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Effects of bark beetle outbreaks and salvage logging on two avian flagship species in mountainous forests, capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*)

Master Thesis

for obtaining the academic degree Master of Science

in Wildlife Ecology and Wildlife Management

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Vienna, April 2017

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Declaration in lieu of oath

I herewith declare in lieu of oath that this thesis has been composed by myself without any inadmissible help and without the use of sources other than those given due reference in the text and listed in the list of references. I further declare that all persons and institutions that have directly or indirectly helped me with the preparation of the thesis have been acknowledged and that this thesis has not been submitted, wholly or substantially, as an examination document at any other institution.

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ABSTRACT

An increasing growing stock and climate change have led to an ongoing increase of natural disturbances in European production forests. The consequences are huge economic losses, but also a promotion of structural and biological diversity in affected stands. The responses to natural disturbances by different species are manifold and depend on the affiliation to a structural component that gets influenced by natural disturbances and post-disturbance management strategies. In this study, I used the different habitat preferences of capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) as an example to analyse how bark beetle outbreaks and the subsequent management measures affect the forest structural attributes in early successional stages and in the end the presence of forest grouse species via combining aerial photography, high-resolution airborne light detection and ranging (LiDAR), and presence data of both capercaillie and hazel grouse. My results revealed that hazel grouse presence was higher in salvage-logged and unlogged stands compared to vital stands, whereas the capercaillie seems to avoid salvage-logged forest stands. Within 22 years of forest succession effects on forest structural components by post-disturbance management disappear. Indirect biological effects of bark beetle infestations like the development of dwarf shrubs, pioneer vegetation and young conifers in affected stands, which serve as important food source, are more important for the occurrence of capercaillie and hazel grouse than effects that arise from forest structural components. The spatial and temporal variability of bark beetle infestations create a mosaic of different early successional stages within unaffected forest stands, that meet the different requirements of both forest grouse species. Because of the negative impact of salvage-logged forest stands on the capercaillie, I conclude that salvage logging procedures should be renounced at least in some disturbed areas to obtain all the possible advantages for both grouse species.

Keywords: natural disturbance, LiDAR, habitat selection, Tetraoninae, forest succession

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1. INTRODUCTION

Mountain forests are important ecosystems since they provide numerous ecosystem services like provision of wood, climate regulation, water purification and recreation (Kulakowski et al., 2016a; Leverkus et al., 2015). Due to intensive economical use over the last centuries and diverse human impacts, forests underwent multiple alterations, which led to a loss of biodiversity and old-growth forest structures (Bengtsson et al., 2000; Paillet et al., 2010). Although forest managers have tried to supress natural disturbances in European forests (Schelhaas et al., 2003), climate change and an increasing growing stock of conifers have led to an ongoing increase in the frequency and intensity of natural disturbances during the last decades (Schelhaas et al., 2003; Seidl et al., 2014). In Germany, approximately 80% of the trees damaged by windstorms and insect outbreaks are Norway spruce (*Picea abies*), Silver fir (*Abies alba*) and Douglas fir (*Pseudotsuga menziesii*) (Destatis, 2015). The most important insect pest in Central Europe is the European spruce bark beetle (*Ips typographus*) (Wermelinger, 2004). Infestations of *I. typographus* severely damaged commercially used forests (an average of 2.9 million m^3 per year between 1950 and 2000) and led to high economic losses (Schelhaas et al., 2003). Moreover, due to climate change the geographical range of *I. typographus* expands northwards and in higher elevations (Jönsson et al., 2009) making mountain forests more susceptible to bark beetle infestations in future times, especially in combination with windstorms (Seidl et al., 2007).

Apart from the economic damage, natural disturbances like bark beetle outbreaks have several positive consequences on forest structures and biodiversity. Directly after a bark beetle infestation, forest stands are characterized by a huge amount of standing dead wood, a decreased canopy cover as well as an increased structural heterogeneity (Lehnert et al., 2013), followed by highly productive and structural complex early successional stages (Swanson et al., 2011). These dynamic alterations change over the years and provide complex and structural divers habitats which are advantageous to many species (Lehnert et al., 2013; Winter et al., 2015). It has also been considered, that natural disturbance regimes can be used as a forest management tool to regain more natural conditions in homogenised production forests (Angelstam, 1998; Kulakowski et al., 2016b). Bark beetle control measures on the other hand involve the removal of infested or dead trees (salvage logging), which is accompanied by many negative effects on biodiversity and species composition (Jonášová and Prach, 2008; Leverkus et al., 2014; Schmiegelow et al., 2006; Thorn et al., 2016) and consequently reduces the ecologic value of early successional habitats (Swanson et al., 2011). For example, post-fire salvage logging is known to have negative impacts on cup- and cavity-nesting woodpeckers like the hairy woodpecker (*Picoides villosus*) in North America (Cahall and Hayes, 2009) or the black-backed woodpecker, which uses recently burned snags for foraging (Nappi et al., 2003). Woodpeckers profit also from the huge amount of dead wood and the thereby provided food after bark beetle infestations (Edworthy et al., 2011).

Responses on natural disturbances and following management interventions are manifold. Most of the occurring effects are directly observable like the loss of cavity-nesting birds due to the removal of dead wood (Kronland and Restani, 2011; Saab and Dudley, 1998). Others are less clear, like the incurrence of microclimatic extremes due to the removal of standing and lying dead wood, or the impeded growth of seedlings due to mechanical disturbance caused by heavy machinery. Such changes might together lead to an increasing amount of pioneer vegetation and consequently a slower regeneration of the disturbed forest sites (Leverkus et al., 2014). The response of a certain species depends decisively on how strong the species is bound to a structural component that gets influenced by natural disturbances and salvage logging. For example, bark insectivorous birds profit from bark beetle outbreaks while other avian foraging guilds show no response (Drever et al., 2009). On the other hand, farmland birds in Mediterranean pine forests profit from post-fire salvage logging and the concomitant opening of the habitat (Rost et al., 2012). To analyse these effects, it is important to determine the interactions between natural disturbances, subsequent management and forest structural attributes.

Capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) inhabit boreal and mountainous forests in Europe (Storch, 1993). The capercaillie is a flagship species of European forest conservation and listed in Annex I, II and III of the European Council directive on the protection of wild birds (79/409/EEC) (Birds Directive). Although it still inhabits most of its original range, severe declines in Central Europe led to the distinction of several populations and a decline and fragmentation of the remaining ones (Storch, 2007a). The capercaillie population in the Bavarian Forest National Park is one of the last populations in European low mountain ranges (Storch, 2007b). It declined severely during the 20th century, with only approximately 16 birds left in 1954 (Rösner et al., 2014b). In the 80th a huge breeding and release program started releasing more than 1000 individuals. After a slight recovery of the population Rösner et al. (2014a) estimated its current size to be about 500 individuals in the entire Bohemian forest.

The hazel grouse is listed in the Annex I of the Birds Directive. Albeit it is usually common in most parts of its historical range, the hazel grouse populations in Western and Central Europe decreased rapidly since the beginning of the 20th century, leaving small and fragmented populations (Storch, 2007a). The Bohemian Forest contains a large part of the remaining birds outside of the Alps (Müller et al., 2009). In the Šumava National Park, the Czech part of the Bohemian forest, the population is thought to be stable or even slightly increasing since the middle of the 20th century as a consequence of extensive forest succession in large parts of the National Park (Klaus, 2007). Nevertheless, both grouse species are threatened by habitat loss and fragmentation (Åberg et al., 1995; Sahlsten et al., 2010; Storch, 2007b).

Previous studies, that investigated habitat preferences of capercaillie and hazel grouse revealed a contrasting preference of both species for different forest successional stages and the associated forests structures (Table 1). The hazel grouse occurs mostly in early successional stages with a huge number of shrubs and herbaceous plants that provide cover. The distinctly larger and more specialized capercaillie on the other hand occurs mostly in late seral forests with a sparse herb layer and open areas for displaying (Bañuelos et al., 2008).

In this study the different habitat preferences of capercaillie and hazel grouse were used as an example to analyse how bark beetle outbreaks and the subsequent management measures affect the forest structural attributes during early succession and in the end the presence of forest grouse species. Therefor I combined aerial photography with high-resolution airborne light detection and ranging (LiDAR) data and presence data of both capercaillie and hazel grouse to test indirect effects of post-disturbance management on the probability of capercaillie and hazel grouse presence via effects on canopy cover, vertical forest heterogeneity, herb layer and shrub layer.

Table 1. Forest structural attributes that determine the presence of capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*)

	Capercaillie *(Tetrao urogallus)*		Hazel grouse *(Bonasa bonasia)*	
Canopy cover	Sparse	(Sachot et al., 2003)	High	(Vauhkonen and Imponen, 2016)
	Intermediate (30–60%)	(Bollmann et al., 2005)	Diverse	(Schäublin and Bollmann, 2011)
	Moderate (50-60%)	(Storch, 2002)	High	(Ludwig and Klaus, 2016)
	Intermediate	(Graf et al., 2009)		
	Incomplete	(Suter et al., 2002)		
Vertical forest heterogeneity	Two or more vertical strata	(Vauhkonen and Imponen, 2016)	Multiple vertical strata	(Vauhkonen and Imponen, 2016)
	Multi-storeyed tree layer	(Suter et al., 2002)	Well structured	(Müller et al., 2009)
	Structural heterogeneity	(González et al., 2012)	Multi-layered	(Pfandl et al., 2013)
Herb layer	Low	(Sachot et al., 2003)	High	(Vauhkonen and Imponen, 2016)
	Average	(Vauhkonen and Imponen, 2016)	Close to 50 %	(Sachot et al., 2003)
	Rich in ericaceous shrubs	(Bañuelos et al., 2008)	Rich field layer	(Åberg et al., 2003)
Shrub layer	Mixed regeneration	(Teuscher et al., 2011)	Dense	(Schäublin and Bollmann, 2011)
	Less than 25%	(Storch, 2002)	Dense	(Ludwig and Klaus, 2016)

2. MATERIAL AND METHODS

2.1 Study area

All data were collected in the Bavarian Forest National Park in southern Germany (48º54′N, 13º29′E). The park is part of one of the largest continuous forested regions in Central Europe, the Bohemian forest, which comprises the Šumava National Park in the Czech Republic as well. Together it is the largest connected extensive forest area in Central Europe (Bässler et al., 2010). The national park consists of mixed mountain forests in areas under 1150 m composed of Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba)* and high montane forests in areas above 1150 m naturally dominated by Norway spruce (Bässler et al., 2010). Annual precipitation ranges between 1200 and 1800 mm, and mean annual temperature ranges between 3.8 and 5.8 °C.

During the 18th and 19th century the whole area has been disturbed several times by wind storms and subsequent bark beetle infestations. In 1880 only approximately 26% of the old-growth forest remained. Since 1983 the infection of the forest stands by bark beetles continued and was accompanied by a severe windstorm in January 2007 (Fink et al., 2009), which created a windthrow of approximately 1000 ha in the development zone of the national park, where salvage logging interventions are required by law. The windthrow has been reconditioned by logging operations almost entirely leaving only four compact areas with altogether 50,000 m^3 of wood (Thorn et al., 2014). The benign-neglect strategy in the natural zone led to increased structural heterogeneity and created together with the salvage-logged areas in the development and buffer zone a mosaic of stands killed by *I. typographus*, cleared areas and vital stands nearby (Beudert et al., 2015; Thorn et al., 2016).

2.2 Species data

Capercaillie and hazel grouse droppings were collected year-round by a group of trained volunteers in 2010 and 2011. Based on an existing habitat suitability map for capercaillie (Teuscher et al., 2011) a 50-ha grid system was established, including the entire potential habitat in the Bohemian forest. Grids were scored for fresh capercaillie droppings in sets of two. Hazel grouse droppings were collected as well, but without a detailed sampling design. Droppings of capercaillie and hazel grouse were stored in thermal packs during the field work and afterwards frozen at -20°C till they were genetically analysed. Geographic coordinates of all records were determined with a handheld GPS device resulting in 479 presence records, 90 records for hazel grouse and 389 records for capercaillie (Fig. 1).

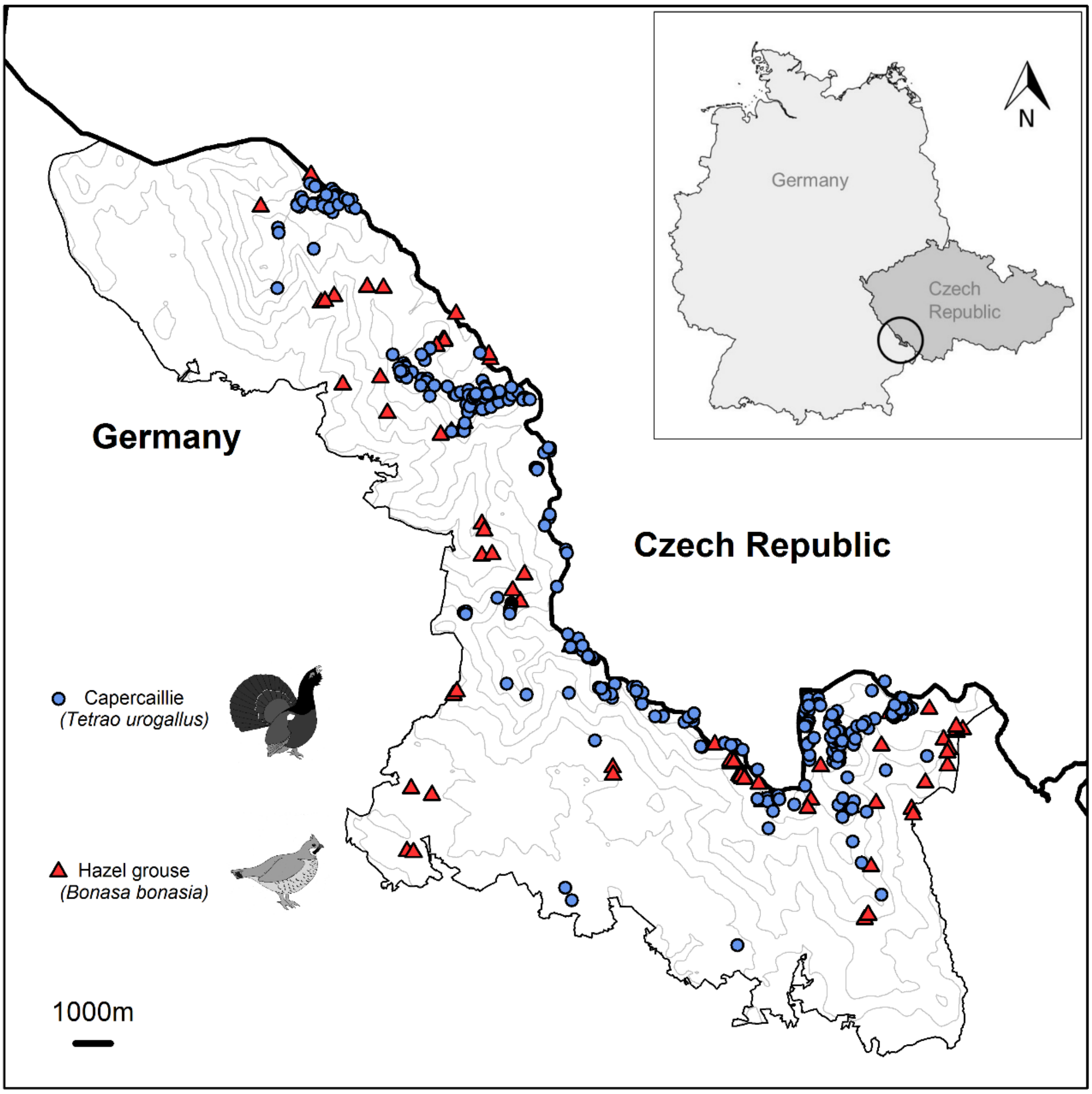

Figure 1. Presence records of capercaillie (*Tetrao urogallus*), and hazel grouse (*Bonasa bonasia*) from 2010 and 2011 in the Bavarian Forest National Park, Germany. The map in the right upper corner shows the location of the study area in Germany at the border to the Czech Republic. The interval between elevation contour lines is 100 m.

2.3 Forest structural attributes

I used LiDAR data to acquire information on forest stands in a 60-m surrounding of every presence point and 4790 additional random points in the same area for comparison. The study area was scanned with a Riegl LMS-Q680i sensor in July 2012 at a flight height of 650 m and an average point density of 30 points m^{-2} (Latifi et al., 2015). Points were aggregated into 10 m × 10 m grids.

I selected canopy cover [%], vertical forest heterogeneity [m], herb layer [%] and shrub layer [%] to represent forest structural attributes in the grouse habitat. The stand layers were calculated based on different LiDAR metrics using the original high-density point cloud (for details, see Latifi et al., 2017). Canopy cover was defined as vegetation density in the upper two thirds from the top height, which is based on 20% trees with largest diameter at breast height (Latifi et al., 2015). Calculation of the canopy cover included the density of laser points for the entire stand height, the mean stand height, the standard deviation of stand height as well as its interaction with forest habitat types. Vertical forest heterogeneity is the standard deviation of the mean height of all returns from minimum to maximum height in the 10 m × 10 m grids in a 60-m radius. A high standard deviation indicates a high structural heterogeneity, i.e. a high number of trees with different heights in the 60-m radius, and a small standard deviation indicates that trees have rather the same height (Latifi et al., 2015). I differentiated between a vegetation layer < 1 m, including grasses, dwarf shrubs and small saplings (herb layer) and a vegetation layer between 1 m and 5 m, including shrubs and large saplings (shrub layer). Calculation of the herb layer included the percentage of laser points located between 0 m and 1.5 m of stand height, a cover understorey metric (n (height < 2 m) / n (height < 60 m)), the height skewness of laser points located between 0 m and 1.50 m and the interaction between habitat types and the cover understorey metric. Calculation of the shrub layer included the height skewness of laser points located between 1.50 m and 5 m and a shrub metric (n (height < 0.5 m) / n (height < 5 m)).

2.4 Bark beetle outbreaks

Since 1988 bark beetle infestations were documented every year in late summer or early autumn by infrared aerial photographs (Heurich et al., 2010; Kautz et al., 2011). Every grid was observed yearly from 1988 to 2011 weather it was infested by bark beetles or not and weather salvage logging has been applied in the following year or not (Kautz et al., 2011). If the forest stands in a grid cell had never been infested through the years, the grid was classified as forest, if it had been infested sometime between 1988 and 2011 and salvage-logged in the following year, it was classified as salvage-logged and if it had not been salvage-logged after an infestation the grid was classified as unsalvaged. Heavily disturbed plots have a high amount of salvage-logged and/or unsalvaged areas, that were created within the time span of 22 years, therefore, representing early seral stages.

2.5 Statistical analyses

All statistical analyses where carried out in R 3.3.1. (www.r-project.org). I created 4790 pseudo-absence points in the study area in QGIS 2.14.3 (www.qgis.org). Via the intersect tool in QGIS I assigned every presence point and the 4790 additional random points all 30 m x 30 m grid cells of the bark beetle layer that lied within a 60-m radius. Afterwards I calculated the percentage of the different forest types (forest, salvage-logged or unsalvaged) for every 60-m circle.

To test the influence of post-disturbance management strategies on forest structural components and the influence of both post-disturbance management strategies and forest structural components on the probability of grouse presence, I used piecewise structural equation modelling (SEM) including different individual models for every response variable (Shipley, 2013, 2009). First I used different general linear models (GLM) to test the influence of the forest structural components and the post-disturbance management strategy on the grouse presence/absence. Because the elevation above sea level affects several other variables it was included in the GLM. To control for spatial autocorrelation, I created a distance-weighted autocovariate and included it in the GLM (function autocov_dist from spdep package (Augustin et al., 1996)) (Table 2). Second, I used different linear models (LM) with canopy cover [%], vertical forest heterogeneity [m], herb layer [%] and shrub layer [%] as response variables and the percentage of salvage-logged and unsalvaged forest stands and elevation as predictors as well as the distance-weighted autocovariate as fixed effect (Table 2).

Furthermore, I applied a correlation test on percentage of unsalvaged and salvage-logged forest stands and elevation, to test whether bark beetle infestations are influenced by elevation.

Table 2. Statistical models that were combined in the piecewise structural equation modelling (SEM). I used general linear models (GLM) for capercaillie (Tetrao urogallus) and hazel grouse (Bonasa bonasia) presence with the forest structural components, the percentage of salvage-logged and unsalvaged forest stands and elevation as predictors as well as a distance-weighted autocovariate (DWA) as fixed effect. Linear models (LM) were used to test the influence of percentage of salvage-logged and unsalvaged forest stands and elevation on the different forest structural components including DWA as fixed effect.

Model type	Response variable	Predictors
GLM	Capercaillie presence/absence	Canopy cover [%] + vertical forest heterogeneity [m] + herb layer [%] + shrub layer [%] + unsalvaged [%] + salvage-logged [%] + elevation + DWA
GLM	Hazel grouse presence/absence	Canopy cover [%] + vertical forest heterogeneity [m] + herb layer [%] + shrub layer [%] + unsalvaged [%] + salvage-logged [%] + elevation + DWA
LM	Canopy cover	unsalvaged [%] + salvage-logged [%] + elevation + DWA
LM	Vertical heterogeneity	unsalvaged [%] + salvage-logged [%] + elevation + DWA
LM	Herb layer	unsalvaged [%] + salvage-logged [%] + elevation + DWA
LM	Shrub layer	unsalvaged [%] + salvage-logged [%] + elevation + DWA

3. RESULTS

Only the canopy cover was influenced by the post-disturbance management strategies. It increased with increasing amount of salvage-logged forest stands. Vertical heterogeneity and canopy cover decreased with increasing elevation, while the herb layer increased with increasing elevation. Bark beetle infestations were independent from elevation.

Analysis of grouse presence data and forest structural attributes revealed that capercaillie and hazel grouse presence increased with increasing elevation. Elevations of the whole study area varied between 600 and 1400 m a.s.l., while presence data of capercaillie and hazel grouse were found in elevations between 740 and 1360 m a.s.l.

Capercaillie occurrence was clustered. Probability of capercaillie presence decreased with increasing percentage of salvage-logged forest stands and with increasing herb layer. Probability of hazel grouse presence on the other hand increased in unsalvaged as well as salvage-logged forest stands and decreased with increasing herb layer (Table A.1).

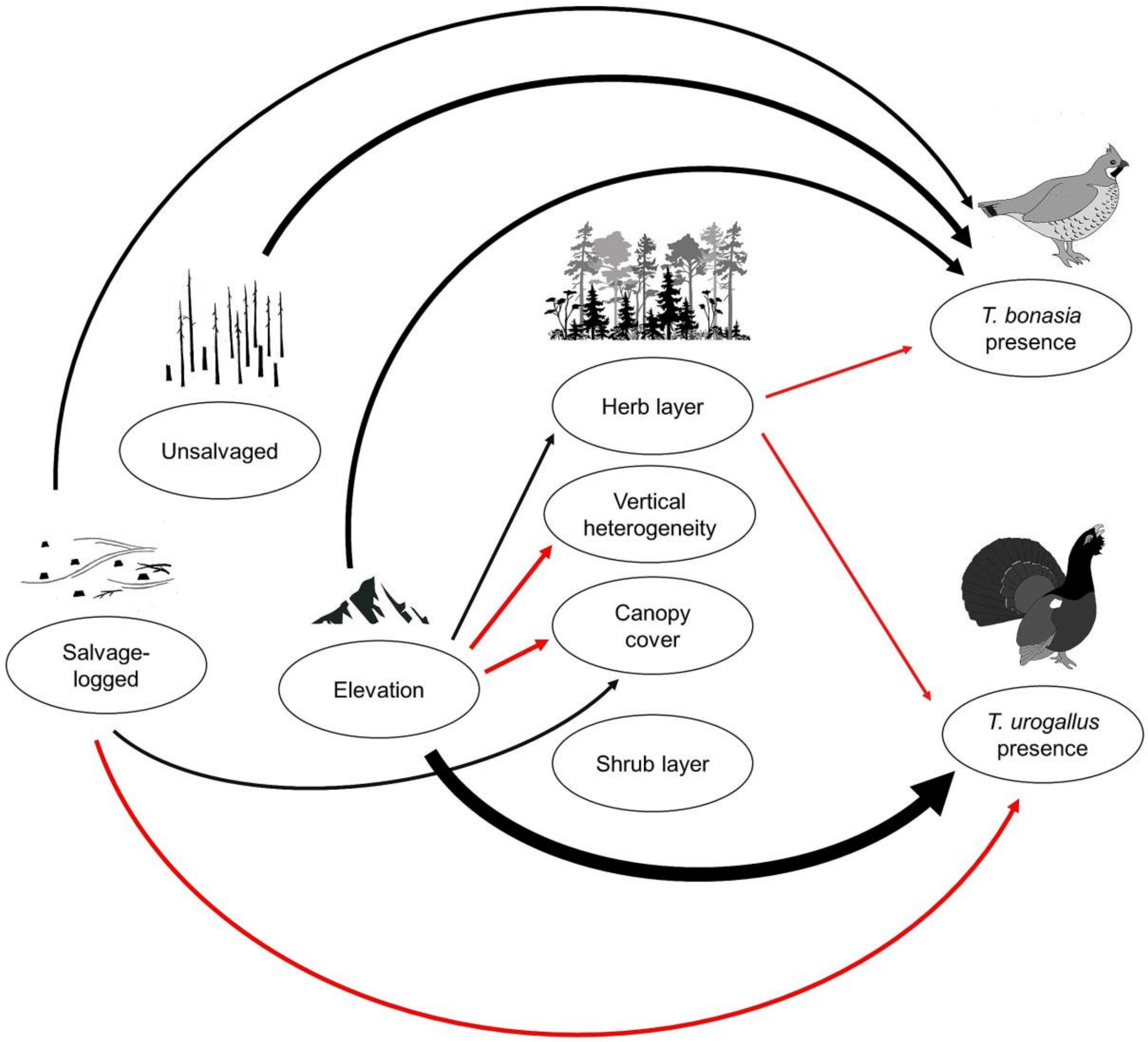

Figure 2. Results of the structural equation model with the post-disturbance management strategies and the elevation on the left, the forest structural attributes in the middle and the grouse presence on the right. Black arrows illustrate a positive, red arrows a negative influence on a response variable. Line width increases corresponding to the z-values.

4. DISCUSSION

My results revealed that the hazel grouse benefits from early seral forest stands that had been disturbed between 0 and 22 years ago, whether they were salvage-logged or not. Contrary to the capercaillie, whose probability of presence was significantly lower in salvage-logged stands. Because the species data was originally gathered for surveys within the scope of population biology, a sample effect should be considered, especially for the hazel grouse. Due to the fact, that droppings were only collected in selected areas and in the case of the hazel grouse even without a specific concern, it should be assumed that a huge proportion of potential habitat has been neglected. Forest stands with a dense understorey, difficult terrain for searching, but suitable habitat for the hazel grouse, have probably been searched only to a minor degree.

Apart from the canopy cover, there were no impacts of post-disturbance management strategies on forest structural components. Because bark beetle infestations in the study area took place in a time span of 22 years, the analysis comprised very diverse forest stands in early successional stages. To redevelop a closed canopy can take up to an entire century for a disturbed forest stand dependent on site factors and seed sources (Swanson et al., 2011). But still, the developments after a natural disturbance can vary greatly. A study in the Šumava National Park revealed that herbaceous vegetation directly after salvage logging differed not significantly from unsalvaged areas, but the development afterwards was different (Jonášová and Prach, 2008). Also, the tree species composition may differ in salvage-logged and unsalvaged sites. In unsalvaged forest stands regeneration consisted of spruce and rowan (*Sorbus aucuparia*), in salvage-logged forest stands pioneer species like birch (*Betula pubescens*), aspen (*Populus tremula*) and willow (*Salix aurita*) were present (Jonášová and Prach, 2004). By contrast, a study from Switzerland concluded that post-disturbance management strategies had no influence on the species composition. Tree species that were dominant before the disturbance gained dominance 20 years after the disturbance independent of the treatment (Kramer et al., 2014). My results showed that within 22 years, salvage-logged and unsalvaged forest stands have no significant differences regarding the forest structural attributes. Due to the huge impact of site factors on early succession (Swanson et al., 2011) and the fact that these site factors vary greatly throughout the whole National Park it is not possible to detect interrelations between the different post-disturbance management strategies and the forest structural components.

The fact that the observed forest stands had been infested up to 22 years ago might also explain my results that revealed an increase of the canopy cover with increasing percentage of salvage-logged forest stands. In many infested areas plantations were carried out after salvage logging interventions, hence within the time-span of 22 years a closed canopy could redevelop faster than in unsalvaged forest stands. Furthermore, the estimate of the interrelation between percentage of salvage-logged forest stands and canopy cover is very low (Table A.1).

Indirect effects caused by insect infestations and post-disturbance management strategies that are beneficial for the hazel grouse could be changes in species composition. After a bark beetle outbreak, unsalvaged forest stands are still dense and treetops are mainly intact. The forest consists of standing dead wood, a few unaffected living trees, lying dead wood and natural regeneration in form of saplings and shrubs. Over the years treetops and standing dead wood collapse gradually and forest stands are homogenised (Jonášová and Prach, 2008). The increased canopy opening and concomitant increased solar radiation (Fontaine et al., 2010) in disturbed forest stands promote open habitat species (Koivula and Spence, 2006; Rost et al., 2012; Swanson et al., 2011), new structures develop and herb and shrub layer increase. At the same time, upcoming pioneer vegetation like rowan and willow serve as important food resource for the hazel grouse (Sachot et al., 2003). Hence, independent of the different post-disturbance management strategies suitable conditions emerge for the hazel grouse in early successional stages. The disturbance itself seems therefore beneficial, independent of the subsequent management strategy, which is in line with the observations of the hazel grouse population in the Bohemian Forest, whose increase is linked to the abandonment of agricultural area and the following succession (Klaus and Ludwig, 2015).

Despite its preference for multi-layered forest stands with a dense understorey (Table 1) my results showed a negative impact of the herb layer on hazel grouse presence. One possible explanation is that in this case a dense herb layer, which I defined as vegetation up to 1 m, might consist, especially in salvage-logged forest stands, mainly of natural or planted spruce regeneration and grasses unsuitable for the hazel grouse, which needs certain soft wood species as food resource (Mathys et al., 2006). Müller et al. (2009) described the importance of rowan for the hazel grouse as winter food as well as root plates for sand bathing and grit ingestion. Such habitat parameters were not observed in my study, but will certainly play an important role in the habitat selection. Furthermore, precisely those components are generally not present in single-layered production forests, but in disturbed forest stands (Müller et al., 2009) and might explain the high probability of hazel grouse occurrence in salvage-logged and unsalvaged areas. Hence, forest structural attributes alone seem not sufficient to explain the preference of the hazel grouse for disturbed forest stands. Furthermore, classifications of stand layers are commonly vague in scientific literature, which complicates the comparison of results regarding the habitat preferences of a specialist like the hazel grouse.

Habitat requirements of the capercaillie are quite different. My results revealed a negative influence of salvage-logged areas on capercaillie presence. A study in Switzerland showed that the capercaillie prefers sparse, well-structured and open forests (Graf and Bollmann, 2008). Especially during rearing of the chicks open areas provide insects, berries and seeds as food resource (Graf and Bollmann, 2008), which can be found in unsalvaged forest sites.

Clear cuttings on the other hand are unsuitable habitats, which was already shown in a study in the Carpathian Mountains (Mikolás et al., 2015) and was explained by the low food availability and shelter for offspring right after a clear cutting (Lakka and Kouki, 2009). Furthermore, salvage logging may damage herbaceous vegetation like bilberry (Atlegrim and Sjöberg, 1996), an important food resource for the capercaillie (González et al., 2012; Storch, 1993). Nevertheless, a possible explanation for the preference of the capercaillie for unsalvaged forest stands could be, that an increasing amount and diversity of insects occur after natural disturbances (Bouget and Duelli, 2004), a major food source for chicks during their early development (Lakka and Kouki, 2009).

On the other hand, judging by my results forest stands with a high herb layer are unsuitable for the capercaillie. These results are in contrast with other studies that pointed out the importance of dwarf shrubs for capercaillie (Storch, 1993). But still, there are also studies, that found a preference of the capercaillie for old-growth single-layered forest stands (Bollmann et al., 2005), for grazed forests with a sparse herb layer (Sachot et al., 2003) and an avoidance of forest sites with dense understorey (Sachot et al., 2003). The line between an unsuitable dense understorey and a beneficial amount of dwarf shrubs might be too thin to allow an appropriate differentiation based on strictly mathematical LiDAR data. A more detailed analysis of the vegetation below 1 m including information about the plant species composition might allow a better insight into the interrelations between bark beetle infestations, the ground vegetation and the grouse occurrence. In addition to that, presence data was mostly gathered during winter, whereas LiDAR data was gathered during summer. Structural compositions especially of the lower stand layers are quite different when covered with a thick blanket of snow. Open areas with a dense herb layer could become a snow covered plain without any structures nor cover in winter, even if they might be suitable habitat during the rest of the year. During winter, on the other hand, the presence of feeding trees, mainly silver fir and pines, and trees for sleeping with protruding branches are of main importance (Suter and Graf, 2008), which altogether might explain the seemingly negative impact of the herb layer on capercaillie presence.

Forest structural attributes were mainly influenced by elevation. This could be explained by the huge difference between the forest stands situated on the slopes, the forest stands in the low-lying areas and those on the hillsides. The latter, lying between 1060 and 1250 m ASL, show huge amounts of even-aged spruce stands. 93% of the forest are declared as threatened by bark beetle infestations (Heurich, 2001), which is all in line with the lack of vertical heterogeneity with increasing elevation. My results showed no impacts of elevation on the percentage of disturbed forest stands, consequently, the reduced canopy cover and increased herb layer shown by my results imply that natural regeneration in higher elevations might be inhibited by less favourable conditions (Heurich, 2001).

CONCLUSIONS

Indirect biological effects of bark beetle infestation are more important for the occurrence of capercaillie and hazel grouse than effects that arise from forest structural components. Such indirect biological effects might be the creation of bare soil caused by a dieback of spruce trees as well as the development of dwarf shrubs, pioneer vegetation and young conifers after an infestation, which serve as important food source. At the same time, open areas are suitable lekking sites for the capercaillie. The natural regeneration that develops over the years also prevents cover for the hazel grouse, which is not present in pre-disturbance single-layered production forests. Hence, the spatial and temporal variability of the bark beetle infestations create a mosaic of different early successional stages within unaffected forest stands, that meet the different requirements of both forest grouse species. Heterogenous site factors in the entire Bavarian Forest National Park lead to a diversification of both salvage-logged and unsalvaged forest stands with the result that effects of the different post-disturbance management strategies following a bark beetle infestation on the forest structural components get lost during 22 years of forest development. Nevertheless, because of the negative impact of salvage-logged forest stands on the capercaillie, I conclude that some beneficial indirect effects occur only in unsalvaged forest stands, among them an increasing amount and diversity of insects as well as the growth of dwarf shrubs. Bark beetle infestations can create suitable habitat for hazel grouse and capercaillie, but to obtain all the possible advantages for both grouse species salvage logging procedures should be renounced at least in some disturbed areas.

ACKNOWLEDGEMENTS

I would like to thank Simon Thorn and Jörg Müller for supervising this master thesis and helping with the statistical analysis and all the questions and problems that arose during project. Further I would like to thank Hooman Latifi and Marco Heurig for their help with processing of the LiDAR data. I also thank Sascha Rösner for providing the species presence data as well as the Department of Conservation and Research in the Bavarian Forest National Park, that provided the LiDAR raw data.

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6. APPENDIX

Table A.1. Results of the structural equation model testing the influence of forest structural components, post-disturbance management strategies (percentage of unsalvaged and salvage-logged forest stands) and elevation above sea level on the occurrence of capercaillie (*Tetrao urogallus*) and hazel grouse (*Bonasa bonasia*) with generalised linear models including a distance-weighted autocovariate (DWA). The influence of post-disturbance management strategies and elevation on the different forest structural components was tested with linear models including a DWA. Boldface indicates significance.

Response variable	Predictor	Estimate	Std. Error	z-value
T. urogallus	**DWA**	**2.37 E1**	**1.67**	**1.41 E1**
	Elevation	**5.63 E-3**	**5.17 E-4**	**1.09 E1**
	Salvage-logged [%]	**-3.31 E-2**	**1.02 E-3**	**-3.23**
	Herb layer	**-3.62 E-2**	**1.65 E-2**	**-2.19**
	Unsalvaged [%]	3.37 E-3	1.73 E-3	1.95
	Vertical heterogeneity	7.19 E-2	4.29 E-2	1.68
	Shrub layer	1.97 E-2	1.19 E-2	1.66
	Canopy cover	-6.22 E-3	7.20 E-3	-8.63 E-1
B. bonasia	**Unsalvaged [%]**	**1.44 E-2**	**2.96 E-3**	**4.87**
	Elevation	**2.57 E-3**	**6.55 E-4**	**3.93**
	Salvage-logged [%]	**1.56 E-2**	**4.80 E-3**	**3.25**
	Herb layer	**-5.19 E-2**	**2.54 E-2**	**-2.05**
	Vertical heterogeneity	1.15 E-1	6.70 E-2	1.71
	Canopy cover	-1.58 E-2	1.12 E-2	-1.4
	Shrub layer	1.26 E-2	1.91 E-2	6.66 E-1
	DWA	1.17 E-1	1.73	6.76 E-2
Vertical heterogeneity	**Elevation**	**-4.36 E-4**	**1.65 E-4**	**-2.64**
	Unsalvaged [%]	1.25 E-3	8.63 E-4	1.45
	DWA	-6.20 E-1	5.83 E-1	-1.07
	Salvage-logged [%]	9.98 E-4	1.53 E-3	6.51 E-1
Canopy cover	**Elevation**	**-4.62 E-3**	**1.43 E-3**	**-3.23**
	Salvage-logged [%]	**3.20 E-2**	**1.33 E-2**	**2.41**
	Unsalvaged [%]	1.46 E-2	7.48 E-3	1.90
	DWA	-3.64	5.22	-6.99 E-1
Shrub layer	DWA	-8.33 E-1	1.78	-4.69 E-1
	Salvage-logged [%]	-1.84 E-4	4.39 E-3	-4.18 E-1
	Elevation	1.61 E-4	4.74 E-4	3.38 E-1
	Unsalvaged [%]	-2.38 E-4	2.47 E-3	-9.62 E-2
Herb layer	**Elevation**	**1.15 E-3**	**5.31 E-4**	**2.18**
	Salvage-logged [%]	9.62 E-3	4.91 E-3	-1.96
	Unsalvaged [%]	-4.29 E-3	2.76 E-3	-1.55
	DWA	-1.72	1.99	-8.67 E-1