.92
<i>Fagus sylvatica</i>	27	4.0	0.82	4.24	0	54.55
<i>Sorbus aucuparia</i>	27	4.0	0.34	1.13	0	13.20
<i>Abies alba</i>	26	3.9	1.49	5.34	0	41.72
<i>Acer pseudoplatanus</i>	7	1.0	0.18	1.22	0	19.94
<i>Larix decidua</i>	4	0.6	0.20	1.64	0	29.44
<i>Salix caprea</i>	4	0.6	0.06	0.32	0	4.88
<i>Alnus incana</i>	3	0.4	0.06	0.54	0	7.84
<i>Pinus cembra</i>	2	0.3	0.18	1.69	0	27.33
<i>Betula pubescens</i> subsp. <i>carpatica</i>	1	0.1	0.02	10.21	0	3.41
Others (<i>Fraxinus excelsior</i> , <i>Ulmus glabra</i> , <i>Pinus sylvestris</i> , <i>Populus tremula</i>)	2	0.3	0.08	0.68	0	9.90
All species	670 ± 591	100	27.02	20.54	0.08	104.50

Data collection

The research was conducted in the years 2016–2017 in 600 circular sample plots established at a spacing of 500 m × 500 m in a compact grid, referenced to as the AtPol geobotanical grid, covering the area of approximately 210 square kilometres. The range of variability of the permanent sample plots in the elevation gradient ranged from 817 to 1797 m a.s.l. In each plot, all the mature trees (alive and dead) of at least a DBH (diameter at breast height, i.e. 1.3 m) of 7 cm were measured (DBH, position, tree height of all individuals) and mapped within the circular area of 0.05 ha, and their species identity and status (alive or dead) were recorded. Due to the high variability of seedlings and saplings densities, we decided to limit the number of measured young trees. In each sample plot, we measured 30 specimens representing each size class (seedlings: height < 0.5 m, short saplings: 0.5 m < height < 1.3 m, tall saplings: height > 1.3 m and DBH < 7 cm) situated closest to the plot centre, but at a distance not exceeding 12.62 m, which determined the borders of the 0.05 ha sample plots. For each young tree, the species identity, height and distance from the centre of the plot were recorded. The distance to the individual situated farthest from the plot centre was used to determine the area covered by each size class and to calculate the density of seedlings and saplings.

On the basis of the distances to the individual most remote from the plot centre, we calculated densities for seedlings, short saplings and tall saplings; in many plots we encountered less than 30 individuals of a given size class—see Supplementary Information (Table S1). The number of individuals of a given species in a given size class and given plot were then used in the statistical analyses described below. For the central point of each sample plot,

we also had data concerning the elevation (from the digital model of the terrain, resolution 10 m), bedrock type (from the geological map of the Tatra Mountains, scale 1:30 000, Bac-Moszaszwili et al. 1979), soil type (Skiba 2002) and potential solar radiation. The latter was calculated in Arc-Map Solar from the digital model of the terrain, on the basis of exposure and slope inclination, and expressed in kWh per area (m²). For each sample plot, we also calculated the stand characteristics on the basis of the mature tree measurements; basal area (BA) of live trees, stand density index (SDI) and tree mortality, defined as the ratio of stem volume of dead trees (standing or fallen) to the volume of live trees plus dead trees together and expressed as % values. The environmental factors and stand characteristics used for developing the models are listed in Table 3.

Statistical analyses

To analyse the relationship between the number of young trees and environmental factors, we employed *boosted regression trees* (BRTs; Elith et al. 2008), a statistical technique frequently used for investigating forest disturbance drivers (Albrecht et al. 2012). We did our analyses for the combined seedlings, short saplings and tall saplings, described later in the text as ‘young trees’; our analysis was confined to the five most abundant species: *P. abies*, *F. sylvatica*, *A. alba*, *A. pseudoplatanus* and *S. aucuparia*. The analyses were conducted for each species separately and for all species combined. The independent variables were: elevation [m], bedrock type (geology), soil type and potential solar radiation (kWh/m²) as well as the basal area of living trees (m²/ha) and tree mortality [%]. Basal area represented the availability of resources, especially light, for the young trees. The variable “tree mortality” represented the recent

Table 3 Explanation and description of predictors

Predictor	Explanation	Average value	Range (min.–max.)
ELEV	Elevation (m a.s.l.)	1220	817–1797
SLO	Slope (%)	21	0–64
SOL	Potential solar radiation (kWh/m ²)	1 025 910	534 962–1 350 621
SOIL	Soil type*	–	–
GEO	Geology–bedrock type**	–	–
BA	Basal area of living trees (m ² /ha)	27.40	0.08–104.50
SDI	Stand density index	495	0–1785
MOR	Mortality—% of dead trees by volume	41.00	0–100

*Soil types: Lithic leptosols; Regosols; Dystric Folic Leptosols; Skeletic Podzols; Dystric/Eutric Skeletic Leptosols; Calcaric Folic Leptosols; Calcaric Leptosols; Cambisols

**Bedrock types: other loams; gravels; sandstones; shales; conglomerates; limestones; dolomites. regolith; gneisses; granodiorites; granites

increase in the availability of resources due to the death of the mature trees as a result of disturbances. We developed models based on how well the observed data can be explained (training data correlation) and how well the model predicts the excluded data (coefficient of variation—CV correlation) (Elith et al. 2008). In comparison with traditional regression analyses, where we compared the coefficients of determination based on data relationships, BRTs generated the relative importance values of each predictor variable in the model, making them robust alternatives.

We also calculated the BRT models in an alternative way, using the stand density index (SDI) instead of BA. To do that, we employed the equivalence coefficients for converting the SDI from one species to the other, developed by Pretzsch and Biber (2016). All BRT models were fitted with R using the `gbm.step` function in the `gbm` package (Ridgeway 2018; Elith and Leathwick 2017) with a Gaussian response distribution and tenfold cross-validation procedures (Elith et al. 2008). These models were defined with levels of complexity (number of nodes) of three and learning rates of 0.0001 to produce 1000 trees per model. Bag fractions (the proportion of data to be selected at each step) were set to 20 to optimize the predictive power. Finally, models were reduced to the most important and relevant predictor variables using the `gbm.simplify` function (Elith and Leathwick 2017).

As two of the analysed species—*A. alba* and *F. sylvatica*—have distinct upper elevation limits in the Tatra Mountains, we developed climate envelopes for both species and conducted analyses for these species both within and outside their respective climate envelopes. The climate envelope for *A. alba* was developed on the basis of de Rigo et al (2017), and for *F. sylvatica*—on Ammer et al. (2008). Then, we conducted the analyses for all species together within the climate envelope for *F. sylvatica* and beyond that envelope.

Basal area affects the availability of resources, but in case of conspecific trees it also represents the seed source

availability. To address our second hypothesis, we calculated linear regression between the BA of given species among mature trees (as dependent variable) and the number of young trees (seedlings and saplings together) as an independent variable. Linear regression is one of the basic approaches in modelling the relationship between variables and we have chosen it, since using it we can calculate the direction and the force of relationship between the variables. All LR models were fitted with R using the `lm` function in the stats package (<https://www.rdocumentation.org/packages/stats/versions/3.6.2>).

Results

Species composition

In forest regeneration, the average number of tree species was 3.29 per plot, while for mature trees it was 1.74 species per plot. Tree regeneration was very unevenly distributed. The average density was highest for seedlings (87 ind./100 m²), lower for short saplings (10 ind./100 m²) and lowest for tall saplings (9 ind./100 m²) (Table S1). At the level of the entire dataset, there were large differences in species composition of young trees compared to the mature stands (Fig. 1, Fig. S2). We focused upon comparisons between mature trees and tall saplings, which have already gone through the stage of high mortality and therefore are quite likely to eventually replace the mature trees in the future. The largest difference was the lower percent share of *P. abies* among tall saplings in comparison with mature trees, while in *S. aucuparia* the share among tall saplings was almost 10 times higher than among mature trees (Fig. 1). The other species, which was much more abundant among the tall saplings compared to the mature trees, was *A. pseudoplatanus*. In the case of *F. sylvatica*, the share among the tall saplings

Fig. 1 Species composition of mature trees and tall saplings in the Tatra N.P

was higher than among the mature trees, while for *A. alba* that difference was small (Fig. 1).

Effects of environmental factors and stand characteristics upon distribution of young trees

When using BA as the proxy for mature stand density, the most important factor explaining the distribution of young trees was elevation. This is clearly visible when comparing the densities of young trees along the elevation gradient (Fig. S3). The species strongly confined to lower elevations was *A. alba*. Two deciduous trees—*F. sylvatica* and *A. pseudoplatanus*—were less affected by elevation, although both had distinct upper elevation limits (1400 and 1420 m a.s.l., respectively). *P. abies* occurred up to the most elevated plots, but the abundance of the young trees decreased slightly with elevation. *S. aucuparia* was the only species that not only occurred up to the highest plots, but also increased in abundance with higher elevation (Fig. S3). The stronger reaction of *A. alba* to elevation (as compared to *F. sylvatica*) was supported by the results of the BRT analyses conducted within climate envelopes for both species; elevation explained over 70% of variation in abundance of young trees of *A. alba*,

while for *F. sylvatica* the respective value was less than 30% (Table 4).

The other factors played different roles for various tree species. Bedrock type was the second most important factor for *A. pseudoplatanus*; it was also relatively important for *F. sylvatica*, and less so for *A. alba*. Potential solar radiation along with tree mortality at the sample plot level was important factors in the case of *S. aucuparia*, and slightly less important for *F. sylvatica*. For *P. abies*, the important factor (apart from elevation and BA) was the slope (Fig. 2a). The analyses conducted separately within and beyond climate envelopes showed that also bedrock was among the most important factors for all tree species taken together beyond the climate envelope for *F. sylvatica* (Table 4). In addition, soil types significantly influenced the abundance of young trees, and within the climate envelope for *F. sylvatica* they were even slightly more important than bedrock type. Potential solar radiation and slope were the least significant environmental factors in our analyses (Fig. 2a, Table 4).

It is also important to note that the measures characterizing mature stands—BA and tree mortality—also played essential roles in shaping the abundance of young trees. The species that responded most strongly to BA was *P. abies*; in the case of *S. aucuparia*, the reaction was weaker (Fig. 2a).

Table 4 Results of BRT analyses (% of variation explained) conducted within the climatic envelope for *F. sylvatica* (1364 m a.s.l.) and *A. alba* (1428 m a.s.l.) and beyond these envelopes for all species within the climatic envelope/ beyond the envelopes

	All species		<i>Fagus sylvatica</i>	<i>Abies alba</i>
	≤ 1364 m a.s.l	> 1364 m a.s.l	≤ 1364 m a.s.l	≤ 1428 m a.s.l
Elevation (m a.s.l.)	38	13	29	71
Geology—bedrock type	16	34	24	7
Soil type	17	29	3	3
Slope (%)	8	8	14	7
Potential solar radiation (kWh/m ²)	9	5	16	8
Basal area of living trees (m ² /ha)	5	7	9	3
Mortality (%)	8	5	5	1

Fig. 2 Results of analysis with Boosted Regression Trees showing the relative importance of environmental factors for the occurrence of young trees (seedlings, short saplings and tall saplings together): **a** Employing BA as the measure of stand density, **b** employing SDI as the measure of stand density. *ELEV* elevation; *SLO* slope; *SOL* potential solar radiation; *SOIL* soil type; *GEO* bedrock type; *BA* basal area; *SDI* stand density index; *MOR* % mortality of mature trees

The species that was least affected by BA (and little affected by tree mortality) was *A. alba*. In the analyses conducted for all species together within and beyond climate envelopes for *F. sylvatica*, the importance of stand factors was less pronounced than of most of the environmental variables; within the climate envelope, tree mortality was more important than BA, and beyond the climate envelope it was the opposite (Table 4).

When employing the SDI index instead of BA, the results were quite different. In general, SDI was a more important factor than BA. In the case of *F. sylvatica*, SDI explained over 99% of variation (Fig. 2b). In this set of analyses, elevation was even more important than before in the case of *A. alba* and *A. pseudoplatanus*, while less important for *P. abies*, *S. aucuparia* and, of course, *F. sylvatica*. The analyses employing SDI showed also a larger importance of slope for *P. abies* and of geology for *A. pseudoplatanus* (Fig. 2b).

Relationship between basal area and number of young trees of given species

The relationship between the basal area of mature trees and the number of seedlings and saplings differed strongly

Table 5 Strength of relationship between basal area of a given species and number of young trees (seedlings and saplings together) of that species per sample plot

Species	Slope	Intercept	R^2	AIC	Number of observations
<i>Abies alba</i>	−0.26	4.23	0.02	4575	122
<i>Acer pseudoplatanus</i>	−0.78	5.06	0.14	4128	33
<i>Fagus sylvatica</i>	−0.007	4.87	0.34	3455	73
<i>Picea abies</i>	−0.28	3.37	0.02	5545	573
<i>Sorbus aucuparia</i>	1.00	3.01	0.01	5284	151

among the five analysed species (Table 5). The positive relationship was found in *S. aucuparia*, although the low value of R^2 and high AIC indicates a poor fit. In the case of *F. sylvatica*, the slope was close to zero, indicating lack of relationship. In *P. abies* and *A. alba*, the relationship was negative, and the fit was very poor (Table 5). The strongest negative relationship was found in *A. pseudoplatanus*, but in that case the number of observations was very low.

Discussion

The density of natural regeneration (over 100 ind./100 m²) recorded in this study was twice as high as the density found in naturally regenerated areas after windstorms in the Swiss Alps (Kramer et al. 2014) and comparable to the densities of seedlings recorded after large-scale disturbances in the Slovakian part of the Tatra Mountains (Budžáková et al. 2013). The paucity of natural regeneration in the Alps has been attributed to the low accumulation of dead wood, which is an important substrate for germination and seedling establishment of *P. abies*, especially at high elevations (Wohlgemuth et al. 2017). The amount of dead wood in the Tatra N. P. is very high; some of dead wood has been accumulated during storms and bark beetle outbreaks in the 1990's, so after more than 20 years it has been decayed enough to serve as a substrate for regeneration (Zielonka 2006).

The process of natural regeneration following large-scale disturbances leads to a more diverse species composition among young trees compared to the composition of mature stands. In that respect, the results are in agreement with the findings of earlier studies (Harmer and Morgan 2009; Bolte et al. 2014; Szwagrzyk et al. 2018). A large role in this process is played by *S. aucuparia*; the importance of that species for regeneration following disturbances was documented in several studies (Jonášová et al. 2010; Żywiec et al. 2013). The role of *S. aucuparia* seems to be especially pronounced in subalpine *P. abies* forests (Żywiec and Ledwoń 2008), but can also be very important in mixed stands of the

montane zone, where typical pioneer species, like *Betula pendula* and *Populus tremula*, are rare (Kramer et al. 2014).

Our first hypothesis—that species with higher requirements for temperature and soil fertility should be more affected by environmental filtering—was partly supported by the results of this study. The species least affected was *P. abies*, occurring in all vegetation belts up to the timberline and on all types of bedrock (Bodziarczyk et al. 2019). Elevation affected strongly the distribution of young trees of *A. alba*. Two deciduous species—*F. sylvatica* and *A. pseudoplatanus*, also decreased with increasing elevation and had distinct upper elevation limits. *F. sylvatica* and *A. pseudoplatanus* were also strongly affected by the type of bedrock, which is in accordance with the first hypothesis. In the case of *S. aucuparia*, the effect was the opposite, as there were more young trees as the elevation increased.

For a mountainous area, the importance of elevation is not surprising. Similar trends of a negative relationship between the density of natural regeneration and elevation were also found in the foothills of the Swiss Alps after severe windstorms in 1990 and 1999 (Priewasser et al. 2013; Kramer et al. 2014) and in Yellowstone National Park following the 1988 wildfires (Turner et al. 2004). Whether this is a result of seed source limitation (Mencuccini et al. 1995), or limited germination and survival rates of seedlings in harsh climate at higher elevations is an open question.

Basal area represented the availability of resources, especially light, for the young trees. According to the results of the analysis conducted using BRT, the importance of the BA of live trees was greater than the importance of tree mortality, and that was true for all analyzed tree species. When we replaced BA with SDI, the results were even more pronounced, and in the case of *F. sylvatica* SDI explained almost the entire variation in the number of young trees. The variable “tree mortality” represented the recent increase in the availability of resources due to the death of the mature trees as a result of disturbances. In the wind disturbed lowland forests, the importance of tree mortality was greater than the importance of the BA of living trees (Szwagrzyk et al. 2017). As in the case of Tatra N.P., much of the recorded mortality occurred after the year 2002 (Sproull et al. 2017), and the effects of these disturbances on the development of natural regeneration could be delayed. Probably they will be more apparent in the future.

The fact that bedrock type and soil were less important than elevation and the measures of stand density (BA or SDI) is surprising in the cases of *F. sylvatica* and *A. pseudoplatanus*, which according to earlier publications from the Tatra Mountains were mostly confined to the limestone and dolomite bedrock (Piękoś-Mirkowa and Mirek 1996). The greater importance of BA, and especially SDI as compared to bedrock type was striking in case of *F. sylvatica*, which is a shade-tolerant species as it is able to regenerate even in

relatively dense stands (Wagner et al. 2010). The relatively low importance of the bedrock and soil types in shaping the distribution of the young trees can be partly attributed to the fact that the base-rich geological substrates (limestone, dolomite, sandstone) occur mostly at lower elevations, while the granite bedrock is more common at higher ones (Piotrowska et al. 2015). Therefore, the effects of elevation could mask the effects of the bedrock type and soil on the distribution and abundance of the tree species among the young trees. An alternative explanation for the relatively low importance of the bedrock type and soil could be the activity of the park managers in the last few decades; species like *F. sylvatica* and *A. alba* have been planted under the canopy of *P. abies* stands at lower elevations during the long-lasting action of the conversion of *P. abies* monocultures to mixed stands. *F. sylvatica* has been planted not only in the areas of limestone/dolomite bedrock, but also on the glacial moraine deposits with granite or on sandstones and shales.

Potential solar radiation was not important for the abundance of regeneration in most of the tree species; the only exception was *S. aucuparia*, with a relatively high importance of the index of potential solar radiation. That could be explained by the biology of that species, which is shade intolerant, but also sensitive to heat and drought, so it thrives in open and semi-open areas in high mountain locations. We expected that the steep south-facing slopes would have a higher abundance of natural regeneration compared to other aspects, but apparently these effects were less pronounced than the effects of the elevation.

Seed dispersal is one of the most important mechanisms in vegetation dynamics (Clark et al. 1999; McEuen and Curran 2004), so we expected strong effects of seed source availability in the case of species that have lower dispersal abilities. That hypothesis was not confirmed by the results, as the relationship between the basal area of mature trees and the number of young individuals turned out to be mostly negative. The only exception was *S. aucuparia*, where that relationship was positive, although the fit was very poor. Relationship between basal area and number of young trees was very close to zero in the case of *F. sylvatica*, which has the largest seeds among the tree species growing in the Tatra Mountains. The only mode of long-distance dispersal for that species is zoochory, especially dispersal by birds (Wagner et al. 2010), and at medium distances also by rodents (Kempter et al. 2018). However, most of the seeds do not travel long distances, and therefore the seedlings appear relatively close to the mature trees (Canham et al. 2014). We suppose that in the case of beech the positive effect of local seed source is balanced by the negative effect of shading by the mature beeches present in the forest canopy. In both conifers, the relationship between basal area and number of young trees is negative, indicating that shading by mature trees probably outweighs their role as

seed source; this is not surprising, as seeds of *P. abies* and *A. alba* are wind-dispersed and do not depend strongly on the local seed source. Similar effects were recorded in North American boreal conifers after wildfire disturbances (Brown et al. 2015). The lack of a difference between *P. abies* and *A. alba* is surprising, despite a large difference in their seed mass (Cremer et al. 2012). However, according to a recent publication (Gratzer and Waagepetersen 2018), the differences in the mean dispersal distances between *P. abies* and *A. alba* (33.7 m; 22.6 m, respectively) are much smaller than the respective differences in seed mass.

Relatively strong negative relationship between BA and the number of young individuals was found in *A. pseudoplatanus*. Maple seeds are spinning samaras, travelling with strong winds over moderately large distances (Horn et al. 2001). However, studies conducted on the closely related species *Acer opalus* Mill. showed that dispersal limitations are among the most important factors affecting the regeneration dynamics of that species (Gómez-Aparicio et al. 2007). The fact that in the Tatra Mountains the role of local seed source in *A. pseudoplatanus* was not confirmed is surprising. However, we need to take into account that this surprising result was based upon a small number of observations.

Conclusion

Although environmental filtering plays a major role in the distribution and abundance of young trees, in several cases historical factors mask the influences of environmental variability. This is especially pronounced in *F. sylvatica* and *A. pseudoplatanus*. In case of *F. sylvatica*, seed source limitation could retard the process of regeneration of that species and limit its share among the next generation of trees.

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Availability of data and materials The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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