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Mixed-severity natural disturbances promote the occurrence of an endangered umbrella species in primary forests

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ABSTRACT

Primary forests are characterized by high vertical and horizontal stand diversity, which provides habitat for a diverse range of species with complex habitat requirements. Detailed knowledge of related ecological processes and habitat development of primary forest species are essential to inform forest management and biodiversity conservation decisions, but relationships are not well documented. We collected dendrochronological data and inventoried numerous structural elements in permanent plots throughout the primary temperate forests within the Carpathian Mountains. We fit and compared multiple predictive models to quantify the importance of 200 years of natural disturbance dynamics on the occurrence probability of an umbrella species – the capercaillie (*Tetrao urogallus*). We showed that a mixed-severity disturbance regime ranging from low through moderate to high severity disturbances is required to generate diverse forest habitats suitable for capercaillie. The variation in natural disturbance severity and its timing promoted key structural habitat elements, such as low natural regeneration density, low mature tree density, high ground vegetation cover, availability of forest gaps, and abundance of standing deadwood. This study demonstrates the importance of natural disturbance in maintaining the variety of conditions necessary to support primary forest specialist species. Managers of protected areas should be mindful that natural disturbances generate habitat for the capercaillie in mountain Norway spruce forests. Further intervention is unnecessary. Conservation planning and forest reserve design should shift focus to the large-scale spatial requirements needed to ensure that a wide range of forest developmental phases are represented in protected areas.

1. Introduction

The rich levels of biodiversity found in primary forests are a consequence of their high structural variability and habitat continuity (Franklin, 2000; Gao et al., 2015). Throughout Europe, primary forests now cover less than one percent of the contemporary landscape and pressure to convert primary forest cover to structurally simplified forests managed for timber production continues to increase (Knorn et al., 2013; Wallenius et al., 2010). To fully understand the consequences of the loss of forest structural complexity on biodiversity, quantifying the relationship between structural variability in primary forests and the abundance of related indicator species is necessary.

The structural variability of primary forests arises largely as a consequence of natural disturbances (Franklin et al., 2002; Franklin and Pelt, 2004; Trotsiuk et al., 2014; Čada et al., 2016, Meigs et al., 2017). Disturbance results in structural reorganization, reduction in living tree densities, increased canopy openness, heterogeneous regeneration of trees and ground vegetation, and increased standing and lying dead

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wood (Donato et al., 2012). As a source of environmental variation, natural disturbances put evolutionary pressure on forest populations (Holling, 1987). Species consequently adapt to the conditions provided by disturbance and forest development; for example, abundances of various bird species are associated with unique configurations of vertical complexity in forest stands (Hansen et al., 1995). Identifying the importance of specific structural elements and their relationship with disturbance is critical for understanding the loss of biodiversity in structurally simplified managed forests (Gao et al., 2015; Mori and Kitagawa, 2014).

Capercaillie (*Tetrao urogallus*) is a typical Eurasian forest specialist bird representing an important umbrella species of species-rich forest habitats (Suter et al., 2002). Large and complex habitats characterized by structural heterogeneity, rich ground vegetation, and high habitat connectivity improves its reproductive success and viability (Bollmann et al., 2005; Braunisch and Suchant, 2008; Graf et al., 2009; Lakka and Kouki, 2009). It is a species well known to a wide audience, which makes it a flagship species for promoting the conservation of forest ecosystems and biodiversity (Storch, 2007). One of the largest, although declining, European population of capercaillie, lives in the Carpathians (Klinga et al., 2015). This mountain range comprises the largest remaining continuous temperate forest ecosystem in Europe; it accounts for more than two-thirds of temperate European primary forests (Veen et al. 2010). Structural heterogeneity in the primary spruce forests throughout the Carpathian Mountains is driven by windthrows and bark beetle disturbances occurring at a wide range of severities (Janda et al., 2017). Capercaillie especially require forests with rich ground vegetation cover, which is directly influenced by the amount of light penetrating the main canopy to the forest floor (Storch, 2007). The variability in natural disturbances induces tree mortality, hence disturbances are expected to play an important role in providing habitat for the capercaillie.

Most studies addressing the relationship between the habitat use of forest specialist species and natural disturbances analyzed the effects of recent disturbances (e.g., Beudert et al., 2015). The effects of long-term disturbance and developmental dynamics on species habitat relationships are only poorly understood (Mori, 2011). It is predicted that natural disturbance regimes will be altered due to climate change (Seidl et al., 2014), which emphasizes the need to understand the impacts of historic natural disturbance dynamics on species of high conservation concern. Poor understanding of past processes increases the uncertainty in future predictions (Thom et al., 2017), and, therefore, the uncertainty in conservation management decisions is also greater.

To address this knowledge gap, we used retrospective dendroecological methods to perform the first quantitative analysis linking natural disturbance history to the habitat requirements of capercaillie. Because species responses to structural variability are potentially complicated, we adopted a multi-model strategy by assessing models of increasing flexibility to provide contrast between more parsimonious versus complicated explanations. The size of our data set permitted further evaluation of model predictive performance using out-of-sample data (Shmueli, 2010), thus improving our assessment of the biological relevance of our findings, an approach critically needed in ecology (Houlahan et al., 2017). The two main research questions addressed were: (1) Can the past natural disturbance regime in the primary forests of the Carpathians explain current capercaillie occurrence? (2) Which disturbance variables and primary forest structures are the best predictors of capercaillie occurrence?

2. Materials and methods

2.1. Study area

This study was conducted in the mountain forests of Giumalau (37,500 ha) and Calimani (24,000 ha), a core zone of capercaillie distribution in the Carpathian Mountains (Fig. S1). Based on the inventory of Romanian primary forests (Veen et al., 2010), we selected two primary Norway spruce (*Picea abies* (L.) Karst.) mountain forest stands in Giumalau (110 ha) and Calimani (40 ha) located between 1300 and 1650 m a.s.l. Norway spruce is the dominant tree species with a minor component (< 5%) of rowan (*Sorbus aucuparia* L.) and stone pine (*Pinus cembra* L.). The understory of the study areas is dominated by bilberry (*Vaccinium myrtillus* L.), *Calamagrostis villosa,* greater wood-rush (*Luzula sylvatica* (Huds.) Gaudin), and wavy hair-grass (*Avenella flexuosa* (L.) Trin.). The average annual temperature in the study region is between circa 2.4 and 4.0 °C; the mean annual precipitation ranges between 1100 and 1650 mm and increases with altitude (FAO, 2010). Snow cover is present for the duration of 139–208 days per year and contributes to up to 500 mm of the total annual precipitation.

2.2. Habitat data

To obtain capercallie and forest structure data, we simulated a 141.4 by 141.4 m grid over the two selected primary forest stands. Within each grid, a permanent circular study plot (1000 m^2) was established to sample forest stand structure and past disturbance history (see Svoboda et al., 2014 for more details). The total of 104 permanent study plots were used to record the following habitat characteristics: diameter at the breast height (DBH), status of all trees ≥10 cm (live and dead), natural regeneration density of tree species in three height classes (0.5–1.3 m, 1.3–2.5 m, and > 2.5 m), ground vegetation height (mean height of dominant layer), and proportion of forest floor covered by bilberry, an important food source for capercaillie (Storch, 2002; Broome et al., 2014).

2.3. Stand age structure and disturbance history variables

Age structure and disturbance history reconstructions were based on a dendroecological study reconstructing disturbance histories of the surrounding region (Svoboda et al., 2014) Twenty-five living dominant trees per plot were randomly selected (using a random number generator) and cored to produce a cross-dated ring-width series collection of 2600 tree cores from all study plots. Mean age, median age, minimum and maximum tree age, mean age of five oldest trees, and interquartile range of age were calculated for each plot (see Table S1).

Variables characterizing the disturbance history covering the last 200 years of individual plots, including the maximum disturbance severity, time since the maximum disturbance, and diversity of disturbance severities represented by the disturbance index, were derived to describe the disturbance histories (Svoboda et al., 2014). Disturbance index (DI) represents the diversity of disturbance severities in time per plot characterized by the commonly used Shannon index of diversity (Svoboda et al., 2014). Low values (i.e., −3) indicate low severity disturbances that occurred frequently over 200 years; the maximum

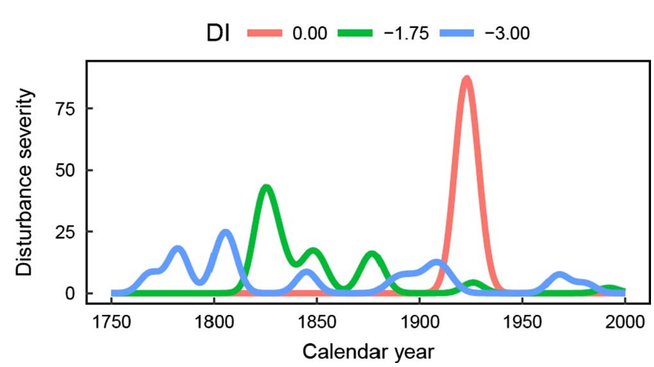

Fig. 1. Example of disturbance histories in plots with disturbance index value 0 (red color), −1.75 (green color) and −3 (blue color). Disturbance severity represents the canopy removal. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)