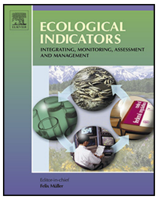
Ecological Indicators xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Response of bird assemblages to windstorm and salvage logging — Insights from analyses of functional guild and indicator species

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ARTICLE INFO

Article history:
Received 2 April 2015
Received in revised form 3 June 2015
Accepted 17 June 2015

Keywords:
Forest management
Biodiversity
Breeding season
Coniferous forests
Natural disturbance
Logging
Harvesting

ABSTRACT

Natural disturbances, such as fire, windstorms and insect outbreaks, are important drivers of biodiversity in forest ecosystems, but at the same time cause large economic losses. Among the natural disturbances in Europe, windstorms cause the highest economic loss. After such storms, damaged forest stands are commonly salvage logged to restore economic value. However, such interventions could affect species assemblages of various taxonomic groups, including breeding birds. Despite these potential effects, investigations of the impacts of post-storm logging are largely lacking. We thus investigated assemblages of breeding birds in 21 logged and 21 unlogged windstorm-disturbed forest plots and 18 undisturbed, control forest plots using fixed-radius point-stop counts three, five and seven years after a windstorm within the Bavarian Forest National Park as part of the European Long-Term Ecosystem Research Network. We recorded 2100 bird individuals of 55 bird species. Bird assemblages were predominantly altered by the consequences of the windstorm and affected only to a minor degree by subsequent logging of storm-felled trees. Nevertheless, bird species richness was significantly reduced by post-storm logging within the first season. In general, the windstorm led to a shift in bird assemblage composition from typical forest species towards open- and shrub-land species. Assemblages of logged and unlogged disturbed plots consisted mainly of long-distance migrants and ground-foraging bird species, whereas assemblages of undisturbed control plots consisted of resident species that forage within vegetation. Both unlogged and logged storm-felled coniferous forest stands were inhabited by endangered or declining bird species, such as Water Pipit (*Anthus spinoletta*) on logged plots and Eurasian Redstart (*Phoenicurus phoenicurus*) on unlogged plots. Indicator species analyses suggested that species of unlogged storm disturbed plots depended on storm-created legacies, such as pits and snags, for foraging and nesting. Hence, we recommend reducing post-storm logging of these legacies to support species restricted to unlogged disturbed forest. To increase the diversity of breeding birds on the landscape scale, diverse logged and unlogged post-disturbance stands should be provided, which could be gained by a partial benign neglect strategy of storm disturbed forest stands.

1. Introduction

Stand-replacing natural disturbances, such as fire, windstorms or outbreaks of pest species, are part of the natural dynamics in many forest ecosystems (Swanson et al., 2011). Owing to climate change, the frequency and extent of natural disturbances have increased considerably in recent decades and will theoretically continue to increase in the future (Kurz et al., 2008; Seidl et al., 2014), thus intensifying discussions on how to manage large areas of disturbed forest. On one hand, increasing demands for timber products compel forest managers to intervene rapidly in

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http://dx.doi.org/10.1016/j.ecolind.2015.06.033
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Please cite this article in press as: Thorn, S., et al., Response of bird assemblages to windstorm and salvage logging — Insights from analyses of functional guild and indicator species. Ecol. Indicat. (2015), http://dx.doi.org/10.1016/j.ecolind.2015.06.033

affected stands through post-disturbance or salvage logging, a common practice in boreal and temperate forests to restore economic value (Donato et al., 2006; Nappi et al., 2004; Stokstad, 2006). On the other hand, natural disturbances can enhance both the structural complexity of forest stands and the biodiversity of numerous taxonomic groups (Beudert et al., 2015; Bouget and Duelli, 2004). Hence, the species richness and community composition of a variety of taxa are affected by post-disturbance logging, but the strength and direction of such effects might depend on the taxonomic group, type of disturbance, and time after intervention (Lindenmayer et al., 2008). Furthermore, specific functional guilds, such as taxa dependent on dead-wood resources, can display a distinct response to post-disturbance logging, even if the overall reaction of the respective taxonomic group is weak (Thorn et al., 2015).

Breeding bird species are frequently used as indicators of forest composition or stand age in boreal and temperate forest ecosystems (Hart et al., 2012; Juutinen and Mönkkönen, 2004; Moning and Müller, 2009). Numerous studies around the globe have focused on the effect of natural disturbances on assemblages of breeding birds, but most were carried out in forests damaged by wildfire and only for periods of less than five years (Azeria et al., 2011; Cahall and Hayes, 2009; Castro et al., 2010; Choi et al., 2014; Hutto and Gallo, 2006; Rost et al., 2012). Investigations of the impact of post-storm logging on breeding bird assemblages are generally scarce (e.g. Lain et al., 2008; Zmihorski, 2010) and particularly lacking for Norway Spruce (*Picea abies*) forests. Norway Spruce is the economically most important tree species in Europe and comprises major parts of the continent's forests (Brus et al., 2011). Furthermore, the growing stock of mature spruce forests has been increased in the past century through forest management (Schelhaas et al., 2003). However, mature spruce forests are prone to large-scale storm damage and accompanied outbreaks of insect and fungal pests, which makes mature spruce stands the most common post-disturbance logged forest type in Central Europe (Schroeder, 2010; Seidl et al., 2011).

To quantify the impacts of post-storm logging on breeding bird communities in forests dominated by Norway Spruce, we surveyed breeding birds in logged and unlogged storm-disturbed forest stands as well as in vital mature spruce stands, three, five and seven years after a major windstorm. In particular, we investigated (1) whether post-storm logging decreases species richness of breeding bird assemblages or causes changes in their community composition; (2) whether the relative abundance of functional guilds (nest position, migration, foraging) differ in logged and unlogged storm-damaged forest and mature undamaged forest, which could explain alterations in species richness or community composition (Azeria et al., 2011; Kroll et al., 2012); and (3) which bird species characterize these different forest plots, as judged by an extended indicator species analysis (De Cáceres et al., 2010).

2. Material and methods

2.1. Study area and bird surveys

The study was carried out within the high montane forests of the Bavarian Forest National Park in south-east Germany, which is part of European Long-Term Ecosystem Research Network and covering a total of 24,250 ha. Forest stands above 1000 m a.s.l. are naturally dominated by Norway Spruce, with low proportions of Mountain Ash (*Sorbus aucuparia*), European Beech (*Fagus sylvatica*) and Silver Fir (*Abies alba*). The average annual temperature ranges from 3.5 to 7 °C, and the average annual precipitation varies between 1200 and 1800 mm (Bässler et al., 2010).

In January 2007, the storm Kyrill affected a high proportion of central European coniferous forests, resulting in 62 million uprooted trees (Fink et al., 2009). In the Bavarian Forest National Park, approximately 1000 ha of mature spruce forest was felled by the storm, which made it the most extensive windthrow for more than a century (Thorn et al., 2014). Most of these storm-felled trees were logged, except for those in four compact areas of around 150 ha total, but no plantings were conducted within our study area. After logging was completed in 2007, we established 21 plots in unlogged disturbed stands, 21 plots in logged disturbed stands and 18 plots in undisturbed mature spruce forest stands; the plots were arranged along six major sampling transects. The minimum distance between the census points was 100 m, and plot altitude ranged from 1100 to 1300 m a.s.l. (for details on spatial distribution of plots and photographes of study plots see Appendix).

Bird censuses were performed five times per year from mid-March to mid-June in 2010, 2012 and 2014. This schedule ensures detection of early resident breeding birds as well as late-arriving long-distance migrants (Südbeck et al., 2005). We used transect-based point-stop counts with a fixed radius of 50 m around the centroid of each plot, resulting in 900 (60 plots * five visits per year * three survey years) individual point-stop counts (Hutto et al., 1986; Moning and Müller, 2008). On each plot, all bird individuals seen and/or heard during a time period of 5 min were recorded. Surveys were only conducted on days without rain, with low wind speed, and clear or slightly overcast sky (Bibby et al., 2000).

2.2. Data analysis

Prior to statistical analyses, count data obtained during five visits per year were summed up per plot to obtain bird abundances (sum of recorded bird individuals, i.e. observations) and species richness (number of recorded species per plot). These values reflect the abundance of species on the plots during the censuses and are not necessarily linked to the number of territories present on the plots. However, the number of individuals is the most objectively obtainable data unit and is the most reliable indicator for the habitat use of a species (Haila et al., 2015). We assigned species to nest-type guilds (cavity nester, open-cup nester), foraging guilds (ground forager, vegetation forager, tree-trunk forager) and migration guilds (short- and mid-distance migrant, long-distance migrant, resident) according to Glutz von Blotzheim and Bauer (1985) (see Appendix for guild classification).

All statistical analyses were carried out using the statistical software R 3.0.3 (R Development Core Team, 2015). We fit Poisson linear mixed models by means of the function 'glmer' (R-package 'lme4') to test the effect of plot type (undisturbed forest, unlogged disturbed forest, logged disturbed forest) on species richness and abundances within each study year. We included the plot as random factor to account for repeated measurements on each plot among the three study seasons (Bolker et al., 2009). Furthermore, we added an autocovariate term, calculated as the distance-weighted function of neighbouring plots to account for possible spatial autocorrelation of neighbouring plots using the R-package 'spdep' (Dormann et al., 2007). To model bird abundances within functional guilds, we added the overall bird abundance on the respective plot as a baseline by means of an offset term in the model formula, which disentangles abundance shifts of a specific guild from overall abundance shifts (Bibby et al., 2000; Bolker et al., 2009). The presence of trunk-foraging species was modelled with a binomial mixed model to account for the large number of absence points. Simultaneous comparisons of categorical plot types and adjustment of p-values for multiple testing were done by means of the function 'glht' (R package 'multcomp'; Hothorn et al., 2008).

We used distance based analysis of similarity (ANOSIM, R package vegan) to reveal differences within species community

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