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Tree and stand-level patterns and predictors of Norway spruce mortality caused by bark beetle infestation in the Tatra Mountains

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ABSTRACT

This study investigates temporal shifts in Norway spruce (*Picea abies*) mortality, stand structure characteristics, and stand complexity facilitated by a bark beetle (*Ips typographus*) outbreak that affected an unmanaged subalpine forest region in Tatra National Park, Poland in the late 2000s. Changes in survivorship and stand structure characteristics (diameter (DBH), basal area, height, age, and crown length ratio) of nearly 2500 spatially-referenced trees located in 64 long-term survey plots were compared over four time periods that spanned the duration of the outbreak disturbance event. Stand structure characteristics, topographic factors (slope, elevation, and aspect), and solar equinox radiation were tested as predictors of mortality for multiple stages in the outbreak using boosted regression tree modeling. Our findings showed that: (1) spatial synchrony was not reflective of mortality severity; (2) mortality rates increased significantly as the outbreak progressed; (3) the stand's structure was altered significantly by the outbreak (larger trees were killed most frequently); (4) stand structure characteristics were the best predictors of mortality in all stages of the outbreak, though topographic factors and solar equinox radiation also exhibited moderate to strong predictive power in some stages; and (5) stand complexity decreased significantly as the outbreak progressed. This illustrates the inherently complex nature of bark beetle outbreaks on fine spatial scales and suggests that the extent and severity of spruce mortality during an outbreak event is largely dependent on the relative stage of the outbreak and the structure of the stand.

1. Introduction

The spruce bark beetle, *Ips typographus* (L.) (Coleoptera: Scolytidae), is the most critical disturbance agent of mature Norway spruce (*Picea abies*) (L.) stands in Eurasia (Christiansen and Bakke, 1988; Turčáni and Novotný, 1998; Grodzki et al., 2004). In Central and Eastern Europe, where Norway spruces often grow in monocultures (Grodzki et al., 2004), large-scale bark beetle outbreaks have had rapid and pronounced effects on a variety of landscapes (Schelhaas et al., 2003; Wermelinger, 2004; Seidl et al., 2007; Raffa et al., 2008; Mezei et al., 2014b). Outbreaks can have serious impacts on sustainable timber production and ecosystem functions and services, such as forest carbon balances, soil erosion dynamics, rockfall and avalanche frequency, and a profusion of biotic relationships (Seidl et al., 2007; Raffa et al., 2008; Lindner et al., 2010). Continued climate warming, drought, and storm severity are expected to increase pressure exerted on disturbance dynamics in mountain systems (Dale et al., 2000), and may increase the scale and severity of bark beetle outbreaks (Dutilleul et al., 2000; Seidl et al., 2007; Lindner et al., 2010; Jönsson et al., 2012).

Recent studies have focused on outbreak disturbance triggers, the dynamics of outbreak events, and the underlying factors that predispose forest stands to high levels of mortality. In the high Carpathian Mountains of Central and Eastern Europe, *I. typographus* outbreaks usually initiate after fine-scale pulse disturbances that provide suitable colonization substrates (e.g. blowdown from windstorms) and progress through healthy forests as press disturbances (5–7 years) if climatic and forest structure attributes are ideal (Schelhaas et al., 2003; Kärvemo, 2015). They are influenced by a complex suite of biotic, abiotic, and topographic variables that can cause beetle population and tree mortality dynamics to fluctuate greatly within and among stands (Wermelinger, 2004;

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Grodzki et al., 2006; Hilszczański et al., 2006). During the progradation stage of the outbreak, defined as the period of initial beetle population increase during an outbreak, which is thought to be governed by a combination of topographic, stand structure, and environmental factors (Kautz et al., 2013; Mezei et al., 2014b), bark beetles spread rapidly at large spatial scales, flying distances well beyond 500 m, in search of large, weakened host trees (Wichmann and Ravn, 2001; Wermelinger, 2004). By the outbreak's culmination, marked by epidemic beetle population levels and high tree mortality rates, attacks become more proximal to previously infested host trees (Jakuš et al., 2003) and selection is dictated less by topographic and environmental factors (Mezei et al., 2014b). During this stage, beetle populations grow large enough to overwhelm healthy trees with robust defense systems (Jakuš et al., 2011). In the retrogradation stage, defined as the period of relative decrease in a beetle population during an outbreak, spatial spread remains minimal and tree mortality rates lower as suitable host trees become limited (Jakuš et al., 2003; Turčáni and Hlásny, 2007; Grodzki et al., 2010).

Though the overall comprehension of bark beetle outbreaks in high-elevation forests has increased in recent years, our understanding of spruce susceptibility remains poorly developed on fine spatial scales (Jakuš et al., 2003; Turčáni and Hlásny, 2007; Svoboda and Pouska, 2008; Kautz et al., 2013). Moreover, the idiosyncratic behavior of beetle populations in varying outbreak stages related to spread, host preference, landscape heterogeneity, and mortality severity requires further investigation to expand our understanding of dynamic disturbance pressures and their related effects (Grodzki et al., 2010; Oliver et al., 2010; Nelson et al., 2014; Mezei et al., 2014b). Few studies have incorporated long-term, tree-level survey data taken at multiple points prior to an outbreak and at disparate stages over the course of an outbreak's progression. Additionally, predictive factors relating to forest structure and topography have been difficult to untangle due to the confounding effects of anthropogenic activity, including land management practices aimed at minimizing outbreak impact (Lindelöw and Schroeder, 2001; Grodzki et al., 2003; Kautz et al., 2013). In Central Europe, nearly all Norway spruce stands are actively managed via salvage logging, thus opportunities to observe natural patterns and drivers of bark beetle outbreaks in this region are severely limited.

We incorporate five time points of patch-level, spatially-referenced survey data taken over a four-decade-long period from a protected, unmanaged forest to examine long-term changes in Norway spruce mortality and living forest stand structure relative to a bark beetle outbreak in the subalpine zone of the Polish Tatras. Our analysis includes two time points of pre-outbreak survey data (taken approximately 7 years prior and 25 years prior to the outbreak., respectively) and three time points of mid-outbreak survey data (taken during the outbreak's progradation stage, culmination stage, and retrogradation stage). Our aim is to uncover spatio-temporal trends of stage-specific tree mortality in hopes of better understanding the mechanisms that influence spatial synchrony, mortality severity, and host selection. We use boosted regression tree modeling to predict the relative importance of stand structure, topographic, and environmental variables relative to mortality severity during each period and over the course of an outbreak. We also assess temporal changes in stand complexity for each period and relate these results to host selection. We sought to address the following questions:

(1) Does the extent of spatial synchrony relate to mortality severity?
(2) Do mortality rates increase significantly as the outbreak progresses?
(3) Is the structure of the surviving stand significantly affected by the outbreak over time?
(4) Do stand structure, topographic, and environmental factors predict mortality prior to each outbreak period, and if so, are they consistent throughout the outbreak lifecycle?
(5) Does stand complexity change significantly over time, and if so, do these changes relate to bark beetle host selection?

2. Methods

2.1. Study area

Our study was conducted in the High Tatra Mountains in the Gąsienicowa valley of Poland. The Tatra Mountains are the highest mountain chain of the Carpathian arch and are located on the border between Poland and Slovakia. The study area comprised a section of subalpine forest in the Małopolskie province of Tatra National Park (Tatrzański Park Narodowy; abbr. TPN) that has been protected from human intervention (e.g. salvage logging) for the last 60 years. The elevation of our study area ranged from 1300 to 1550 m. The annual precipitation in this region is 170 mm and the mean annual temperature is 2.7 °C; the mean temperature of the coldest month (January) is −6.0 °C and the mean temperature for the warmest month (July) is 11.1 °C (Niedźwiedź, 1996). The dominant tree species in the subalpine forest is the autochthonous Norway spruce (*P. abies* L.) H. Karst. Here, Norway spruce grows in monoculture with very small admixtures of rowan (*Sorbus aucuparia* L.). At higher elevations (1550–1900 m), dense thickets of dwarf mountain pine (*Pinus mugo* L.) form a distinct vegetation belt. Swiss stone pine (*Pinus cembra* L.) occurs mainly at the timberline. At lower elevations (900–1200 m), mixtures of Norway spruce, European beech (*Fagus sylvatica* L.), and silver fir (*Abies alba* L.) dominate the landscape (Mirek and Piękoś-Mirkowa, 1992). The shrub layer of the study area is poorly developed and the herb layer is dominated by mosses and European blueberry (*Vaccinium myrtillus* L.) (Mirek and Piękoś-Mirkowa, 1992). The study area covers 170 ha, and varies in aspect and slope. From the late 2000s–2014, this area was affected by an intense bark beetle (*I. typographus*) outbreak. Bark beetle outbreaks occurred over large parts of the Tatra Mountains during this period and were triggered by a major wind storm at lower elevations.

2.2. Field methods and response variables

We resurveyed 64 long-term circular sample plots (0.05 ha each; 3.2 ha in total) in October of 2014. Plots were systematically arranged and established in 1973 for monitoring forest dynamics (Jagiełło et al., 1978). They were resurveyed in 2002 (Holeksa et al., 2006). In 2011 and 2012, TPN employees monitored the survivorship of trees and the progression of bark beetle infestation. Each plot was spatially mapped in 1973; individual trees were spatially referenced and numbered. Only Norway spruce trees were mapped and recorded during this initial survey. The collection of plots allowed for patch-scale inferences related to tree mortality in the study area caused by a bark beetle outbreak that inflicted the region from the late 2000s–2014.

In each plot, the survivorship (living or dead) of every mapped spruce in the dataset (or stand) was assessed. Diameters at breast height (DBHs) of living mapped spruces were also recorded; dead trees were recorded but not measured. These data were aggregated with previous years' data, which included survivorship assessments (1973, 2002, 2011, and 2012) and measurements of tree height, DBH, crown length, and age (2002) to portray temporal changes in mortality and stand structure (see Holeksa et al., 2006; Szewczyk et al., 2011 for data collection methods). Survey years were defined as relative outbreak stages based on mortality