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Long-term responses of canopy–understorey interactions to disturbance severity in primary *Picea abies* forests

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Abstract

Questions: How do canopy–understorey interactions respond to variation in disturbance severity over extended periods of time? For forests with different disturbance histories, do light availability and understorey cohort densities converge towards a common old-growth structure, or do historical legacies influence populations indefinitely?

Locations: Remnants of primary spruce (*Picea abies* (L.) Karst.) forests throughout Germany, Slovakia, Ukraine and Romania.

Methods: A disturbance history of >200 yr was reconstructed from 11 278 tree cores collected from forest plots ($n = 520$). Understorey tree densities of two size classes and hemispherical photo-based light availabilities were inventoried and modelled as functions of the severity of the main disturbance and time since the event.

Results: Variation in understorey tree densities had a hump-shaped distribution through time. Stem densities were approximately static in the least disturbed sites, and declined in relation to disturbance severity over approx. 100 yr. Similar to patterns of stem densities, initially high understorey light availability also reached a minimum at 100 yr, which indicated crown closure. Following this, light availability and stem densities both increased as stands transitioned from stem exclusion to understorey re-initiation. The effect of disturbance severity on understorey densities and patchiness in light availability persisted for >200 yr.

Conclusions: Long-term trends in canopy–understorey interactions validate current conceptual models of forest development. Furthermore, we empirically validate that these conceptual models generalized over gradients in disturbance severity. Higher disturbance sites exhibited a more even-aged character with more pronounced periods of stem exclusion, canopy closure and understorey re-initiation; forests with low-severity disturbance histories yielded a more stationary uneven-aged structure. The model identified the extent of variation in disturbance severity within which these *P. abies* forests are able to regenerate and retain their monospecific character, which is increasingly relevant as disturbance regimes continue to shift under global climate change.

Keywords
Bark beetle; Canopy openness; Disturbance regime; Mountain forest; Natural regeneration; *Picea abies*; Primary forest; Saplings and poles; Understorey light availability; Wind storms

Nomenclature
Kubát et al. (2002)

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Introduction

Canopy cover regulates understorey light availability and, consequently, the performance of the regenerating saplings that will eventually dominate forest canopies (e.g. Canham et al. 1990; Caspersen & Kobe 2001; Bače et al. 2015). Disturbances, like wind storms or insect outbreaks, reduce canopy cover, increase light transmission and can initiate population cycles whereby understorey cohorts increase in size to fill canopy gaps and are subsequently repopulated by incoming recruitment (Oliver 1980; Franklin et al. 2002). The majority of empirical research into canopy–understorey interactions deals with the initial responses of understorey populations to recent disturbances (e.g. Lang & Knight 1983; Nagel et al. 2006). However, developmental dynamics unfold over centuries (Kashian et al. 2005) and empirical investigations into the full cycle of understorey response and re-initiation are consequently rare.

Following a disturbance, forest structure transitions through a sequence of successional phases defined by developmental shifts in the constraints on recruitment, growth and mortality (Oliver 1980; Franklin et al. 2002). Canopy removal is accompanied by a pulse of seedling recruitment and increased sapling growth rates. In the stem exclusion phase, saplings compete to increase in size, density-dependent thinning becomes an important cause of mortality, and canopy closure occurs as light penetration to the forest floor is minimized (Assmann 1970). In the understorey re-initiation phase, occasional canopy tree deaths permit increased light penetration and the gradual repopulation of understorey cohorts (Cumming et al. 2000). The stand reaches the old-growth phase after long periods of low disturbance, where an approximately stationary uneven-aged structure develops to reflect continuous gap creation and recruitment (Peet & Christensen 1980; Coomes et al. 2003). Quantitative treatments of the entire developmental cycle are rare, but several features are necessary to parameterize key aspects of canopy–understorey interactions: the baseline densities of understorey cohorts at equilibrium, the duration of time between disturbance and canopy closure, and the relationship between post-canopy closure gap dynamics and understorey re-initiation. Furthermore, the conceptual model outlines the development of a single cohort in horizontally homogeneous conditions following complete canopy removal by a stand-replacing event; how long-term responses of development generalized over gradients in canopy removal, or disturbance severity, is poorly quantified (Romme et al. 1998; Kashian et al. 2005).

Variation in disturbance severity influences the magnitude, patchiness and duration of increased light availability (Liu & Hytteborn 1991; Nicotra et al. 1999) and, presumably, long-term understorey population dynamics. In simple monospecific cases, understorey populations will fluctuate in correspondence with canopy removal as more individuals are recruited into adult cohorts. Declining sapling densities due to out-going recruitment will be offset by incoming recruitment from recent germinants. Anticipating the outcomes of canopy–understorey dynamics among multiple competing species is likely to become more complicated, because gap size variation influences interspecific variation in growth and survival (Sipe & Bazzaz 1995). However, regeneration strategies evolve under the regularity of disturbance patterns and insulate populations against stark compositional transitions (Gutschick & BassiriRad 2003; Johnstone et al. 2016). For example, shade-tolerant conifers maintain cohorts of advanced regeneration that have a significant size advantage over dispersal-dependent species upon canopy removal (Messier et al. 1999). The capacity of regeneration strategies to promote self-replacement is limited to a range of post-disturbance conditions (i.e. gap size), but these thresholds are unspecified for many forest types (Johnstone et al. 2016; Kulakowski et al. 2017).

Our objective was to produce an empirical model of canopy–understorey interactions in monospecific *Picea abies* (L.) Karst temperate mountain forests that span the range of developmental phases invoked in standard conceptual models, and can also be generalized to variation in post-disturbance conditions. Dendroecological methods were used to reconstruct local disturbance histories in fragments of primary forests distributed throughout Central and Eastern Europe. Disturbance history reconstruction allowed sites to be stratified by disturbance severity and time since disturbance (Lorimer & Frelich 1989), and could be analysed as a chronosequence. Understorey light conditions, along with sapling and pole stem densities, were additionally inventoried to address the following questions:

1. How do understorey cohort densities change with time since disturbance? Do densities of understorey cohorts with different disturbance histories converge towards an old-growth phase (Peet & Christensen 1980; Kashian et al. 2005), or do sites with different histories diverge in terms of population structure?
2. Is the increase in light availability larger in magnitude over a longer period in more severely disturbed plots? How do light conditions change after canopy closure to influence understorey re-initiation?
3. Is there an effect of disturbance severity on the proliferation of other species, implying a limited ability of spruce to sustain monodominance? *Sorbus aucuparia* L. (rowan) is a common light-demanding understorey tree in the region, and is known to infiltrate large gaps and arrest the

development of *P. abies* stands (Hofgaard 1993; Żywiec et al. 2013).

Methods

Study site

Inventory plots were placed in remnants of primary forest throughout the Romanian, Slovakian and Ukrainian Carpathians and in the National Park Harz, Germany. Prior efforts have used tree-ring methods to empirically reconstruct the natural disturbance regime of these inventoried locations (e.g. Svoboda et al. 2014; Trotsiuk et al. 2014; Janda et al. 2017; Meigs et al. 2017). Study sites ranged in altitude from 1000 m (Germany) to 1700 m a.s.l. (Romania; Fig. 1). The average annual precipitation ranges from 800 to 1400 mm, and the annual temperature ranges from 2 to 4 °C (UNEP 2007). More detailed information about the study area is presented in Appendix S1. Satellite imagery, first-hand knowledge of local people and on-site inspections focused on signs of former human influence (e.g. cut stumps), were used to delineate polygons of primary forest fragments (15–300 ha); they were primarily in remote areas with minor human influence, such as where steep slopes restrict access for logging or grazing. More detailed information regarding the selection of primary forest fragments is presented in Appendix S2. In each polygon (henceforth stand), we placed six to 60, 1000 m^2 (or 500 m^2 in structurally homogenous stands with high stem densities; n = 90) circular plots using a stratified random design (Svoboda et al. 2014). In total, we established 520 plots in 31 stands. Norway spruce dominated tree species composition in the study area (99.6% of trees ≥10 cm DBH and 80.0% for regeneration ≥50 cm in height and <10 cm DBH), while rowan was also relatively abundant in the understorey layer (0.2% of trees ≥10 cm DBH and 17.9% for regeneration). Other rarer species included *Pinus cembra* L., *Abies alba* Mill., *Acer pseudoplatanus* L. and *Betula* spp. (in total 0.2% for trees ≥10 cm DBH and 2.1% for regeneration).

Data collection

Understorey tree densities were comprehensively inventoried from 2010 to 2014. All individuals ≥0.5 m in height within forest plots were identified to species, and densities were recorded for two height classes: saplings (height 0.5–1.3 m) and poles (height > 1.3 m and DBH < 10 cm). At each plot, six hemispherical photographs (one in the plot centre, and five distributed 12.1 m from the plot centre at 72° intervals around the plot) were taken 1.3 m above the ground using a circular fisheye lens (Sigma 4.5 mm F2.8 EX DC). The amount and variability of understorey light was analysed using WinSCANOPY software (Regent Instruments, Quebec, CA) using the 'openness' variable. The mean, maximum and coefficient of variation of openness were calculated for each plot, and they were used as response variables to detect mean, maximum and relative variability of light distribution in the understorey. The relative variability of light distribution is hereafter referred to as patchiness of light.

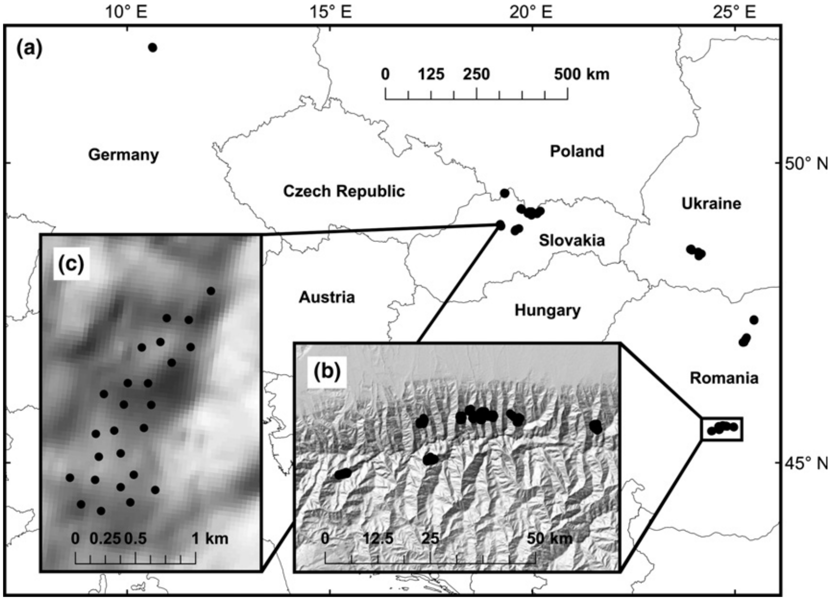

Fig. 1. Distribution of inventory plots at regional (**a**), mountain (**b**) and stand scales (**c**).

Dendrochronology and disturbance reconstruction

We randomly selected 15 or 25 (for 500-m^2 or 1000-m^2 plots, respectively) non-suppressed, live trees (i.e. trees with a significant portion of their crown projection receiving direct sunlight from above; Lorimer & Frelich 1989) per plot for the radial growth analysis and age determination. In rare cases, fewer trees were cored because less than 15–25 individuals were present. Suppressed trees were avoided because their growth patterns may lack information important for disturbance history reconstruction (Splechtna et al. 2005). All trees were cored at a height of 1 m above the ground. In total, 11 278 cores were used to reconstruct plot histories.

Increment cores were dried, cut with a core microtome, measured and cross-dated using standard dendrochronological methods (Speer 2010). Annual rings were measured to the nearest 0.1 mm using a stereomicroscope and Lintab™ sliding-stage measuring device in conjunction with TSAP-WIN™ software (www.rinntech.ds). Cores were initially cross-dated visually using the marker year approach (Speer 2010), and were then verified with PAST4 software (www.sciem.com) and, subsequently, COFECHA software.

Individual tree growth patterns were investigated to identify when individual trees were released from canopy suppression and recruited into the adult cohort. Two modes of canopy recruitment were considered: open-canopy recruitment and growth release. Open-canopy recruitment was indicated in trees with high initial growth rates. Mean growth rates of individuals from the time they were 4 cm DBH and over the following 5 yr were compared to a growth rate threshold. This threshold was determined by a logistic regression comparing tree ring-derived sapling growth rates, mean over 5 yr following 4 cm DBH, under closed canopies and among gaps of 500 m^2 ($N_{\text{suppressed}} = 46$, $N_{\text{not suppressed}} = 41$). Individuals with a mean growth rate exceeding 1.7 $mm \cdot yr^{-1}$ were categorized as open-canopy recruits (Svoboda et al. 2014).

To identify the release of individuals from canopy suppression, a set of growth rate changes was compiled and compared to a boundary line that conditions responses on formed growth rates (Black & Abrams 2003). Ten-year running means were estimated along ring-width series. The differences between adjacent 10-yr means were then calculated. The boundary line is an exponential function that models the upper limit of variation of percentage growth changes as a function of prior growth rates. This method scales the release criteria to pre-disturbance growth rates, which reduces the number of falsely detected releases (Black & Abrams 2003). We used a boundary line function calibrated for *P. abies* from trees throughout Central European spruce forests by Splechtna et al. (2005). Growth rate changes exceeding 20% of the boundary line value were treated as gap releases. We also decided that the detected growth pattern had to be sustained for at least 7 of the 10 yr used to calculate adjacent means (Fraver et al. 2009). Gap releases were only searched for during the interval when individuals were <25 cm DBH; trees >25 cm DBH were assumed to be in the canopy stratum (Lorimer & Frelich 1989).

Both releases types were converted to total canopy area disturbed in each decade (Lorimer & Frelich 1989). Crown radius was estimated for each cored tree and a regression was fit between crown area and DBH ($R^2 = 0.61$, $P < 0.001$, crown area = 0.4631 × DBH + 0.8948; Svoboda et al. 2014). Crown areas of released trees were summed for the decade of relese, and this quantity was divided by current plot-level crown areas to produce an estimate of proportion of crown area released in each decade (Lorimer & Frelich 1989). For a thorough description of disturbance history reconstructions, see Svoboda et al. (2014).

To account for the protracted nature of some disturbances and release tree responses, disturbance severity was further integrated over a running window of three decades, and local maxima in this smoothed disturbance profile were used as point estimates of disturbance severity; the largest local maximum was treated as a plot main disturbance (Svoboda et al. 2014). Years since the main disturbance were calculated as the year of data collection (2010–2014) minus the year of maximum severity. For recently disturbed plots, where the current canopy area disturbed was larger than dendrochronologically detected maximum disturbance severities, the severity was expressed by current canopy openness. Current canopy openness was calculated as the difference between mean canopy closure of the whole data set and current canopy closure of a given plot. Distributions of time since disturbance and disturbance severity across countries and stands are shown in Appendices S3 and S4.

Statistical analyses

Temporal patterns in stem density variation were investigated by modelling the coefficients of variation in log-transformed stem densities among time-since-disturbance classes (20 yr) using spline regressions. Independent spatial regression models were fitted to assess how spruce and rowan densities in the two different height classes, mean, maximum and variation of understorey light availability respond to both disturbance severity and the number of years since the main disturbance. We used a GAMM to fit a linear combination of smoothed functions of several predictor variables (plus one smooth interaction of time and severity), while additionally considering random spatial effects, which allowed us to account for systematic variability in space (Wood 2006). Altogether, four full models for regeneration densities (two species and two height categories) and three models for mean, maximum and variation of understorey light availability were used. For the *i*-th stand and *j*-th plot, we used the following model:

$$Y_{ij} \sim \mathrm{NB}(\mu_{ij}.P_{ij}, \theta); \text{for stem density}$$

$$Y_{ij} \sim N(\mu_{ij}.P_{ij}, \sigma_u^2); \text{for understorey light characteristics}$$

$$\begin{aligned}\log(\mu_{ij}) = \beta_0 + b_i + s_{\mathrm{loc}}(x_{ij}, y_{ij}) + s_{\mathrm{time}}(\mathrm{time}_{ij}) \\ + s_{\mathrm{severity}}(\mathrm{severity}_{ij}) \\ + s_{\mathrm{time*severity}}(\mathrm{time}_{ij}, \mathrm{severity}_{ij})\end{aligned}$$

$$b_i \sim N(0, \sigma_b^2)$$

Expected values of either log-transformed light or sampling quantities ($\log(u_{ij})$) were considered a function of several factors. A set of spatially variable functions (smoothed, penalized splines), including s_{loc}, reflects the smooth spatial trend; s_{time} reflects the (smooth) marginal effect of time since disturbance; s_{severity} reflects the (smooth) marginal effect of disturbance severity; and $s_{\mathrm{time*severity}}$ reflects the (smooth) interaction of time and severity (obtained as a tensor product spline). The vector b_i is a set of independent random effects for individual stands and β_0 is the model intercept; σ_b^2 is the variance among random effects. Observed densities were modelled as a negative binomial (NB), with a rate of u_{ij} and probability of success θ. Observed light values were modelled as a normal distribution with mean u_{ij} and variance σ_u^2. All parameters were estimated based on the optimization of the penalized likelihood function. P_{ij} is an offset applied to correct for variation in plot sizes. Means and standard deviations of variables used in the analyses are displayed in Appendix S5.

Results

Variation in regeneration densities

Variation in regeneration densities among plots increased during the first 100 yr after disturbance, and decreased within the next 100 yr for both height classes of spruce (Fig. 2). This unimodal relationship was confirmed by spline regression ($P = 0.001$, deviance explained = 86.4% for saplings; $P = 0.002$, deviance explained = 86.9% for poles).

Understorey light

The model for mean understorey light availability explained 54.7% of the deviance, with a significant spatial term ($P < 0.001$), random stand effect ($P = 0.026$) and time since disturbance effect ($P < 0.001$; Table 1). A spatial term ($P < 0.001$) and years since disturbance effect ($P < 0.001$) explained 52.9% of deviance in maximum light availability. The model for patchiness in light explained 37.4% of the deviance with a spatial term ($P = 0.024$), stand effect ($P < 0.001$), years since disturbance ($P < 0.001$), disturbance severity ($P = 0.001$) and the years × disturbance interaction ($P = 0.037$). The amount of understorey light decreased since the main disturbance, and remained at a

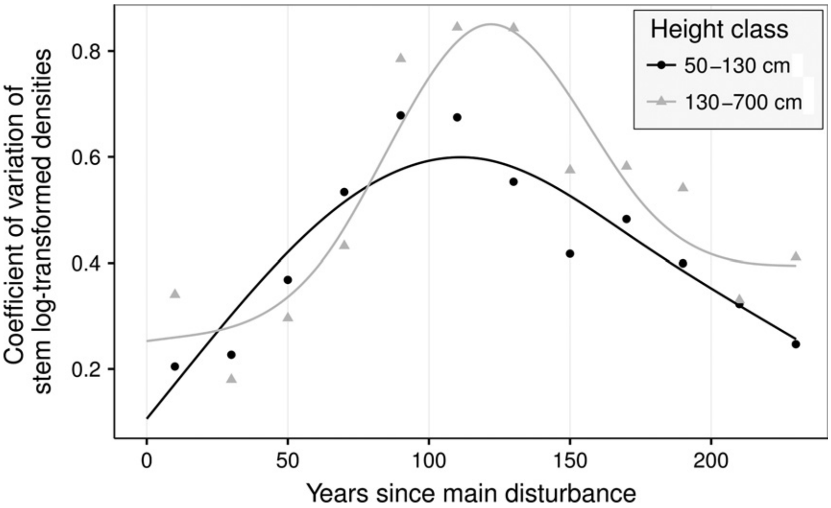

Fig. 2. Coefficients of variation in log-transformed spruce densities in different time-since-disturbance (20 yr) classes for two height classes of regeneration. The black line and circles represent height class 50–130 cm (saplings) and grey line with triangles represents height class 130–700 cm (poles). The points represent exact values and curves represent the spline regressions.

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Table 1. Results of GAMMs for influence of time since main disturbance, severity of the main disturbance and their interaction on tree densities and understorey light availability characteristics. The response variables for understorey light availability followed a Gaussian distribution, whereas a negative binomial distribution was appropriate for tree densities. The results displayed are: explanatory variables included in the model, their significance (based on Chi-squared or F-tests, values of $P < 0.05$ are in bold). Also given are the overall percentages of deviance explained (dev) for the model. Estimated degrees of freedom (edf) indicate linearity: edf = 1 represents a linear relationship, edf $\geq$ 2 represent a significant non-linear relationship.

Response Variable	Explanatory Variable	edf	*F*	*P*	dev
Mean Understorey Light Availability	Random spatial effect	27.3	5.5	**0.000**	54.7%
	Random effect of stand	4.7	0.3	**0.026**	
	Smooth main effect of Years since main disturbance	3.7	10.0	**0.000**	
	Smooth main effect of Disturbance severity	1.0	1.7	0.191	
	Interaction between main effects	2.3	1.7	0.163	
Maximum Understorey Light Availability	Random spatial effect	26.7	5.1	**0.000**	52.9%
	Random effect of stand	4.6	0.2	0.065	
	Smooth main effect of Years since main disturbance	3.6	10.5	**0.000**	
	Smooth main effect of Disturbance severity	1.0	0.0	0.960	
	Interaction between main effects	1.9	0.8	0.386	
Patchiness of Understorey Light (CV)	Random spatial effect	2.0	3.7	0.024	37.4%
	Random effect of stand	20.1	5.3	**0.000**	
	Smooth main effect of Years since main disturbance	1.2	21.0	**0.000**	
	Smooth main effect of Disturbance severity	1.0	10.9	**0.001**	
	Interaction between main effects	2.1	3.0	**0.037**	

Response Variable	Explanatory Variable	edf	χ^2	*P*	dev
Spruce 50–130 cm (Saplings)	Random spatial effect	2.0	34.8	**0.000**	48.0%
	Random effect of stand	23.9	148.1	**0.000**	
	Smooth main effect of Years since main disturbance	2.9	15.9	**0.001**	
	Smooth main effect of Disturbance severity	1.0	5.9	**0.016**	
	Interaction between main effects	3.1	4.4	0.373	
Spruce 130–700 cm (Poles)	Random spatial effect	13.8	99.2	**0.000**	43.0%
	Random effect of stand	8.7	16.0	**0.002**	
	Smooth main effect of Years since main disturbance	3.6	40.7	**0.000**	
	Smooth main effect of Disturbance severity	2.4	38.5	**0.000**	
	Interaction between main effects	2.7	8.4	**0.042**	
Rowan 50–130 cm (Saplings)	Random spatial effect	6.4	57.7	**0.000**	63.7%
	Random effect of stand	17.7	73.4	**0.000**	
	Smooth main effect of Years since main disturbance	3.6	29.1	**0.000**	
	Smooth main effect of Disturbance severity	1.0	0.2	0.618	
	Interaction between main effects	1.2	1.2	0.394	
Rowan 130–700 cm (Poles)	Random spatial effect	6.6	57.5	**0.000**	59.6%
	Random effect of stand	16.8	57.7	**0.000**	
	Smooth main effect of Years since main disturbance	3.0	18.3	**0.001**	
	Smooth main effect of Disturbance severity	1.2	0.2	0.706	
	Interaction between main effects	4.2	7.8	0.212	

low level until ~150 yr since disturbance, but then began to rise gradually (Fig. 3; Appendix S6). The patchiness of light became lower through time following moderate to high severity disturbance events. The patchiness of light was constantly higher on plots under a low-severity disturbance regime; it exhibited a U-shaped pattern, declining and then increasing later during stand development (Fig. 3).

Spruce regeneration densities

Densities of small spruce saplings (50–130 cm in height) were significantly influenced by time since disturbance ($P = 0.001$), disturbance severity ($P = 0.016$), a spatial term ($P < 0.001$) and a random stand effect ($P = 0.001$), which explained 48.0% of the deviance (Table 1). Spruce poles (130–700 cm in height) were influenced by time since disturbance ($P < 0.001$), disturbance severity ($P < 0.001$), time x disturbance interaction ($P = 0.042$), a spatial term ($P < 0.001$) and a random stand effect ($P = 0.002$), which explained 43.0% of the deviance. Both sapling and pole densities were most stable after low-severity disturbances (Fig. 4). Following disturbance, sapling densities declined to a minimum at ca 100 yr of development. Pole densities follow a similar

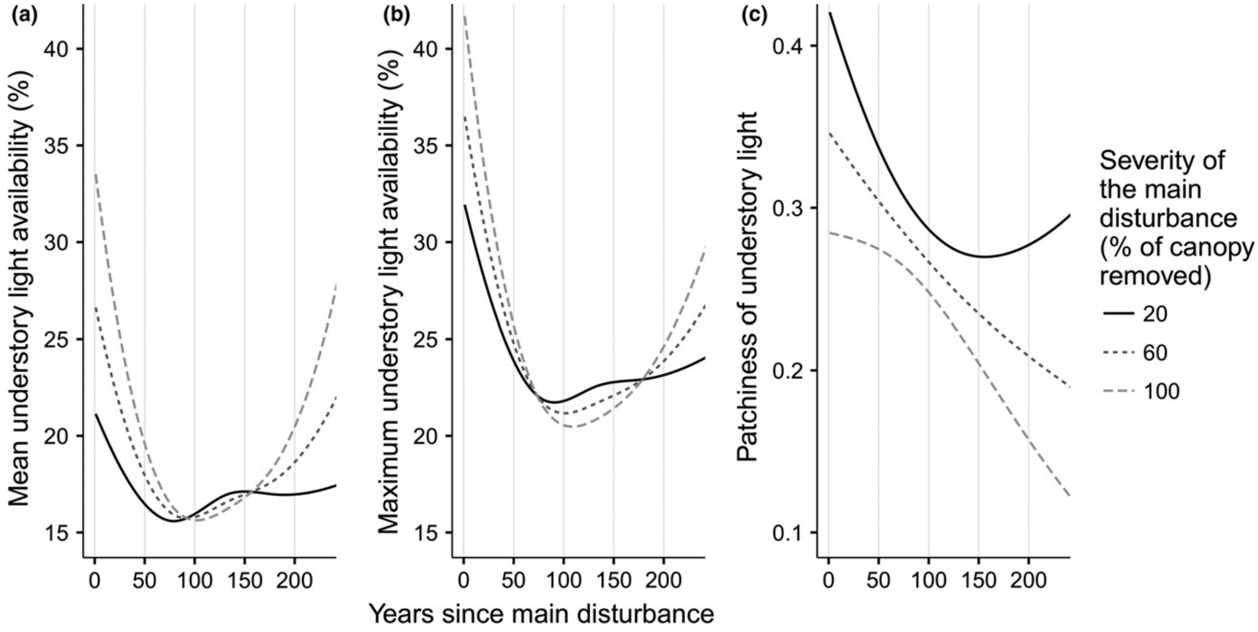

Fig. 3. The influence of time since main disturbance, severity of the main disturbance event (percentage of disturbed canopy) and their interaction on mean understorey light availability (**a**), maximum understorey light availability (**b**) and patchiness of understorey light (coefficient of variation) (**c**) at 1.3 m above the ground.

profile, reaching a minimum at ca 100 yr of development, but exhibit a larger fluctuation in stem densities in response to disturbance severity (Fig. 4; Appendix S7).

Rowan regeneration densities

Rowan sapling densities were significantly influenced by time since disturbance ($P < 0.001$), a spatial term ($P < 0.001$) and a stand effect ($P < 0.001$), which explained 63.7% of the deviance (Table 1). Rowan poles were significantly influenced by years since disturbance ($P = 0.001$), a spatial term ($P < 0.001$) and a random stand effect ($P < 0.001$), which explained 59.6% of the deviance. Rowan densities were highest shortly after disturbance, and rapidly decreased thereafter (Fig. 4; Appendix S7). After reaching a minimum (~100 yr), densities gradually increased.

Discussion

Investigations of canopy–understorey interactions tend to focus on initial responses of understorey populations following a stand-replacing event (e.g. Cooper-Ellis et al. 1999; Romme et al. 2016) or compare dynamics among various gap sizes in mature or old-growth forests (e.g. Canham & Marks 1985; Nagel et al. 2006; Fahey & Puettmann 2008). Our study with a long-term perspective fills an important knowledge gap by simultaneously addressing initial responses of understorey cohorts and their re-establishment many decades later. Understorey densities on low-disturbance sites were more stationary through time, providing a baseline to contrast against high-severity sites. Understorey dynamics in plots recovering from more severe disturbances exhibit a more even-aged character, where the boundaries between developmental phases were more punctuated. We identified critical points in the co-development of light availability and sapling densities, and used these points to integrate our generalized model with stand development concepts (Oliver 1980; Franklin et al. 2002). A summary of our expectations and observations is further provided (Fig. 5).

Canopy closure and stem exclusion

Canopy closure is a critical event in the process of stand development (Assmann 1970; Jennings et al. 1999). We observed a minimization of mean understorey light availability occurring in correspondence with a maximum in the variation of sapling densities among plots following 100 yr of development (Fig. 3a,b). Sapling and pole densities diverged during the first 100 yr following disturbance (Fig. 2) because stem densities declined in proportion to disturbance severity (Fig. 4). Conceptually, this corresponds to the transition between stand initiation and stem exclusion, which becomes more pronounced as disturbance severity increases.

A reduction in sapling densities implies that the incoming recruitment of smaller individuals into the size

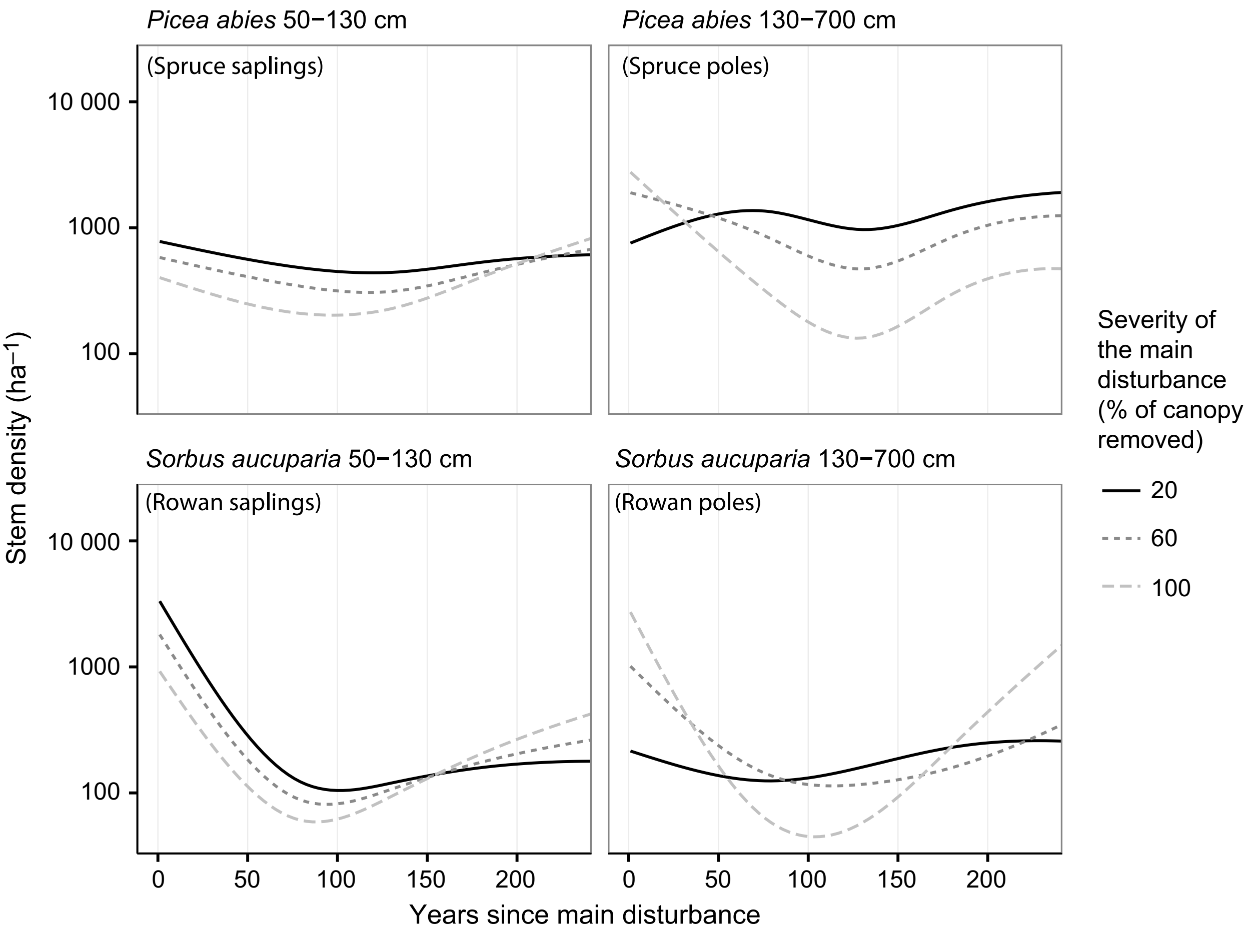

Fig. 4. The influence of time since main disturbance, severity of the main disturbance event (percentage of disturbed canopy) and their interaction on density of spruce and rowan saplings (50–130 cm) and poles (130–700 cm).

categories we analysed is outpaced by the out-going recruitment of saplings into larger size classes and mortality. Sapling densities decline in proportion to disturbance severity, implying that a larger proportion of understorey cohorts respond to fill larger canopy openings. As saplings increase in size, they fill the new gap and understorey light availability declines. Although spruce seedlings can survive with no height growth for many years (Messier et al. 1999; Hytteborn & Verwijst 2011), recruitment to the upper strata is strongly light limited and, as established individuals replace canopy cover, they inhibit incoming recruitment (Messier et al. 1999).

Post-disturbance light levels (intercepts on Fig. 3) were estimated to be highest in the most disturbed sites, but this signal was statistically not significant. This is counter-intuitive, but Canham et al. (1990) concluded that the role of gap size in determining understorey light availability was less important than the height of the bordering canopy and latitude (Canham et al. 1990). More observations from recently disturbed sites would improve confidence in our estimates of variation in initial light conditions immediately following disturbances.

Understorey re-initiation

After canopy closure, variation in understorey densities decreased due to a corresponding increase in both light availability and sapling densities. As we observed, conceptual models of development anticipate correlated increases in understorey light and sapling densities following canopy closure. Mortality of canopy trees increases understorey light availability, which facilitates the incoming recruitment of seedlings into sapling size classes (Lutz & Halpern 2006). Even following >200 yr of development, sapling densities still vary as a function of past disturbance severity, implying that disturbance has long-term consequences for understorey dynamics (Kashian et al. 2005).

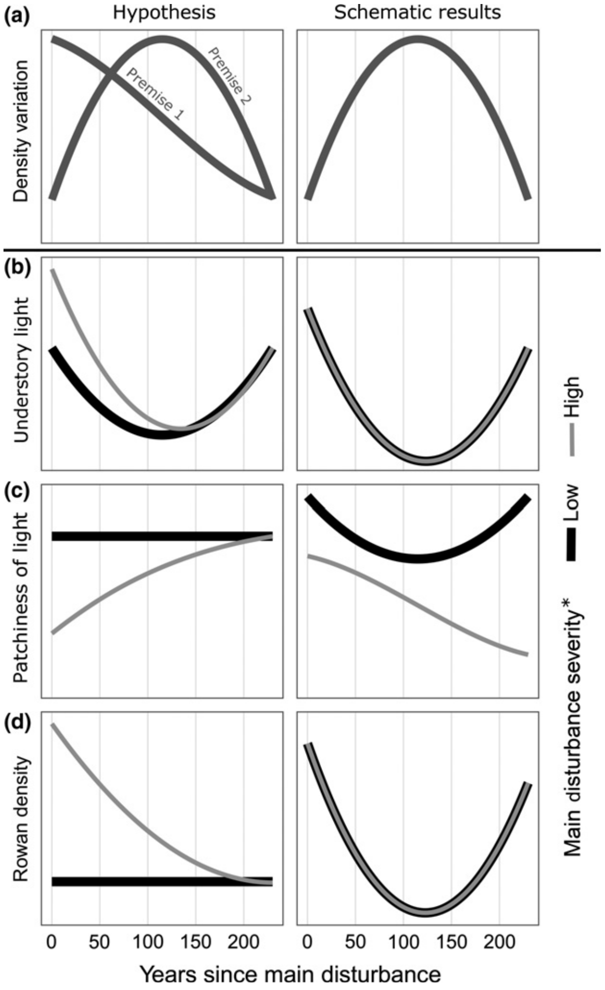

Fig. 5. Graphic summary of hypotheses and significant observed trends. The results show that density-dependent processes do not dampen initially high variation (premise i), but rather that disturbance induced heterogeneity in regeneration conditions, which seeds further divergence (premise ii) (**a**). Results did not confirm that severe disturbances cause a larger, more prolonged increase in light availability (**b**). Light was more uniformly distributed within plots after severe disturbance, but did not converge to patchiness of light found under a low-severity disturbance regime, as was expected (**c**). The results did not show any pronounced effect of disturbance severity on rowan abundance, as was predicted (**d**). *Low-severity disturbance removes 20% of the plot-level canopy, while high severity disturbance removes 100% of the plot canopy. Mean understorey light availability was measured using a fish eye lens, and patchiness of light was expressed as the coefficient of variation of light availability within a plot.

Disturbance severity also has a lasting effect on within-site variation in light availability (Fig. 3c). Light variability at the low end of the severity spectrum followed an intuitive trajectory: variability was high following partial canopy removal, but declined as these small gaps are filled by regeneration, and again increased later in stand development as individual canopy tree deaths contributed to patchiness. Contrary to our expectation that light levels would approach an equilibrium, independent of disturbance history, light variability on heavily disturbed plots declined continuously as mean light availability increased (Fig. 5c). Increasing evenness suggests density-dependent processes, like self-thinning (Kashian et al. 2005; Lutz & Halpern 2006). Persistent divergence in light variability over multiple centuries suggests that stand dynamics do not converge to an equilibrium in less than 250 yr. Canopy patchiness directly impacts the spatial arrangement of saplings in spruce populations, and likely contributes to the vertical and horizontal complexity later in development (Bače et al. 2015).

Regeneration strategies and resilience

Regeneration strategies of late successional species are presumed to buffer ecosystems against large fluctuations in community and ecosystem structure (Messier et al. 1999). Sustaining cohorts of advanced regeneration in anticipation of future canopy gaps is common among shade-tolerant conifers (Messier et al. 1999), and the persistent monospecific character of our *P. abies* study sites exemplifies this trait. The specific character of disturbance agents plays a large role in compositional stability. Central European temperate spruce forests are driven by wind storms and bark beetle outbreaks, which preferentially remove the largest individuals and leave cohorts of advanced regeneration intact (Svoboda et al. 2010). Central European spruce forests can be compared with boreal spruce forests, where fire destroys advanced regeneration, and loss of this competitive advantage permits the infiltration of birch and rowan populations into early successional communities (Hofgaard 1993).

Our approach does not permit us to state with certainty that advanced regeneration is predominantly responsible for filling recently formed canopy gaps; that would require directly observed plots and tracking individuals before and after disturbance. However, indirect evidence exists to support this claim. Understorey population densities at the incidence of disturbance (intercepts in Fig. 4) are similar among low-severity sites, but the least stable densities are on high-severity sites. Saplings thus appear to occur at a high baseline density across a wide range of canopy conditions, implying that there should be sufficient advanced regeneration available to respond to canopy removal. The contribution of post-disturbance recruitment to canopy closure is likely small, given the size advantage of saplings occurring at high baseline densities (Macek et al. 2016). Densities of saplings <50-cm tall rapidly increase after disturbance, but growth remains low, giving a substantial size advantage to advanced regeneration (Zeppenfeld et al. 2015; Macek et al. 2016). These post-disturbance cohorts

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will contribute to the increase in sapling densities during understorey re-initiation.

We also considered whether advanced regeneration was sufficient to ensure self-replacement of spruce following disturbances of all severities. A change in composition from spruce to rowan, a light-demanding understorey species, following the highest severity events was considered one potential outcome (Fig. 5d; e.g. Pajtík et al. 2015). We did not detect a significant effect of disturbance severity on rowan abundance (Fig. 5d), although rowan was encountered at high densities in some stands. The poor dispersal ability of rowan, paired with the competitive advantage provided by advanced regeneration of spruce, appears to sustain the suppression of rowan under the current disturbance regime (Żywiec et al. 2013).

Conclusions

A retrospective approach was used to construct a model that specified the time scale of understorey cohort responses to disturbance. Our dendroecological approach fills a gap in empirical inquiry into stand dynamics by producing a long-term, quantitative representation of stem exclusion and understorey re-initiation, and largely validates accepted, but untested, development theory (Oliver 1980; Franklin et al. 2002). In this low-diversity system, sapling densities at locations differing in disturbance history converge towards a common baseline, but disturbance effects persist for >200 yr.

Our study supports the premise that the persistence of the monospecific character of temperate spruce forest, despite variation in disturbance severity, is due to the strategic advantages of advanced regeneration. Our findings estimated boundaries to the limit of variation in disturbance severity that *P. abies* can sustain to maintain monospecific character. Inspection of our model predictions suggests that understorey cohorts are lowest ca 100 yr after the most extreme events. It is likely that at this point of minimization in stem densities, *P. abies* populations are most vulnerable to large shifts in composition.

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Supporting Information

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

Appendix S1. List of stands and their environmental conditions.

Appendix S2. Description of delineation of primary forests in each country.

Appendix S3. Distribution of time since disturbance and disturbance severity across countries.

Appendix S4. Distribution of time since disturbance and disturbance severity across stands.

Appendix S5. Means ± SD of variables used in the analyses, per stand and country.

Appendix S6. Probability density of maximum understorey light availability as a function of the influence of time since main disturbance and severity of the disturbance.

Appendix S7. Probability density of stem densities as a function of the influence of time since main disturbance and severity of the disturbance.

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