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Mapping of mountain temperate forest recovery after natural disturbance: a large permanent plot established on Czech-German border

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Abstract
Natural regeneration following large-scale disturbance is a basic attribute of forest resilience. However, in the intensively managed forest ecosystems in Europe these processes are not well understood which also limits the options for silvicultural management in these ecosystems. To overcome this shortfall, we have established a large (20 ha) permanent research plot in mountain spruce forest of the Bohemian Forest Ecosystem in 2018, 20 years after one of the largest forest disturbances in Central Europe, left without forestry interventions. The spatial positions of all living trees and dead wood, including low stumps and young regeneration above 50 cm in height were recorded. In total we measured 29 464 positions of 6 species. All live individuals were tagged for permanent monitoring of mortality and growth. As a result of the data analysis the tree spatial structure of the pre-disturbance generation was more heterogeneous compared to a commercial forest. After the disturbance, it became even more heterogeneous, with very pronounced aggregation at all spatial levels, from meters to hundreds of meters. This implies that the spatial pattern of regeneration varies, even over the homogeneous environmental conditions. Explaining this large spatial variability is challenging. Current post-disturbance structure is hardly attainable by any human planting intervention. This shows the high value of non-interventional approach for nature conservation. The further purpose of the research plot is to investigate the development of the abundance and composition of species, biomass and dynamics of spatial distribution of tree individuals. The plot also offers a possibility to add further opportunities for research.

Key words: cross-border plot, Forest Geo, bark beetle, disturbances, Norway spruce, spatial pattern

Introduction

Large scale disturbances such as windstorms or bark beetle outbreaks play an important role in the mountain Norway spruce (*Picea abies* (L.) Karst.) forest dynamics in Central Europe (Čada et al. 2013). The European spruce bark beetle, *Ips typographus* (L., 1758), is considered as the most dangerous pest in Norway spruce stands throughout Euroasia

(Wermelinger 2004). Most damages are recorded in forests with changes towards a simpler forest structure caused by human plantations (Jonášová & Prach 2004). But in strictly protected areas where natural conditions prevail and original species composition is preserved, bark beetle is a natural part of forest dynamic, sometimes even considered as a keystone species (Müller et al. 2008). These ecosystems are likely adapted to the disturbance regime (Čada et al. 2016). After the dieback of parent stands, regeneration (stand-replacement) often depends on the amount of advanced regeneration established before the disturbance (Heurich & Jehl 2000, Svoboda et al. 2012, Macek et al. 2017). Outbreaks of bark beetle cause rapid canopy opening, increase of light availability and high amount of dead wood in the affected forests which is beneficial for many forest species (Beudert et al. 2015). Disturbances caused by bark beetle are also important drivers of changes in the forest structure (Raffa et al. 2008). Increasing temperatures and reduced precipitation resulting from global warming will increase the number of possible bark beetle generations per year and their survival through winter periods and will also decrease the vitality of trees which will be less able to resist an attack. Therefore we can expect an increase of the number and severity of bark beetle outbreaks (Lausch et al. 2011, Seidl et al. 2017). Understanding how forests respond to bark beetle disturbance is therefore critical to forest conservation, climate and forest protection (Keane et al. 2009, Anderson-Teixeira et al. 2014). In Central Europe, the forest structure was studied mainly on a small scale level in permanent research plots up to 1 ha (Wild et al. 2014, Bače et al. 2015), however, for a profound understanding of the natural processes and ecological interactions following the bark beetle outbreak, it is necessary to monitor the forest on a larger spatial scale (Anderson-Teixeira et al. 2014).

Two national parks were found in the Bohemian Forest Ecosystem: The Bavarian Forest National Park (NP) in 1970 and the Šumava National Park (NP) in 1991. These two parks together protect more than 22 000 ha of mountain spruce forests, one of the largest complexes in Central Europe (Čížková et al. 2011). Most of these forests are currently in early successional stages after several successive disturbances, mostly due to wind throws and bark beetle outbreaks (Zeppenfeld et al. 2015). On both sides of the border, non-intervention management is applied and most of these forests are left to natural processes. In this area (the area of Central Europe) we have never had a chance to study forest dynamics, spatial patterns and changes of the forest structure on a larger scale plot situated in a mountain spruce forest. Therefore we established a large (20 ha) cross-border plot partly in the area of Šumava NP and partly in the Bavarian Forest NP in summer 2018. The plot is situated exactly on the border between Czech Republic and Germany in an area of former iron curtain which divided Western and Eastern Europe from 1945 to 1989. The plot serves as a symbol of good cross-border cooperation between both national parks and shows that there are no borders for nature anymore. But the main purpose of the research plot is to investigate the development of the abundance and composition of species, biomass and the dynamics of spatial distribution of tree individuals. Current knowledge shows that spatial pattern and process play an important role in the assembly, dynamics, and functioning of tree communities (Wild et al. 2014). The spatial patterns reflect the ecological processes of the system and affect the placement of the tree individuals as well as the quality of their features (Velázquez et al. 2016). The analysis of large spatial point pattern will provide the possibility to extract this information.

The plot was established according to the methodology of the international CTFS-ForestGEO network (Anderson-Teixeira et al. 2014) and we aim to include this plot in this network.

It consists of forest research sites in tropical and temperate climatic zones. Currently, the intensity and scale of the network remains unprecedented in forest science tracking the fate of 6 million individual trees. Within each plot all stems with diameter ≥1 cm are identified to species, mapped, and regularly recensused according to the standardized protocols (Condit et al. 1998). This study was done in the non-intervention area of mountain spruce forest 20 years after dieback of the maternal stands due to bark beetle outbreak. We used this exceptional dataset from cross-border plot to achieve the following objectives:

1) Introduce the newly established cross-border permanent research plot with area of 20 hectares. Focus on the permanent monitoring of spatial pattern of all woody species.
2) Describe species composition, density and horizontal structure of natural regeneration on this plot.
3) Compare structure of the forest before bark beetle disturbance and 20 years after that.

Methods

Study area and permanent study plot establishment

The area of interest is located on the border between the Bavarian Forest NP on German side and Šumava NP on Czech side in central part of the Bohemian Forest (Fig. 1; 48°56'56" N, 13°28'6" E). The cross-border rectangular 20 ha (400×500 m) permanent study plot was established in the core zone of both parks. In 2017 the plot was stabilized geodetically using grid of squares with a size of 20×20 m for consequent precise data collection of tree individuals. The network was delimited in the third class of geodetic accuracy (which means with a divergence 0.14 m).

The elevation of the plot varies between 1200–1220 m a.s.l. The mean annual temperature is 4°C and yearly precipitation is about 1500 mm (Tolasz et al. 2007), which is exceptionally high in both countries. The bedrock is composed of stromatitic biotite migmatite with sillimanite and cordierite. Soils are shallow and poor, dominated by podzols. The naturally monospecific Norway spruce forests cover the whole plot and grow in high elevations of the whole Bohemian Forest (>1150 m a.s.l.), with minor share of Common rowan *Sorbus aucuparia* L. (Neuhäuslová et al. 1998). Vegetation communities are formed by *Calamagostio villosae-Piceetum* Hartmann (with patches dominated by *Calamagrostis villosa* (Chaix) J.F. Gmel., *Deschampsia flexuosa* (L.) Trin.; Neuhäuslová et al. 1998). Most of the stands in the area of our plot are currently in early successional stages after an outbreak of bark beetle that caused mature trees mortality between the years 1995 and 1996.

Data collection

In 2018 (July–November), the exact spatial position (the middle of a trunk in the rooting place) of standing tree individuals was measured for all (both living and dead) trees higher than 0.5 m and for dead trees in the height range from 0.1 to 0.5 m while having the base diameter greater than 0.2 m. Information about status (living or dead), species, damage (healthy-suitable for height measurements, heavily bent or tilted, broken top or trunk) were recorded. Each recorded living tree was labelled by an aluminium tag. The tags were attached on a branch with a loose wire in the height of 1.3 m. In case of the smallest trees, the wire was fastened around the trunk with the sufficient loose wire for growth. In case of bigger trees without branches in the bottom zone the tag was nailed in the bark of the tree.

Tree positions were collected with a laser range-finder and a magnetic compass (IFER-MMS, Field-Map Technology, 2016, http://www.fieldmap.cz). The equipment was placed on a tripod providing the required measurement accuracy, where the utmost divergence was 0.4 m. The measurement was performed from the stabilized geodetic points. Diameter at breast height (DBH) was measured and recorded to the nearest millimetre for all individuals with height ≥1.3 m when diameter at this height was ≥10 mm. In case of dead trees (snags and stumps) with the height lower than 1.3 m, the diameter (instead of DBH) was measured in the bottom of the break point. The measuring point for DBH was set to 20 mm under the trunk's irregularity in case of bulky trunks or trunks with obvious swelling. Multiple-trunk trees were considered as unique individuals if the trunk was divided under 1.3 m and if the DBH of a single trunk was ≥10 mm. DBH and the diameter of trees with diameter <60 mm was measured with the calliper, whereas DBH of trees with diameter ≥60 mm was measured by the girthing tape. The point of DBH measurement was marked by long-term colour stripe for future repetitive measurements.

The height to the nearest cm was measured for all individuals with height <2 m (we measured height from year 2017). Five hundred living undamaged trees with height ≥2 m were chosen using stratified (by height classes and 1 ha square cell) random selection.

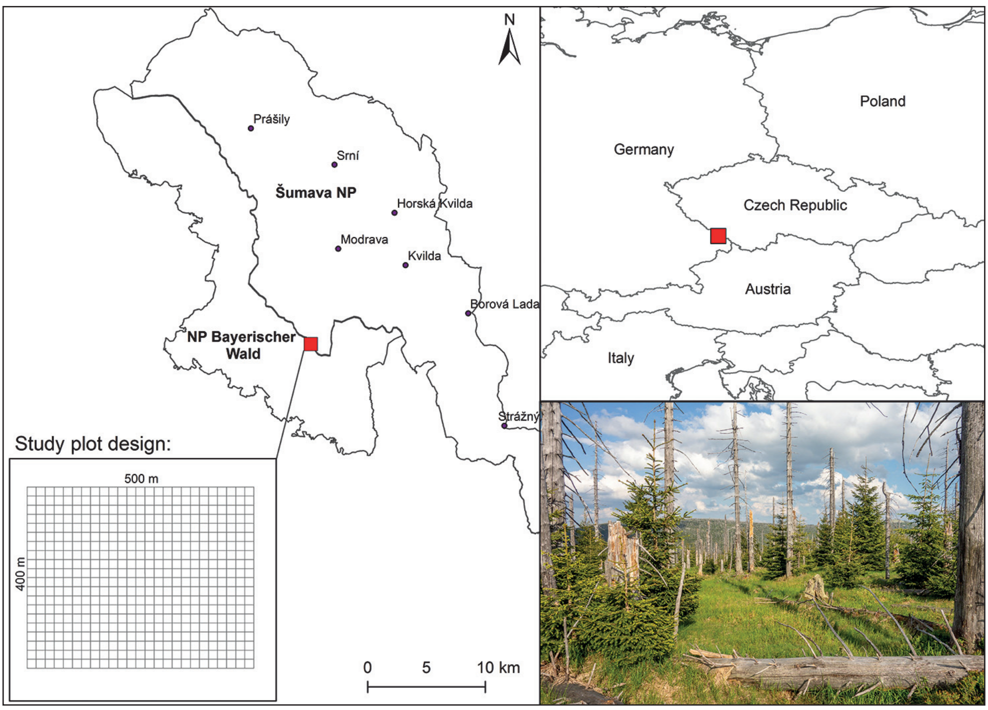

Fig. 1. The location of the cross-border permanent plot and its design (rectangular 20 ha plots - 400×500 m). A geodetically stabilized grid of squares with a size of 20×20 m was used for data collection. The photograph in the lower right-hand corner shows our plot 20 years after the dieback of mature stands (during fieldwork in 2018).

These were measured to calibrate allometric functions of the plot. If a regenerated individual had a withered top, the whole tree was measured; in addition to that the value for the highest living leaf was recorded. The length of the tree was marked in case the trees inclined more than 45° from the vertical axis. The height of the trees was measured with extendable measuring rod in case of trees with height <4 m and the Vertex III altimeter (Haglöf Sweden AB) in case of higher individuals.

Data analysis

To evaluate the structure of tree species before and after a disturbance, we assume that currently dead individuals were alive before the disturbance (i.e. 20 years ago). We know that the mortality of vast majority of individuals will occur within a narrow time frame around the year of disturbance (Bače et al. 2015, Macek et al. 2017). To distinguish young trees that were present before the disturbance (advance regeneration) from those established during and after the disturbance, a 2-meter limit was chosen, which roughly corresponds to the growth rate of the spruce regeneration in local conditions (Macek et al. 2017). The mean and standard deviation of tree number per plot were calculated on 20×20 m squares to demonstrate spatial variability in a scale of tens of meters. To evaluate changes in spatial structure we compare the size of treeless patches (gaps in canopy) before a disturbance (given by the position of dead trees) and 20 years after the disturbance (given by the position of currently living trees). The "empty space distance F-function" with Kaplan-Meier edge correction was used in the spatstat package of R (Baddeley et al. 2015). The empty space distance F is the distance from an arbitrarily fixed location to the nearest point of the pattern. The visualization of empty spaces without tree individuals in the research plot was performed by the "distmap" function from the same R package, which computes a distance map of the tree positions and returns it as a pixel image.

Results and discussion

Composition of species and the structure of natural regeneration

The observed density of tree individuals is 1473 per hectare. The following species occur on the plot: Norway spruce (97.6%), Common rowan (2.1%), European beech (*Fagus sylvatica* L.) (0.2%). The share of all other species (Grey alder *Alnus incana* (L.) Moench; Silver birch *Betula pendula* Roth; Silver Fir *Abies Alba* Mill.) was lower than 0.1%. The composition of tree species is described in more detail in Tab. 1 and is consistent with other results from mountain spruce forests (Jonášová & Prach 2004, Bače et al. 2015, Nováková & Edwards-Jonášová 2015), where a good regeneration of spruce and rowan was observed. Sporadic number of pioneer species can be explained by the absence of soil disturbance (wind throws), which are not common in case of bark beetle outbreak (Heurich 2009). Most of the mature large-diameter-dimension spruce trees (29.1% of all spruce individuals) are dead (Fig. 2). Living individuals predominate in smaller diameter classes. Almost all rowan individuals are alive (97.2%). Most of the regeneration (72% of all living trees) is higher than 2 m. A significant mortality of regeneration is not expected in the near future. High mortality rate of saplings was recorded in the younger stages (Jonášová & Prach 2004; Zenáhlíková et al. 2011). With increasing height, the survival rate of saplings increases as well. Macek et al. (2017) reports only 5% mortality rate of regeneration higher than 0.5 meters.

Table 1. Numbers and density of tree species recorded on the plot.

Species	Sum ind.	Number of dead ind.	Number of dead ind. / ha	Number of alive ind.	Number of alive ind. / ha
Norway spruce	28770	8363	418	20407	1020
Common rowan	624	17	0,85	607	30
European beech	65	0	0	65	3
Grey alder	2	0	0	2	0.1
Silver birch	1	0	0	1	0.05
Silver Fir	1	0	0	1	0.05

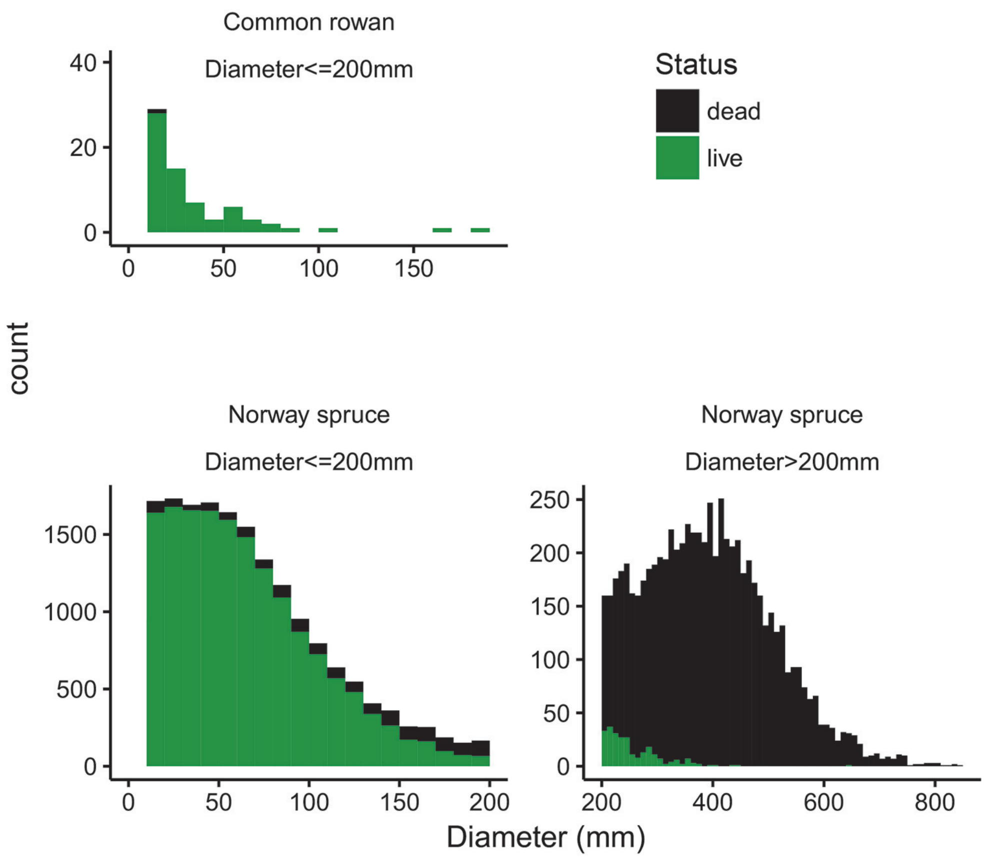

Fig 2. Histograms of the tree diameters categorized by species and status (dead or living). The diameter was measured in the height of 1.3 m. In case of stumps with height lower than 1.3 m, the diameter was measured in the bottom of the break point.

Presence and size of gaps

The spatial heterogeneity of the former tree layer before a disturbance was relatively high. The mean and standard deviation of number of dead trees per square unit of 20×20 m is 16.7±6.4. The values are 15.7±5.4 for dead trees with a diameter ≥70 mm. The post-disturbance tree density and its spatial variation are much higher than the pre-disturbance one: the mean number and standard deviation of number of dead trees on a square unit of 20×20m is 42.3±50.5 and 13.7±14.1 for live trees with diameter ≥70 mm, respectively (Fig. 3).

The spatial pattern of free space distribution in the pre-disturbance time is shown in Fig. 4a. Before a disturbance: considerably aggregated occurrences of dead trees – removed by the disturbance and many gaps with diameter over 10 m are visible in Fig. 4a. Surprisingly, the bark beetle disturbance increased spatial variability of trees even more. Compared to the previous structure, the rate of aggregation on a small scale (in the order of meters) has increased significantly in many sites (Fig. 4b). The most significant result is the shift towards a highly irregular and aggregated occurrence in the middle (tens of meters) and larger (hundreds of meters) spatial scale. This resulted in more pronounced mosaic of dense, sparse and woody areas, and can be distinguished at all spatial scales.

Bigger amount of large-size treeless patches will occur on the plot compared to the state before disturbance. This is shown in Fig. 4, which shows the distribution of the positions of tree species as well as the free (treeless) space distribution. The Fig. 4 can also be seen as an approximate prediction of the crown canopy at the time when the current individuals of natural regeneration reach the maximum crown radius of 5 m. This prediction is valid assuming zero establishment of new individuals and zero mortality of existing individuals. This assumption will be met especially in the first decades of forest succession, when the natural source of seeds from mature trees is absent for some time and when the mortality of individuals forming new forest canopy is minimal (Macek et al. 2017).

If the future projected forest canopy is reduced, compared to the previous canopy, it can be estimated that the post-disturbance regeneration density will be lower than in cases of earlier historical disturbances (Bače et al. 2015, Macek et al. 2017). There are several reasons

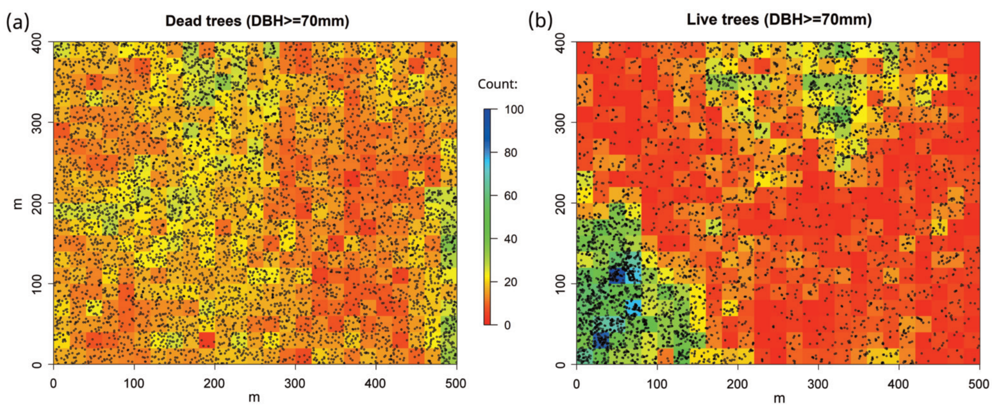

Fig 3. The spatial pattern of dead trees (a) and live trees (b) with diameter ≥70 mm within squares of 20×20 m. The number of individuals is reflected in the colour of the square.

for lower seedling density. First, at the time of the disturbance, some deadwood appropriate for seedling establishment was missing. In the primary mountain spruce forests of Šumava, more than 50% of the spruce regeneration was found on dead wood (Heurich & Jehl 2000, Bače et al. 2012). A substantial part of the dead wood in the forest is formed by lying trunks, and these were previously partially extracted from the ecosystem in the area (Heurich & Jehl 2000, Jonášová & Prach 2004). Second, the crucial limiting factor of natural regeneration density is drought (Donato et al. 2016). Drought due to climate change is an increasingly limiting factor of tree growth in mountain spruce forests in Europe, in one of Europe's most wet forest ecosystems (Primicia et al. 2015, Svobodová et al. 2019). The meta-analysis of densities of regeneration after intensive large-scale disturbances of temperate and boreal forests shows that the regeneration density increases with the average temperature and annual total

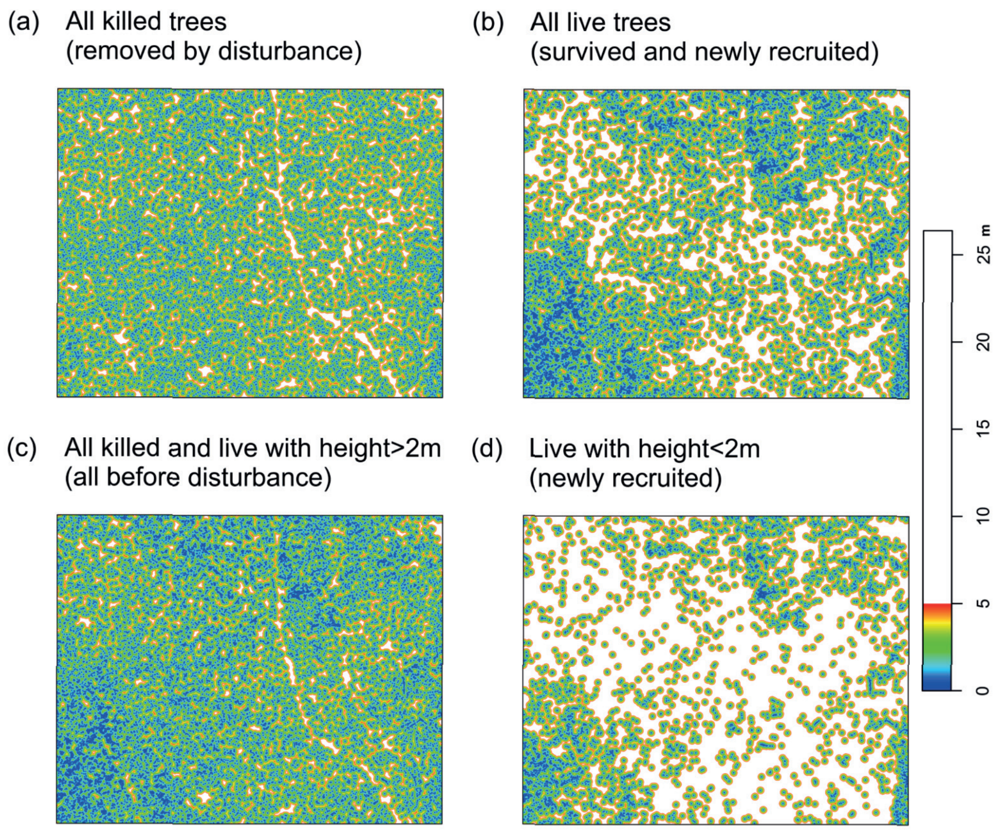

Fig 4. The distance of each pixel from the nearest recorded individual by a colour scale for (a) trees removed by a disturbance, (b) survived the disturbance and newly recruited, (c) all trees before disturbance and (d) only newly recruited trees. A colour scale of up to 5 metres from the nearest individual. White areas have a distance to the nearest individual larger than 5 meters. The state border between Germany and Czech Republic is shown as a white curve in pictures illustrating the pre-disturbance state (a and c), as the border line was artificially kept treeless. The disturbance changed treeless space distribution and the state border disappeared.

precipitation (Nováková 2018). In European mountainous area, the regeneration density decreases with altitude due to lowering of the temperature (Vorčák et al. 2006). In some kinds of forests the synergistic effect of climate warming and a canopy-removing disturbance can cause partial conversion of forest to non-forest ecosystems for some prolonged periods (Donato et al. 2016). However, change to non-forest ecosystems is very unlikely in an area of mountain spruce forests. The tree spatial pattern in these types of forests showed high resilience to stand-replacing disturbance (Wild et al. 2014). Regeneration in sufficient numbers is highly clustered around trees and on other favourable microsites.

The fact that the new post-disturbance generation of the forest has a significantly more heterogeneous structure has many positive consequences. First, the large spatial variability in tree regeneration after a disturbance delays and dampens future bark beetle outbreaks (Seidl et al. 2016). Second, tree spatial variability promotes forest biodiversity. Many red-listed forest species demand open conditions (Winter et al. 2015). And third, the spatial heterogeneous forest with its open spaces has greater aesthetic value (Gundersen & Frivold 2008).

Conclusions

Our established 20 ha plot has been the first large-scale plot in a natural subalpine Norway spruce forest. We had never had a chance to study this type of forest on such a scale. Also the location of the plot is unique, on the border of two countries and two national parks. The site is situated in core zones where no management is applied, in an area more than 20 years after bark beetle outbreak and death of mature stands. Our current data from the first census has already shown that disturbances play crucial role in shaping the forests in the Bohemian Forest Ecosystem and also the regeneration pattern in part of the national parks left to natural development after large scale disturbances by wind and bark beetle was shown. The results from the first census already show that the regeneration after disturbances has altered the forest structure and the newly established forest hides previous effect of the state border. The new forest is more open, but there is regeneration present throughout the whole plot. First census was done in 2018 and brought us very important information about changes in forest structure before and after disturbances. The cross-border plot will be measured again in five years.

In addition to this information the area will serve for a wide range of research. LIDAR scanning was done in 2017. Microclimatic monitoring and vegetation surveys are in progress. The results from the plot can be then used for guiding sustainable forest management, natural resource policies and to monitor the impacts of global climate change. We are also open to cooperate on further research with other research organizations.

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