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

Jerzy Szwagrzyk1, Anna Gazda1, Tomasz Zwijacz-Kozica2, Antoni Zięba2, Barbara Ciesielska3, Janusz Szewczyk1, Kacper Foremnik1, Elżbieta Muter1, Jan Bodziarczyk1

Received: 2 April 2020 / Revised: 15 February 2021 / Accepted: 25 February 2021 / Published online: 12 March 2021 © The Author(s) 2021

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).

Communicated by Claus Bässler.

Anna Gazda
anna.gazda@urk.edu.pl
1 Department of Forest Biodiversity, University of Agriculture in Krakow, al. 29-Listopada 46, 31-425 Krakow, Poland
2 Tatra National Park, Kuźnice 1, 34-500 Zakopane, Poland
3 Institute of Mathematics, Faculty of Mathematics and Computer Science, Jagiellonian University, ul. Łojasiewicza 6, 30-348 Krakow, Poland
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 (Frelích 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 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%.

| Filter        | Species          |
|---------------|------------------|
|               | F. sylvatica     | A. pseudoplatanus | A. alba | S. aucuparia | P. abies |
| Historical    | Strong           | Strong            | Moderate | Moderate     | Weak     |
| Environmental | Strong           | Strong            | Strong   | Weak         | Weak     |

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

| Species                  | Average tree density (ind./ha) | Share in % by number | Basal area (m²/ha) |          |         | Minimum | Maximum |
|--------------------------|-------------------------------|---------------------|-------------------|----------|---------|----------|---------|
|                          | Average                      | SD                  | Minimum           | Maximum  |
| **Picea abies**          | 567                           | 84.6                | 23.60             | 20.28    | 0       | 101.92  |
| **Fagus sylvatica**      | 27                            | 4.0                 | 0.82              | 4.24     | 0       | 54.55   |
| **Sorbus aucuparia**     | 27                            | 4.0                 | 0.34              | 1.13     | 0       | 13.20   |
| **Abies alba**           | 26                            | 3.9                 | 1.49              | 5.34     | 0       | 41.72   |
| **Acer pseudoplatanus**  | 7                             | 1.0                 | 0.18              | 1.22     | 0       | 19.94   |
| **Larix decidua**        | 4                             | 0.6                 | 0.20              | 1.64     | 0       | 29.44   |
| **Salix caprea**         | 4                             | 0.6                 | 0.06              | 0.32     | 0       | 4.88    |
| **Alnus incana**         | 3                             | 0.4                 | 0.06              | 0.54     | 0       | 7.84    |
| **Pinus cembra**         | 2                             | 0.3                 | 0.18              | 1.69     | 0       | 27.33   |
| **Betula pubescens subsp. carpatica** | 1                     | 0.1                 | 0.02              | 10.21    | 0       | 3.41    |
| **Others (Fraxinus excelsior, Ulmus glabra, Pinus sylvestris, Populus tremula)** | 2                           | 0.3                 | 0.08              | 0.68     | 0       | 9.90    |
| **All species**          | 670 ± 591                     | 100                 | 27.02             | 20.54    | 0.08    | 104.50  |

**Table 2** Characteristics of forest stands in Tatra National Park
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

---

**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/m²) | 1 025 910 | 534 962–1 350 621 |
| SOIL      | Soil type*   | –  | –  |
| GEO       | Geology–bedrock type** | – | – |
| BA        | Basal area of living trees (m²/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
was higher than among the mature trees, while for \textit{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 \textit{A. alba}. Two deciduous trees—\textit{F. sylvatica} and \textit{A. pseudoplatanus}—were less affected by elevation, although both had distinct upper elevation limits (1400 and 1420 m a.s.l., respectively). \textit{P. abies} occurred up to the most elevated plots, but the abundance of the young trees decreased slightly with elevation. \textit{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 \textit{A. alba} to elevation (as compared to \textit{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 \textit{A. alba}, while for \textit{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 \textit{A. pseudoplatanus}; it was also relatively important for \textit{F. sylvatica}, and less so for \textit{A. alba}. Potential solar radiation along with tree mortality at the sample plot level was important factors in the case of \textit{S. aucuparia}, and slightly less important for \textit{F. sylvatica}. For \textit{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 \textit{F. sylvatica} (Table 4). In addition, soil types significantly influenced the abundance of young trees, and within the climate envelope for \textit{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 \textit{P. abies}; in the case of \textit{S. aucuparia}, the reaction was weaker (Fig. 2a).

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

| Factor                      | All species | \( \leq 1364 \text{ m a.s.l.} \) | \( > 1364 \text{ m a.s.l.} \) | \( \leq 1364 \text{ m a.s.l.} \) | \( \leq 1428 \text{ m a.s.l.} \) |
|-----------------------------|-------------|-------------------------------|-------------------------------|-------------------------------|-------------------------------|
| 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/m²) | 9        | 5                             | 16                            | 8                             |                                 |
| Basal area of living trees (m²/ha) | 5         | 7                             | 9                             | 3                             |                                 |
| Mortality (%)               | 8           | 5                             | 5                             | 1                             |                                 |
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*, 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*, 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).

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 (Budzáková 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 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).

### Discussion

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 (Żywic and Ledwoń 2008), but can also be very important in mixed stands of the

### 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 |
|----------------|-------|-----------|---------|------|-----------------------|
| *Abies alba*    | −0.26 | 4.23      | 0.02    | 4575 | 122                   |
| *Acer pseudoplatanus* | −0.78 | 5.06      | 0.14    | 4128 | 33                    |
| *Fagus sylvatica* | −0.007| 4.87      | 0.34    | 3455 | 73                    |
| *Picea abies*    | −0.28 | 3.37      | 0.02    | 5545 | 573                   |
| *Sorbus aucuparia* | 1.00  | 3.01      | 0.01    | 5284 | 151                   |

### 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 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.
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 (Prielwasser 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 mixedstands. *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.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s10342-021-01371-2.

**Author’s contribution** Conceptualization was contributed by JB and JSzw; methodology was contributed by JB and JSzw; formal analysis was contributed by BC, AG; investigation was contributed by TZY, AZ, and JB; writing—original draft, was contributed by JSzw, AG, TZY, AZ, BC and JSzw; writing—review and editing, was contributed by JSzw, AG, TZY, AZ, BC, EM, KF, JSzw, JB; visualisation was contributed by BC, AG; supervision was contributed by JSzw; project administration was contributed by JSzw, JB, TZY; funding acquisition was contributed by JSzw, JB, TZY, AG.

**Funding** This research was financed by the Polish National Science Foundation (NCN; No. 2018/31/B/NZ8/02786) and by the Ministry of Science and Higher Education, Republic of Poland in the frame of statutory funds: SUB/040011-D019/2020 Department of Forest Biodiversity, University of Agriculture in Krakow. Collection of data for this study was partially supported by National Forest Funds, transferred to the Tatra National Park in 2016.

**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.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

**References**

Albrecht A, Hanewinkel M, Bauhus J, Kohnle U (2012) How does silviculture affect storm damage in forests of south-western Germany? Results from empirical modeling based on long-term observations. Eur J For Res 131:229–247. https://doi.org/10.1007/s10342-010-0432-x

Ammer C, Bickel E, Kolling C (2008) Converting Norway spruce stands with beech—a review on arguments and techniques. Austrian J For Sci 125:3–26

Bac-Moszaszwili M, Burchart J, Glazek J, Iwanow A, Jaroszewski W, Kotas Z, Westwalewicz-Mogilska E (1979) Mapa geologiczna Tat Polskich, 1:30 000 [Geological Map of the Polish Tatra, 1:30,000]. Wydawnictwa Geologiczne, Warszawa

Bodzianczyc J, Szwagryczk J, Zwiarcz-Kozica T, Zięba A, Szewczyk J, Gazda A (2019) The structure of forest stands in the Tatra National Park: The results of 2016–2017 inventory. For Res Pap 80:12–21. https://doi.org/10.2478/frp-2019-0002

Bolte A, Hilbrig L, Grundmann BM, Roloff A (2014) Understory dynamics after disturbance accelerate succession from spruce to beech-dominated forest—the Siggaboda case study. Ann For Sci 71:139–147. https://doi.org/10.1007/s13595-013-0283-y

Bonada N, Zamora-Muñoz C, Rieradevall M, Prat N (2005) Ecological and historical filters constraining spatial caddisfly distribution in Mediterranean rivers. Freshw Biol 50(5):781–797. https://doi.org/10.1111/j.1365-2427.2005.01357.x

Brown CD, Liu J, Yan G, Johnstone JF (2015) Disentangling legacy effects from environmental filters of post fire assembly of boreal tree assemblages. Ecology 96:3023–3032. https://doi.org/10.1890/14-2302.1.sm

Budzáková M, Galvánek D, Littera P, Šibík J (2013) The wind and fire disturbance in Central European mountain spruce forests: the regeneration after four years. Acta Soc Bot Pol 82:13–24. https://doi.org/10.5586/asbp.2013.002

Burton JI, Mladenoff DJ, Clayton MK, Forrester JA (2011) The roles of environmental filtering and colonization in the fine-scale spatial patterning of ground-layer plant communities in north temperate deciduous forests. J Ecol 99:764–776. https://doi.org/10.1111/j.1365-2745.2011.01807.x
National Park, Slovakia (Central Europe). For Ecol Manag 432:489–500. https://doi.org/10.1016/j.foreco.2018.09.050

Pretzsch H, Biber P (2016) Tree species mixing can increase maximum stand density. Can J For Res 46:1179–1193. https://doi.org/10.1139/cjfr-2015-0413

Prießwasser K, Brang P, Bachofen H, Bugmann H, Wohlgemuth T (2013) Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. Eur J For Res 132:231–240. https://doi.org/10.1007/s10342-012-0670-1

Ridgeway G (2018) The gbm package. Generalized boosted regression models (Documentation on the R Package ‘gbm’, version 2.1.4.). https://cran.r-project.org/web/packages/gbm/gbm.pdf. Accessed 16 Oct 2018

Sheffer E, Canham CD, Kigel J, Perevolotsky A (2013) Landscape-scale density-dependent recruitment of oaks in planted forests: More is not always better. Ecology 94:1718–1728. https://doi.org/10.1890/12-2121.1

Skiba S (2002) Mapa gleb Tatrzańskiego Parku Narodowego. In: Przemiany środowiska Przyrodniczego Tatr (electronic version, zwektoryzowana przez TPN). Wyd. TPN—PTPNoZ, Kraków—Zakopane, pp 21–26

Sproull GJ, Bukowski M, Zwijacz-Kozica T, McNutt N, Szwagrzyk J (2017) Landscape-level spruce mortality patterns and topographic forecasters of bark beetle outbreaks in managed and unmanaged stands in the Tatra Mountains. Pol J Ecol 65:24–37. https://doi.org/10.3161/15052249PJE2017.65.1.003

Szwagrzyk J, Gazda A, Dobrowolska D, Chećko E, Zaremba J, Tomski A (2017) Tree mortality after wind disturbance differs among tree species more than among habitat types in a lowland forest in northeastern Poland. For Ecol Manag 398:174–184. https://doi.org/10.1016/j.foreco.2017.04.041

Szwagrzyk J, Gazda A, Dobrowolska D, Chećko E, Zaremba J, Tomski A (2018) Natural regeneration following wind disturbance increases the diversity of managed lowland forests in NE Poland. J Veg Sci 29:898–906. https://doi.org/10.1111/jvs.12672

Talebi K (2010) Beech regeneration research: from ecological to institutional claims in published maps and institutional affiliations. For Ecol Manag 259:2172–2182. https://doi.org/10.1016/j.foreco.2010.02.029

Wild J, Kopeczký M, Svoboda M, Zenáhlíková J, Edwards-Jonasová M, Herben T (2014) Spatial patterns with memory: tree regeneration after stand-replacing disturbance in Picea abies mountain forests. J Veg Sci 25:1327–1340. https://doi.org/10.1111/jvs.12189

Wagner S, Collet C, Madsen P, Nakashizuka T, Nyland RD, Saghe-Talebi K (2010) Beech regeneration research: from ecological to silvicultural aspects. For Ecol Manag 259:174–184. https://doi.org/10.1016/j.foreco.2010.02.029

Willis JL, Walters MB, Farinosi E (2016) Local seed source availability limits young seedling populations for some species more than other factors in northern hardwood forests. For Sci 62:440–448. https://doi.org/10.5849/forsci.15-143

Wohlgemuth T, Schwitter R, Bebi P, Sutter F, Brang P (2017) Post-windthrow management in protection forests of the Swiss Alps. Eur J For Res 136:1029–1040. https://doi.org/10.1007/s10342-017-1031-x

Yang QS, Shen GC, Liu HM, Wang ZH, Ma ZP, Fang XF, Zhang J, Wang XH (2016) Detangling the effects of environmental filtering and dispersal limitation on aggregated distributions of tree and shrub species: life stage matters. PLoS ONE 11:e0156326. https://doi.org/10.1371/journal.pone.0156326

Zielonka T (2006) When does dead wood turn into a substrate for spruce replacement? J Veg Sci 17:739–746. https://doi.org/10.1111/j.1654-1103.2006.tb02497.x

Zmudzka E, Nejedlík P, Mikulová K (2015) Temperatura, wskaźniki termiczne [Temperature, thermal indices]. In: Dąbrowska K, Guzik M (ed.) Atlas Tatr. Przyroda nieożywiona [Atlas of the Tatra Mountains—Abiotic Nature], Tatrzański Park Narodowy, Zakopane

Żywiec M, Ledwont M (2008) Spatial and temporal patterns of rowan (Sorbus aucuparia L.) regeneration in West Carpathian subalpine spruce forest. Plant Ecol 194:283–291. https://doi.org/10.1007/s11258-007-9291-z

Żywiec M, Holeksa J, Wesołowska M, Szewczyk J, Zwijacz-Kozica T, Kapusta P (2013) Sorbus aucuparia regeneration in a coarse-grained spruce forest—a landscape scale. J Veg Sci 24:735–743. https://doi.org/10.1111/j.1654-1103.2012.01493.x

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.