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Response of mountain *Picea abies* forests to stand-replacing bark beetle outbreaks: neighbourhood effects lead to self-replacement

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Summary

1. Large, severe disturbances drive many forest ecosystems over the long term, but pose management uncertainties when human experience with them is limited. Recent continent-scale outbreaks of bark beetles across the temperate Northern Hemisphere have raised major concerns as to whether coniferous forests will regenerate back towards pre-outbreak condition and meet possible reforestation objectives. To date, however, analyses of post-outbreak regeneration across broad spatial and temporal scales have been rare, and entirely lacking for many regions.

2. Following a series of large, severe (~99% overstorey mortality) outbreaks of spruce bark beetles *Ips typographus* in Central Europe, we capitalized on an extensive forest inventory data set (n = 615 plots across ~7000 ha) to evaluate regeneration dynamics in Norway spruce *Picea abies* forests across the Bohemian Forest Ecosystem (spanning Germany and the Czech Republic). We asked whether neighbourhood effects (conspecific advance regeneration of spruce) would support prompt regeneration back to spruce forest, or whether the rapid, severe canopy mortality would overwhelm this influence and promote pioneer and broadleaf species. We tracked 15 years of post-outbreak regeneration dynamics (occupancy, density, height, composition) of all tree species and evaluated initial variations in successional pathway and structure.

3. Median tree regeneration density increased from ~400 trees ha^{-1} at the time of outbreak to ~2000 trees ha^{-1} within a decade, and occupancy increased from 58% to 76%. The increases were driven by spruce, which primarily recruited from advance regeneration, gradually occupying greater height classes. Only one broadleaf/pioneer species increased in relative proportion, for a brief (< 3-year) period before declining again. Nevertheless, both pure spruce and spruce–broadleaf stands were common and, coupled with wide variations in density and height, contributed to diverse early-successional structure.

4. *Synthesis and applications*. Contrary to common expectations, spruce beetle outbreaks in Central Europe effectively promoted their host in the long term. Outbreak-affected forests are naturally self-replacing even after severe canopy mortality, when positive neighbourhood effects of conspecific advance regeneration lead to rapid replacement of the dominant species. Thus, natural regeneration may be considered among the most effective ways to meet possible reforestation objectives in forests destroyed by beetles.

Key-words: advance regeneration, Bohemian Forest Ecosystem, disturbance ecology *Ips typographus*, Norway spruce, rowan, *Sorbus aucuparia*, spatiotemporal model

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Introduction

Large, severe disturbances are an integral part of many forested systems (Turner *et al*. 1998; Franklin *et al*. 2002; Swanson *et al*. 2011), but can present uncertainties for forest management when human experience with such events is limited (Dale *et al*. 1998). Understanding how large disturbances interface with management objectives is especially critical within the context of ongoing environmental change (Turner 2010). For example, much of the temperate Northern Hemisphere, including North America and Europe, has experienced continent-scale outbreaks of bark beetles (*Ips* and *Dendroctonus* spp.) in recent decades, affecting tens of millions of hectares of coniferous forests (Raffa *et al*. 2008; Aakala *et al*. 2011; Seidl, Schelhaas & Lexer 2011). Although large disturbances are not unprecedented for these regions (Turner *et al*. 1998; Dobrovolný & Brázdil 2003; Čada, Svoboda & Janda 2013), they have become a critical topic of debate and management uncertainty for forest managers and society (e.g. Müller 2011). Key questions centre on the capacity of forests to regenerate back towards pre-outbreak density and composition. Here, we address these questions through a lens of disturbance ecology theory, evaluating 15 years of post-outbreak natural regeneration dynamics in Norway spruce *Picea abies* (L.) Karst. forests across a large mountain landscape in Central Europe.

Common expectations following stand-replacing disturbances suggest that canopy mortality 'resets' succession by promoting shade-intolerant early seral species (e.g. Oliver & Larson 1996). For example, observations in managed spruce stands in Europe have suggested that pioneer or broadleaf associates including rowan *Sorbus aucuparia* L., willow *Salix* spp., aspen *Populus tremula* L. and birch *Betula* spp. may initially take over the site depending on treatment context (Fischer *et al*. 2002; Jonášová & Prach 2004; Pretzsch *et al*. 2015), leading to a perception of delayed or indirect succession to spruce forest. In contrast, a few studies in unmanaged forests suggest that, in the absence of intervention, spruce regeneration after such events is probable (Jonášová & Prach 2004; Kupferschmid *et al*. 2006; Svoboda *et al*. 2010; Wild *et al*. 2014). However, these small-scale studies have been limited to a few years following disturbance; no studies have tracked post-outbreak regeneration over relatively long time periods and large landscapes.

Frelich & Reich (1999) posed a broadly applicable general disturbance theory that relates how disturbance type and severity interact with autecological traits of canopy species ('neighbourhood effects') to determine long-term forest composition. The direction of neighbourhood effects (positive, neutral, negative feedback) is determined by characteristics of the dominant overstorey tree that influence whether it can replace itself at the time of disturbance. This theory recognizes two types of neighbourhood effects: overstorey–understorey relationships, and disturbance-activated effects that may interact with disturbance severity to control long-term stability or succession of species composition. With respect to Norway spruce, positive neighbourhood effects based on overstorey–understorey relations, like the ability to persist as shade-tolerant advance regeneration, increase the likelihood of spruce replacing itself quickly following disturbance. Similarly, disturbance types/severities that leave the understorey intact are more likely to promote stability in forest composition over time compared to disturbances such as stand-replacing fires, which create mineral soil conditions conducive to the establishment of early-successional species (Frelich & Reich 1999).

Norway spruce appears well-suited to positive neighbourhood effects, but alternative pathways involving early dominance by other, pioneer species are also possible. Like many *Picea* species, reproductive potential of Norway spruce is tied to seed rain frequency and intensity as influenced by mast years and distance to surviving mature trees, and early seed-bearing trees within a disturbed patch (LePage *et al*. 2000; Hanssen 2003; Martínez *et al*. 2013). Relatively high shade tolerance allows spruce to reproduce under extant canopies, often at high densities, and potentially accede if canopy trees are killed (Bauer 2002; Svoboda *et al*. 2010; Wild *et al*. 2014). Alternatively, positive neighbourhood effects may be overwhelmed if disturbances are exceptionally severe (such as rapid, complete overstorey mortality) or if advance regeneration is patchy (Frelich & Reich 1999). Pioneering associates that can thrive in higher light conditions such as willow, aspen, birch and (to some degree) rowan may thus gain dominance due to relatively consistent seed crops and rapid initial height growth (Raspé, Findlay & Jacquemart 2000; Holeksa & Żywiec 2005; Żywiec *et al*. 2013) and then decrease over time as the canopy closes. The relative likelihood of these alternate pathways (direct vs. protracted spruce regeneration) has scarcely been evaluated over broad areas in natural forests of Central Europe.

Norway spruce forests cover much of the montane zone of Central and Eastern Europe and provide an important test bed for these fundamental theories. Wind and bark beetles are the two most important disturbance agents in these regions (Seidl, Schelhaas & Lexer 2011; Brůna *et al*. 2013; Čada, Svoboda & Janda 2013). In the last 30 years, a combination of several warm years, a regional abundance of mature, spruce-dominated forests, and large wind-throw events resulted in an extensive outbreak of the spruce bark beetle *Ips typographus* L. (Lausch, Fahse & Heurich 2011; Seidl, Schelhaas & Lexer 2011; Svoboda *et al*. 2012). From 1996 to 2000, the Bohemian region along the German–Czech border experienced virtually 100% overstorey mortality across >10 000 hectares (Fig. 1; Lausch, Fahse & Heurich 2011). This near-complete mortality differs from most North American bark beetle outbreaks, which commonly range from ~50 to 80% mortality (e.g. Diskin *et al*.

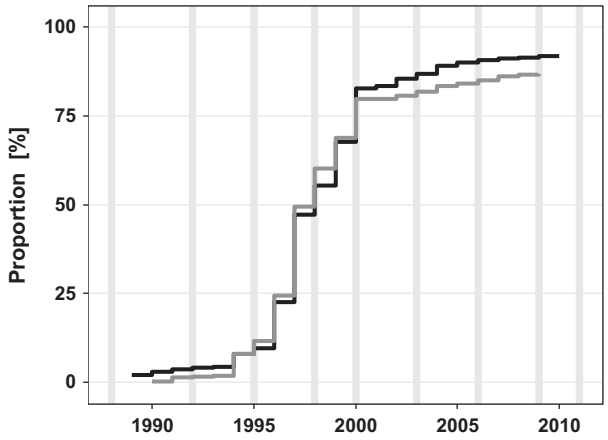

Fig. 1. Progress of canopy dieback due to bark beetle infestation in the Bavarian Forest National Park portion of the study region. Values are the cumulative proportion of infested area to total area (black line) and the number of infested inventory plots to total number of inventory plots (dark grey). Vertical grey lines indicate mast seed events of spruce (M. Heurich, unpublished data).

2011; Donato *et al.* 2013b); thus, it represents an important landscape characterizing the extremes of insect-caused disturbance severity.

In this study, we combined two extensive forest inventory data sets collected from two large protected areas with limited historical human management, Bavarian Forest National Park (Germany) and Šumava National Park (Czech Republic) – hereafter 'Bohemian Forest Ecosystem' – to evaluate broad-scale post-outbreak regeneration in Norway spruce-dominated forests. Our objective was to evaluate the degree to which predictions from neighbourhood effect theory (self-replacement of spruce) were born out in this exceptionally severe and large-scale canopy dieback, and to expand the global scope of post-outbreak regeneration studies which have so far focused on North America (Boggs *et al.* 2008; DeRose & Long 2010; Diskin *et al.* 2011; Donato *et al.* 2013a). Our study builds on previous work (e.g. Jonášová & Prach 2004; Kupferschmid *et al.* 2006; Svoboda *et al.* 2010; Wild *et al.* 2014) by being the first to evaluate regeneration dynamics across a broad spatial extent that corresponds with that of the recent outbreaks. We assessed 15-year trends in regenerating tree density (central tendency, variability), occupancy, growth and co-dominance of associate pioneer/broadleaf species. Specifically, we asked whether spruce was rapidly self-replacing as predicted by theory, or alternatively whether positive neighbourhood effects could be overwhelmed by the extreme severity of the outbreak or highly patchy spruce regeneration, allowing co-dominance or dominance in the short term by pioneer/broadleaf species. Evaluating these questions provides an immediately relevant application of a central forest dynamics theory and informs management objectives for reforestation of extensively disturbed landscapes such as those in Central Europe.

Materials and methods

STUDY AREA

The Bohemian Forest Ecosystem is located in the border region of southeast Germany and southwest Czech Republic (48°57′N 13°26′E) covering 920 km². We focused on elevations, between 1100 and 1453 m a.s.l. The study area is a broad ridge–plateau (13 917 ha) between the peaks Großer Rachel (1453 m a.s.l.), Lusen (1373 m a.s.l.) and Černá hora (1315 m a.s.l.) (Fig. 2).

Climatically, the Bohemian Forest Ecosystem lies in the transition zone of Atlantic and continental influences (Elling *et al.* 1987). In the higher elevations (>1100 m a.s.l), a cold mountain climate prevails with mean annual temperature of ~4 °C and annual precipitation of ~1800 mm. Snow cover can persist up to half a year. The region is underlain by granite and gneiss bedrock; soils are nutrient-poor, with cambisols, (crypto)podzols and organic soils being the most common.

Vegetation cover at upper elevations consists of acidophilic Norway spruce-dominated montane to subalpine forests, belonging to the *Calamagrostio–Piceetum* phytosociological group (Ewald *et al.* 2011). Tree species composition of mature stands throughout the study area was dominated by spruce (98% by stem density), followed by European beech *Fagus sylvatica* L. (1·2%), at lower elevations, and rowan (0·4%) and other species (*Acer pseudoplatanus* L., aspen, *Abies alba* Mill., and birch) in lesser amounts (Heurich 2001; Svoboda *et al.* 2010). The most important pioneer species include aspen, birch and willow. Rowan, while more plastic in shade tolerance, can be an important colonizer of forest gaps if parent trees and/or seed dispersal agents (e.g. birds) are sufficient (Raspé, Findlay & Jacquemart 2000; Żywiec & Ledwoń 2008; Żywiec *et al.* 2013).

DISTURBANCE HISTORY

Human impact on forests in the study area has been relatively low. Windstorms followed by bark beetle outbreaks have frequently disturbed forests in this region (Svoboda *et al.* 2012; Brůna *et al.* 2013; Čada, Svoboda & Janda 2013). The present forest represents a mosaic of selectively logged and unlogged stands of which most parts originated after a moderate- to

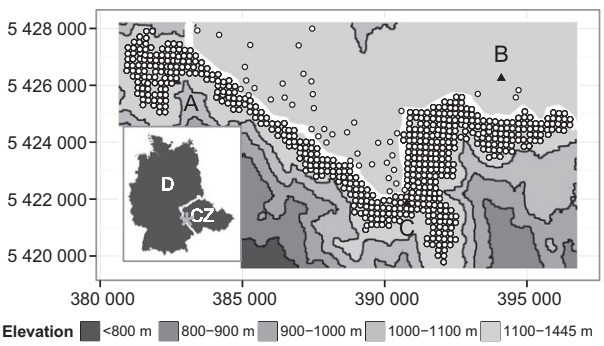

Fig. 2. The study area located along the border (white line) between Germany (D) and Czech Republic (CZ) at elevations exceeding 1100 m a.s.l. White points indicate the location of sampled plots. Black triangles indicate the three peaks that delineate the study area: Großer Rachel (A), Černá hora (B) and Lusen (C). Coordinates refer to UTM WGS 1984.

high-severity disturbance in the mid-19th century (Heurich & Englmaier 2010). According to National Park principles, there has been no forest management in core protection zones, since 1970 in Germany and since 1991 in Czech Republic. Both National Parks were established by ~1990; therefore, we have a unique opportunity to quantify the natural regeneration response to a major *I. typographus* outbreak. The current outbreak began in the 1980s and peaked in 1996–2000, causing mortality of canopy trees on more than 10 000 ha (Fig. 1; Lausch, Fahse & Heurich 2011). Prior to the outbreak, mean mature spruce forest basal area was 46 m^2 ha^{-1} basal area, and overstorey tree density was 262 stems ha^{-1} (median); after the outbreak, basal area was reduced to 2·5 m^2 ha^{-1}, none of which was in the overstorey (see Table S1 in Supporting Information). The age of disturbed stands averaged ~190 years, with large variation across the landscape (V. Čada, unpublished data; Svoboda *et al*. 2012; Čada, Svoboda & Janda 2013).

REGENERATION SAMPLING

We combined two regeneration survey data sets, one from each National park (615 total plots). The German data set included six measurements through time (1996, 1998, 2000, 2002, 2005 and 2011) on each of 572 plots on a systematic 200 × 200 m grid following the standard inventory method (Heurich 2009). Species and height of regenerating trees were recorded within concentric circles whose size depended on the diameter at breast height (d.b.h.) of the trees: trees with d.b.h. <6 cm but >10 cm tall were counted on 25 m², trees with d.b.h. from 6 to 11 cm were counted on 50 m², and trees with d.b.h. from 12 to 29 cm were counted on 150 m² (all classes could contain trees <500 cm tall).

The Czech data included 43 intensively measured plots preferentially located in unmanaged forests of the study area; these do not have temporal replications, but contribute to enhanced spatial representation of post-outbreak regeneration across the region. Sampling occurred from 2008 to 2011 and followed the inventory method of Černý *et al.* (2004): species, height and d.b.h. of regeneration trees were recorded within two non-concentric circles: all trees taller than 10 cm and with d.b.h. <7 cm were counted within a circle of 28·3 m², and trees with d.b.h. from 7 to 29·9 cm were counted within a circle of 154 m².

DATA ANALYSIS

Each survey on a plot is subsequently referred to as a sample. Trees between 10 and 500 cm height were considered regeneration (very few trees >500 cm survived the outbreak), and based on the reference circle area, count data were calculated to regeneration densities and corrected by inclination.

The beetle outbreak was not temporally synchronous (Fig. 1), so we used colour-infrared aerial photography as described in Heurich *et al.* (2010) (see also Kautz *et al.* 2011). Aerial surveys for infestations were conducted each year between July and October, starting in 1988. Analogue images taken before 2003 were digitized while a digital sensor was used afterwards. Spatial resolution of the photographs ranged from ~0·2 to 1 m. Spatial distribution of infested areas was delineated by visual interpretation. A minimum threshold of five trees showing foliage deterioration was used to classify an area as 'infested'. In a 50 × 50 m raster, we calculated the percentage of infested area for each cell. The year in which >50% (>1250 m²) of the raster cell area was infested was taken as the year of canopy mortality, and we assigned a unique time-since-canopy-mortality (defined as sampling year minus year of mortality) to each sample measurement within the raster cell. Sampled plots within raster cells with an infested area <50% were assigned to an age of 0, and putatively represent the regeneration layer immediately prior to the beetle outbreak (individuals >10 cm in height). Analysis was restricted to measurements with a maximum age of 15 years because of low replication in older years, resulting in 3412 samples on 609 plots.

To assess overall trends and variability in post-outbreak regeneration, we tabulated total regeneration densities (stems ha^{-1}) and frequencies (proportion of plots occupied) for the pre-outbreak condition (age 0) and post-outbreak time periods (1- to 5-, 6 to 10- and 11- to 15-year groups). Additionally, species-specific responses to spruce mortality were assessed by plotting regeneration densities over the entire time-since-disturbance interval (15 years). The criterion for support of positive neighbourhood effects was continued population dominance of spruce relative to other species; the criterion for rejection was dominance or co-dominance by any of the pioneer species.

We applied spatiotemporal regression models to assess the temporal response of species-specific and height-specific regeneration abundance to the beetle outbreak. We used a generalized additive mixed model (GAMM) to fit a linear combination of nonparametric smoothing functions of predictor variables while considering random effects (Wood 2006), which allowed us to incorporate variance in space and the autocorrelation associated with repeated measurements. The regression model is given by:

$$Y_{ij} \sim \text{Bernoulli}(1, \pi_{ij})$$

$$\Pr(Y_{ij}) = \pi_{ij}$$

$$\text{logit}(\pi_{ij}) = \alpha + f(\text{space}_{ij}) + f(\text{time}_{ij}) + \varepsilon_j$$

where Y_{ij} denotes the response of sample i on plot j and is a realization of the Bernoulli distribution given by probability π_{ij} and $n_{ij} = 1$ independent trials. The probability π_{ij} is a linear combination of the model intercept α, a function of space ($f(\text{space}_{ij})$) and a function of time ($f(\text{time}_{ij})$). The nonparametric smoothing functions were implemented by a two-dimensional regression spline over the spatial coordinates of each plot ($f(\text{space}_{ij})$) and, in the case of $f(\text{time}_{ij})$, a thin plate regression spline of time-since-canopy-mortality. For the repeated measurements on the German side, each sample site had a random effect added (ε_j) to account for temporal dependence. The predictor term was linked by the logit function to π_{ij}. Parameters were estimated by Laplace approximation.

We evaluated two different responses: (i) a species-specific response to assess relative species dominance after the outbreak, and (ii) a height-growth response to assess the potential development of the regeneration layer after the outbreak. For the former, we divided regeneration densities into density of spruce and total density of other species combined and then applied a GAMM with the proportion of both groups as the response variable. An analogous model was fitted for rowan. All other species observed in the plots were too rare to be modelled. For the second, we defined three density thresholds and fit models for the proportion of samples reaching this density threshold. Target thresholds were (i) 0 stems ha^{-1} in order to model presence–absence; (ii) 500 stems ha^{-1}, which represents the typical density of an old-growth spruce forest in the study region; and (iii)

1500 stems ha^{-1}, which conservatively assumes a ~30% survival rate (Rammig *et al.* 2007) to reach the old-growth density level. The regeneration density models were applied on three data subsets: (i) the entire data set (>10 cm); (ii) individuals of intermediate height (>100 cm); and (iii) the tallest individuals that will likely be the first to contribute to the future canopy layer (>300 cm).

STAND STRUCTURE ANALYSIS

We evaluated basic relationships between species composition, stand density and height structure in order to elucidate apparent variations in early structural development. Using data from 11–15 years post-dieback (the latest stage of development), we computed the relative frequency of plots falling into each of four compositional classes (spruce only, spruce–broadleaf mix, broadleaf only and neither present). We compared the first three classes in terms of tree density, mean height and the range of heights within each plot. Height class distributions of regenerating trees were calculated for pre-disturbance samples and three post-outbreak periods (1–5, 6–10 and 11–15 years). For all data analyses and graphical displays, we used R statistical software (R Core Team 2014) with extension packages *gamm4* (Wood & Scheipl 2013) and *ggplot2* (Wickham 2009).

Results

TEMPORAL TRENDS IN REGENERATION DENSITY AND COMPOSITION

Stem density and frequency of stocking increased following the beetle outbreak. Prior to the outbreak (age class 0), regeneration was present in 58% of plots; this increased to 64%, 71% and 76% at five, ten and 15 years, respectively (Table 1). Median regeneration densities increased fivefold, from ~400 stems ha^{-1} pre-outbreak to ~2000 stems ha^{-1} nearly a decade later (Table 1). These increases were driven almost entirely by rapid recruitment of spruce (Fig. 3). Although mean spruce establishment was variable, and low for the first 5 years, after the fifth post-outbreak year it had doubled in density compared to other species (Fig. 3). Non-spruce species were dominated by rowan, which remained stable in density throughout the post-disturbance period. Other fast-growing, pioneer species including birch, aspen and willow were only rarely detected in the first 12 years post-disturbance. In the last 3 years, mean values increase due to high beech regeneration densities (>5000 stems ha^{-1}) on few lower elevation sites (n = 6).

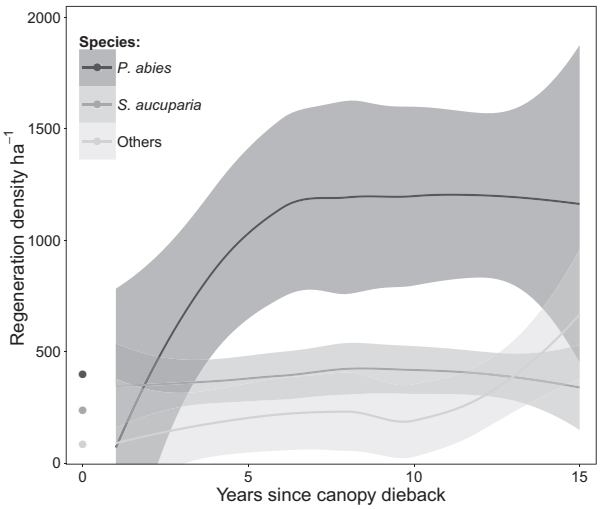

Fig. 3. Temporal trends in regeneration density showing pre-outbreak (year 0) and post-outbreak (1–15) periods in the Bohemian Forest Ecosystem. Data are based on medians for spruce and means for other species because medians were zero for the latter; these data are shown for visual representation of temporal trends only and not quantitative analysis. Smoothed trend lines were calculated by local cubic regression fitting. Semi-transparent grey shades delineate 95% confidence limits.

Temporal changes in regeneration composition over the first 15 years after outbreak showed sharply contrasting trends for the two most abundant species, spruce and rowan. While the relative proportion of rowan increased initially following canopy opening, it strongly decreased soon afterwards and the temporal effect became negative by year three (Fig. 4). Conversely, spruce decreased slightly in proportion for the first few years, followed by a rapid increase up to year 10 (Fig. 4). Afterwards, the increase in proportion of spruce fluctuated but stayed well above 0, indicating increasing spruce dominance of the future forest.

REGENERATION VARIABILITY AND STAND STRUCTURE

Variability in stand structure at the plot scale was high in terms of density, composition and height profiles.

Table 1. Temporal trends in occupancy of plots by regenerating trees (i.e. frequency or stocking) and regeneration density statistics, for all species. Age classes indicate pre-outbreak (0) and different time periods after canopy dieback

	Occupancy		Regeneration densities (trees ha^{-1})			
Age (Years)	# of samples	% Occupied by regeneration	1st quartile	Median	3rd quartile	Max
0	1289	58	0	405	2295	95 536
1–5	1105	64	0	811	3284	282 372
6–10	550	71	0	1360	4772	170 878
11–15	468	76	355	1972	5616	79 985

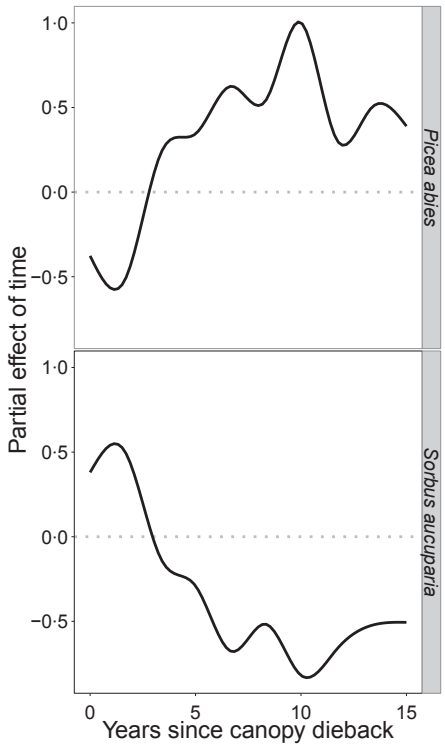

Fig. 4. The effect of time since canopy dieback (smoothed) on the relative proportion of spruce (top) and rowan (bottom) in the sample plots. The partial effect is in units of the linear predictors in the GLMM. The partial effect describes the magnitude of change for each species where increasing dominance by one species is indicated by positive values, 0 indicates no change, and negative values indicate a decreasing proportion for that species. Confidence intervals are very close to the estimates and not displayed.

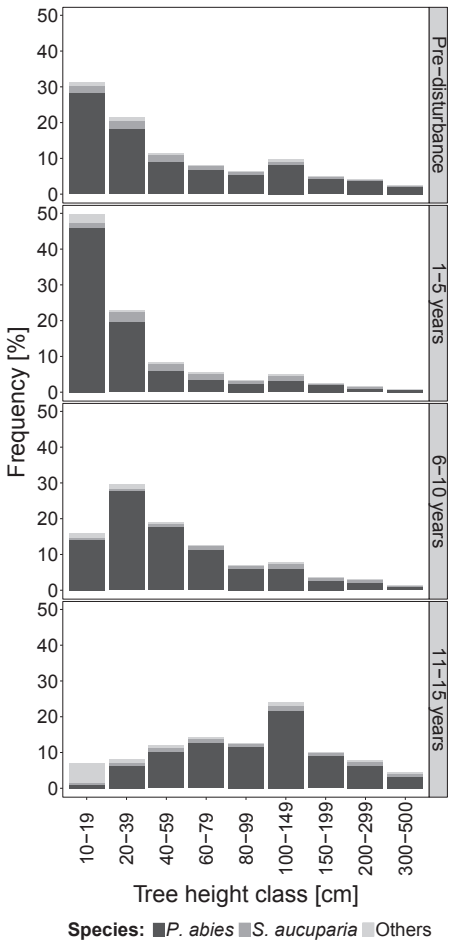

Fig. 5. Height distribution of regenerating tree species before outbreak ('pre-disturbance') and in three subsequent time periods after canopy dieback. Values indicate relative frequencies of trees in each height class based on densities.

Densities ranged over six orders of magnitude within the first five years post-outbreak, narrowing to four orders of magnitude by 11–15 years (Table 1), suggesting fine-scale clustering in tree density. Assessed by composition class, stocked plots were split evenly between spruce only (41% of plots) and spruce–broadleaf mix (31%), with fewer plots containing only broadleaves (4%) (Table 2). Spruce–broadleaf mix was characterized by the highest but most variable tree densities, and greater fine-scale variation in tree heights (Table 2). The broadleaf-only class was characterized by the lowest densities, heights and height variability, post-outbreak (Table 2). Tree height distributions showed not only a shift from shorter to taller trees over time (predominance of trees <20 cm tall before and shortly after disturbance vs. trees 100–149 cm tall by 11–15 years), but also large variation in heights and more equitable representation of height classes with time-since-disturbance (Fig. 5).

Increases in occupancy (i.e. frequency or stocking) differed depending on specific height and density thresholds

Table 2. Relative proportion, density and tree height profile of plots by composition class, at 10–15 years after canopy dieback (median, 1st–3rd quartile)

Composition class	% of plots	Regeneration density (trees ha^{-1})	Tree height within plot (cm)	Range of tree height within plot* (cm)
Spruce only	40·4	2028 (805–4812)	112 (73–170)	87 (15–160)
Spruce + broadleaf mix	31·6	6008 (2893–11 130)	113 (77–170)	130 (84–221)
Broadleaves only	4·1	480 (416–1211)	90 (50–147)	0 (0–34)
Neither present	23·9	0	–	–

*Height range is computed as the height difference between the 10th and 90th percentile tall trees within each plot, to avoid emphasis of outliers.

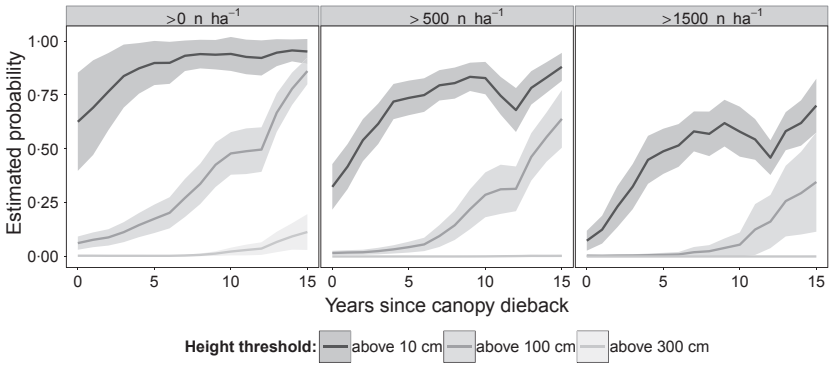

Fig. 6. Estimated probability for each sample to reach a certain density threshold (panels) for trees with a specific minimum height (lines, see legend). Shading indicates pointwise 95% confidence intervals. Site-specific random effects were excluded.

(Fig. 6). For all regeneration of any size (10–500 cm height), the probability of occurrence at >0 stems ha^{-1} was initially 60% and increased to a plateau of over 90% by year 10. At a threshold of 500 stems ha^{-1}, initial probability of occurrence of trees > 10 cm was just ~30%, but by year 10 increased to ~80%. At the most conservative threshold (1500 stems ha^{-1}), initial post-outbreak probability of occurrence was only ~15%, but increased to ~60% in a decade (Fig. 6).

Discussion

Tree regeneration after a severe *I. typographus* outbreak in the Bohemian Forest Ecosystem was driven by strong positive neighbourhood effects that lead to rapid regeneration of the canopy dominant, Norway spruce. Our alternative hypothesis that the extreme severity of the outbreak (~99% canopy mortality) or insufficient advance regeneration could overwhelm neighbourhood effects (conspecific advance regeneration potential), and allow initial dominance by early-successional and broadleaf species, was largely unsupported. Rather, there was an immediate positive response in spruce regeneration after canopy opening that progressed for at least 15 years, independent from site-to-site variation. The relative proportion of spruce in the community initially declined for 2 years before increasing over the rest of the 15-year period, whereas the only other prevalent species, rowan, briefly increased in proportion for 2 years before decreasing over years 3–15. There was a large variation in regeneration density, composition and height structure, suggesting a diversity of successional pathways during an extended pre-canopy closure period.

NEIGHBOURHOOD EFFECTS

That a large-scale spruce beetle outbreak, resulting in near-complete mortality of overstorey trees, could maintain spruce dominance is initially counterintuitive. However, this observation is consistent with the few related studies conducted over smaller spatial and temporal scales (Jonášová & Prach 2004; Kupferschmid *et al.* 2006) and suggests some generalities. A key mechanism by which canopy-removing disturbance benefits spruce is release of a conspecific understorey seedling bank that exists in mature forests and was not disturbed by the outbreak – that is a positive neighbourhood effect (Frelich & Reich 1999). When the understorey is undisturbed, as in most beetle outbreaks, this effect is not overwhelmed even when canopy removal severity approaches 100%. Regardless of the relative shade tolerance of spruce, median advance regeneration densities in this study (400 trees ha^{-1}; Table 1, Fig. 3) were similar to that of the mature overstorey that was killed (500 trees ha^{-1}; Svoboda *et al.* 2010). The extreme severity of the outbreak was apparently insufficient, by itself, to encourage pioneer species to overtake spruce advance regeneration or to exclude additional post-outbreak spruce recruitment.

Consistent with predictions from the neighbourhood effect theory, there was no shift in dominance to shade-intolerant, pioneer species such as birch, willow and aspen. These species were a minor and patchy component of the pre-disturbance forest in both the advance regeneration and canopy layers, but were abundant enough to provide seed sources in portions of the landscape. Despite the ~100% mortality of the spruce overstorey, the outbreak generated little to no exposed mineral soil – the preferred substrate for pioneer species (Jonášová & Prach 2004). Rowan was the only broadleaf species that showed a brief increase in relative proportion after the outbreak (Fig. 4), but this was related to its presence as advance regeneration (Fig. 3), and it quickly decreased again with the massive recruitment of spruce. This dynamic differs from other canopy disturbances such as wind-throw, which leaves intact understories but also exposes new soil via tip-up mounds and thus supports establishment of pioneer species (e.g. *Betula* spp.; Fischer & Fischer 2012); or stand-replacing wildfires which consume understories and expose mineral soil, creating opportunities for pioneers or invader/evader species (e.g. Ilisson & Chen 2009; Johnstone *et al.* 2010). We note that our analysis was not intended to provide a test of local spatial variation or gradients in neighbourhood effects, because there was essentially only one neighbourhood type in these forests: near

spruce trees. Rather, these data allow evaluation of whether predictions from the theory held for this large-scale empirical example, and given the extreme nature of the canopy disturbance.

More broadly, Norway spruce forests in Central Europe share certain key characteristics with the most compositionally stable forest types on Earth, including, surprisingly, tropical forests which are typically characterized by a dominance of late-successional shade-tolerant species, low landscape abundance of pioneer components, and small- to medium-gap-phase recruitment dynamics between larger disturbances (Frelich & Reich 1999). These characteristics were all present prior to the spruce beetle outbreak in this study (Fig. 3, Svoboda *et al.* 2010, 2012) and were also observed by Boggs *et al.* (2008) in white spruce *Picea glauca* forests in Alaska. By contrast, in other forest types with more variable understories that may differ from the overstorey (host) species, bark beetle *Dendroctonus* spp. outbreaks can shift composition by accelerating succession towards more shade-tolerant species (e.g. *Abies lasiocarpa* in forests previously dominated by *Pinus contorta* or *Picea engelmannii*) (Veblen *et al.* 1991; DeRose & Long 2010; Diskin *et al.* 2011). To reiterate, i) abundant advance regeneration of the overstorey species, ii) a disturbance that leaves the ground and understorey intact, and iii) less propagule source for pioneer species, in combination, lend to temporal stability of Norway spruce composition in spruce forests, even through extreme-severity canopy-removing disturbances.

The increasing spruce density over time (Table 1, Figs 3 and 6) indicates that new post-disturbance recruitment was also an important regeneration mechanism. The source and germination timing of this component cannot be known with certainty, as the inventory data include seedlings >10 cm height only; thus, we describe post-outbreak density increases as new recruitment to 10 cm, not necessarily new germination or establishment. In Central and Eastern European spruce forests, seedlings below this height experience high mortality and turnover, but often form a consistent seedling bank exceeding 10 000 ha^{-1} (Svoboda *et al.* 2010). These seedlings can take 5–10 years to exceed 10 cm (Bauer 2002), suggesting that the majority of the recruitment we quantified was likely the release of seedlings dating before or during the outbreak. This interpretation is further supported by the lack of new recruitment of the smallest height class after the first few years (Fig. 5). Semi-regular spruce mast events at 2- to 4-year intervals (Fig. 1) may also contribute new post-disturbance cohorts, but the shape of the recruitment curve (Fig. 6) suggests that post-outbreak seeding was not a primary driver of regeneration.

STRUCTURAL VARIATION AND DEVELOPMENT

The data clearly show that spruce is regenerating in a robust fashion and ought to dominate the forest again, but the process of complete spruce occupation will not be instantaneous (Fig. 5). As increasingly recognized for temperate forests (e.g. Franklin *et al.* 2002; Swanson *et al.* 2011; Tepley, Swanson & Spies 2014), a multidecade establishment period is the normal developmental pathway for Central and Eastern European spruce forests (Svoboda *et al.* 2012, 2014). Fifteen years following outbreak, 28% of plots were yet to be occupied by spruce (Table 2), indicating gaps in spruce regeneration at small scales. Height probabilities showed gradual, ongoing recruitment (Figs 5 and 6). Moreover, stocked plots spanned several orders of magnitude in terms of density and were split roughly evenly between pure spruce and spruce–broadleaf composition.

In combination, the variability in regeneration structure and composition suggests a diversity of successional pathways. Slow height growth and gradual in-filling in parts of the landscape allow an early seral period prior to tree canopy closure, which is increasingly recognized as a structurally complex and functionally rich stage of forest development (Swanson *et al.* 2011). Norway spruce regeneration also typically occurs in highly clustered spatial patterns, due in part to 'safe' microsite fidelity such as dead wood or stem bases (Bače *et al.* 2012; Wild *et al.* 2014); thus, neighbourhood effects perpetuate not only stand composition but also spatial structure through severe canopy mortality. The regenerating forests studied here possess many of the structural features ascribed to diverse early seral forest communities, including abundant legacy dead wood, mixing of conifer and broadleaf vegetation, and horizontal gaps and clumps (Donato, Campbell & Franklin 2012). The greater within-stand diversity in tree heights in spruce–broadleaf mix plots is consistent with the theory that mixing and competition between life forms can increase early vertical complexity (Donato, Campbell & Franklin 2012). Such early seral communities support a high and unique biodiversity (Lehnert *et al.* 2013; Beudert *et al.* 2015) and are rare in Central European landscapes.

CONCLUSIONS

Studies of natural post-disturbance regeneration, a rare opportunity in Central and Eastern Europe, serve as important benchmarks for conservation, ecology and forest management. Results from this study have implications for both natural and managed mountain spruce forests. In terms of meeting reforestation management objectives, the regeneration densities we observed (median 2000 trees ha^{-1}) are well above those observed in mature to old-growth forests in this region (~500 trees ha^{-1}; Svoboda *et al.* 2014) and appear sufficient to return the system to mature forest cover over time – a primary objective for protected forest landscapes. We expect similar outcomes in other forests consisting of tree species with similar autecological profiles because the responses to the outbreak were based on ecological traits of the tree species and a generalizable effect of disturbance (overstorey mortality).

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Data accessibility

Data on regeneration tree measurements and sample site features are archived in the Dryad Digital Repository, entry http://dx.doi.org/10.5061/dryad.sq41r (Zeppenfeld *et al.* 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Comparison of stand structural characteristics before and after the bark beetle outbreak.

Appendix S1. Commented R-code for spatiotemporal model estimation including further variants of models.