



# Landscape-level spread of beetle infestations from windthrown- and beetle-killed trees in the non-intervention zone of the Tatra National Park, Slovakia (Central Europe)



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## ABSTRACT

The European spruce bark beetle (*Ips typographus*) causes widespread Norway spruce (*Picea abies*) mortality in European forests. The pattern of landscape-level tree mortality varies over the course of beetle outbreak and by the presence and location of active breeding sites. Increased understanding of rules governing the unmanaged spread of beetle-induced tree mortality over the landscape would help to optimise management control strategies on the borderline between highly valuable protected areas and surrounding managed forests.

Our study aimed to quantify the dynamics of standing tree infestation patterns from two infestation sources: windthrow and previous-year beetle infestations. Specifically, we (i) evaluated dispersal distances between the nearest infestation source and new infestations, (ii) quantified size and shape of infestation spots, (iii) modelled an infestation gradient and (iv) probability of new infestation during the incipient, peak and decline phases of beetle outbreak. Based on one- and two-year records of colour-infrared aerial photography, taken between 2005 and 2015, we identified windthrown and beetle-killed trees in the non-intervention zone of Tatra National Park, Slovakia (Central Europe).

The size and compactness of infestation spots evolved from small and simple to more extended and complex shapes during beetle epidemics. In total, 40% of infestations were smaller than 100 m<sup>2</sup> and 79% smaller than 500 m<sup>2</sup>. Spot growth dominated over spot initiation, with the mean spot growth extent during peak epidemic (54.8 m). Beetle infestations reached the upper tree line (1605 m a.s.l.). In total, 71% of new infestations emerged within 100 m and 97% within 500 m from an infestations source. Emergence of new infestations varied between infestation sources and phases of beetle outbreak. New beetle infestations emerged near windthrown locations during incipient and peak phases and near source beetle infestations during peak and decline phases following inverse power-law function. We found that the forest within 100 m from the active infestation compared to more distant buffers had the highest risk of infestations. The distance to previous-year infestations should be considered as one of the main factors in determining the risk of subsequent tree mortality, especially if other predictors are absent. If the active wind disturbances or beetle infestations neighbour the border of the unmanaged protected area, the search and sanitation felling of active breeding trees should be concentrated within 500 m from the border of unmanaged protected areas in order to restrain the spread of beetle infestations from nature reserve to surrounding managed forests.

## 1. Introduction

The European spruce bark beetle, *Ips typographus* L., is the largest

cause of biological disturbance in Norway spruce trees in Eurasia (Christiansen and Bakke, 1988; Grégoire et al., 2015; Schelhaas et al., 2003). Climate-change-related increasing seasonal temperatures

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threaten to reduce host tree resistance, facilitate beetle multivoltinism (Fleischer et al., 2016) and completion of sister broods, and hence increase yearly rates of beetle-induced tree mortality (Mezei et al., 2017).

Spruce bark beetle populations develop in endemic and epidemic states, defined in terms of population size, relative to the abundance of available hosts (Mezei et al., 2014; Safirnyik and Carroll, 2006). During times of low population numbers – the endemic phase – *I. typographus* survives long periods on scarce trees with compromised health, randomly distributed over the forest (Sauvard, 2004). A climatic event, such as windthrow (Økland and Berryman, 2004; Økland and Bjørnstad, 2006), or severe drought (Grodzki, 2007; Rouault et al., 2006), lowers the resistance of a large amount of trees, enabling increased beetle colonisation success and beetle density. Beetle populations then transit to an epidemic state, in which beetles kill even healthy trees (Byers and Lofqvist, 1989; Lindgren and Raffa, 2013).

The severity of spruce mortality depends on the relative phase of the beetle epidemic (i.e., the tree-killing phase: Mezei et al., 2014; Safirnyik and Carroll, 2006; Sproull et al., 2015). One to three years after a windthrow event (i.e., in the incipient phase), the majority of beetles feed on windthrown trees, and only few infest standing trees (Schroeder and Lindelöw, 2002), located hundreds of metres from each other (Jakuš et al., 2003). The peak phase starts up to three years after a windthrow event, with the occurrence of massive infestations of healthy trees (Modlinger and Novotný, 2015; Økland et al., 2016; Schroeder and Lindelöw, 2002). The decline of beetle epidemics is likely triggered by exhaustion of suitable brood trees (Økland and Berryman, 2004), unfavourable weather conditions, intraspecific competition (Holuša and Lukášová, 2017; Komonen et al., 2011; Lawson et al., 1997), natural enemies (Grodzki et al., 2010), or a combination of these factors.

The dispersal of individual beetles differs from the spatial distribution of infested trees over the landscape. Individual beetles are assumed to disperse randomly over a forest (Byers, 2000, 1999), until localizing the suitable host tree using olfactory cues (Byers, 2004, 1989). Successful tree infestation relies on the rapid aggregation and collective attack of dispersing beetles on a specific host tree within a short amount of time (Kautz et al., 2011; Louis et al., 2016; Økland et al., 2016). The sole presence of a beetle specimen in a forest therefore does not guarantee successful tree infestation.

On the other hand, the sole presence of a host tree does not predict beetle infestation (Robertson et al., 2007). The spatial distribution of patches of infested trees over the landscape is predicted by stand age and structure (Wermelinger, 2004), tree species composition (Kärvelo et al., 2016), terrain exposure (Netherer and Nopp-Mayr, 2005), elevation (Sproull et al., 2017), solar radiation (Kautz et al., 2013; Mezei et al., 2012; Sproull et al., 2017) and proximity to breeding sites, such as windthrown (Hedgren et al., 2003; Wichmann and Ravn, 2001) and standing beetle-killed trees (Kautz et al., 2011; Lausch et al., 2011). The importance of factors predicting location of new beetle infestation vary over the course of a beetle epidemic (Mezei et al., 2014).

The amount of freshly-infested trees over a landscape approximates the size of the beetle population in a specific time interval (Kautz et al., 2011; Sproull et al., 2017). Remote sensing records the fading needles of dying trees (Rock et al., 1986; Wulder et al., 2006), allowing the identification of beetle infestations on a landscape scale, which is ineffective and costly to survey by terrestrial methods (Lausch et al., 2013; Wulder et al., 2006). Repeated aerial surveys facilitate (i) disclosing progressive changes in patterns of tree mortality over time and space (Delplace, 2008; Heurich et al., 2010; Kautz et al., 2011; Nikolov et al., 2014; Sproull et al., 2017, 2015); (ii) recording the spatio-temporal distribution of infested trees in relation to infestation sources (Kautz et al., 2011); (iii) enable evaluation of the impact of salvage logged and uncleared windthrow on subsequent standing-tree mortality (Nikolov et al., 2014; Økland et al., 2016); (iv) allowing an examination of the transition from windthrow- to patch-driven outbreak dynamics (Økland et al., 2016); (v) analysing the dispersion of beetle infestations

under endemic and epidemic conditions (Kautz et al., 2011; Lausch et al., 2013); and (vi) quantifying the direct impact of the bark beetle on forest stands (Kautz et al., 2011).

Landscape-level analysis of the spread of beetle infestations reveals the spatiotemporal dynamics of such infestations over the forested landscape, and the spatial dependency on two sources of infestation – active windthrown trees (Gilbert et al., 2005; Wichmann and Ravn, 2001) and freshly infested standing trees (Havašová et al., 2017; Kautz et al., 2011; Lausch et al., 2011). One year after a windthrow event, beetles use wind-felled trees as breeding material (Gilbert et al., 2005; Schroeder and Lindelöw, 2002), while windthrown trees serve as focal points for infestations in following years (Hedgren et al., 2003). Windthrown trees decay slowly providing long-lasting breeding resources (Louis et al., 2014) up to three years after the windthrow (Vakula et al., 2007). In the second to third summer, beetles transit to infestation of healthy standing trees (Modlinger and Novotný, 2015; Schroeder and Lindelöw, 2002). New infestations spread over short distances, with 80% of new infestations being located within 250 m of the nearest old attack (Wichmann and Ravn, 2001) with the highest risk of infestation within 100 m of the previous year's infestation (Kautz et al., 2011). Spatial distribution of new infestations follows an inverse power-law distribution with increasing distance from an active breeding site (Kautz et al., 2011).

New beetle infestations show high spatial affinity to previous-year infestations (Kautz et al., 2011; Lausch et al., 2011) with dominant spot growth (Havašová et al., 2017; Jakuš et al., 2003). However, only one study has documented the changing importance of proximity to windthrown infestation sources to beetle-killed trees over the course of a beetle outbreak (Økland et al., 2016). The spatiotemporal dynamics of beetle infestation patterns during epidemics have been addressed by coarse-resolution Landsat imagery (30 m, Havašová et al., 2017; Jakuš et al., 2003), which neglected the identification of individual and small groups of infested trees (< 900 m<sup>2</sup>) over the landscape. A tree-level evaluation of the patterns of tree infestation, spot initiation and growth, and identification of infestation gradients and probabilities near two sources of beetle infestation (infested windthrown and standing trees) would contribute to a more precise identification of the areas at highest risk of infestation in forested landscapes, and thus make forest protection measures in buffer zones surrounding protected areas more effective.

To address this research gap, we quantified windthrown areas and spots of beetle infestation in a part of the non-intervention zone of Tatra National Park (TANAP, Carpathian Mountains, Slovakia) between 2005 and 2015. We aimed to quantify the spatiotemporal dynamics of beetle infestations during incipient, peak and decline phases in relation to two potential sources of infestation – windthrown and standing trees. Specifically, we aimed to: (i) measure the dispersal distances between active sources of infestation and following-year infestation spots; (ii) quantify the size and compactness of infestation spots, spot initiation and growth rates, and orientation and extent of spot growth; (iii) model infestation gradient developed by Kautz et al. (2011) to identify the rules governing the spatial dispersal of tree infestations over time; and (iv) to evaluate the distance-dependent risk of beetle infestation relative to infestation source.

## 2. Material and methods

### 2.1. Study area

TANAP is located in northern Slovakia, in the Tatra Mountains, the highest range in the Carpathian Mountains. In 2004, an extensive windthrow event affected ~12,000 ha of forest stands in the park, followed in 2007 by an extensive bark beetle outbreak (Nikolov et al., 2014; Økland et al., 2016). TANAP is divided into intervention and non-intervention management zones. In the intervention zone, forest management, such as sanitation logging and felling, is applied to mitigate

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