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Structural complexity in managed and strictly protected mountain forests: Effects on the habitat suitability for indicator bird species

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ABSTRACT

Increasing the proportion of unmanaged forests in multi-functional forest landscapes is a primary goal of international and national conservation strategies aiming at restoring natural properties in structurally simplified forests. However, the development of structural features and associated habitat suitability for forest species is largely unknown and even controversially discussed, as the development of newly established reserves is unidirectional and passes through dense maturation stages. This may negatively affect open forest species in the first phase after reserve designation. We evaluated the effects of management cessation on key habitat characteristics of four mountain forest bird species indicative of different structural components: Capercaillie *(Tetrao urogallus)*, Hazel grouse *(Bonasa bonasia)*, Three-toed woodpecker *(Picoides tridactylus)* and Pygmy owl *(Glaucidium passerinum)* across four mountain regions in Central Europe. Habitat suitability was modelled based on 300 forest sites selected independently of their management status, and predicted to an independent dataset of 42 strictly protected forest reserves in the same regions. We then compared forest reserves to managed forests with species presence or absence with regard to habitat suitability and key habitat structures and related both to the time since reserve designation. For all model species, except Pygmy owl, habitat suitability in forest reserves was significantly higher than in managed forests with species' absence, but not different from managed forests with species presence. For the species associated with open forest structures (Capercaillie, Hazel grouse, Pygmy owl) habitat suitability was significantly related to the "reserve age": reserves in the first three decades after management cessation showed a significant decrease in suitability, which increased afterwards up to the maximally recorded time of 100 years. No such correlation was found for the Three-toed woodpecker associated with deadwood and barkbeetle infestations following temporally unpredictable disturbance events. Structural characteristics varied greatly in abundance and distribution, with open structures being related to the time since reserve designation. We therefore recommend focusing on mature, near-natural and structurally diverse forests when designating new strict forest reserves.

1. Introduction

Europe hosts one billion hectares of forest, which cover 45% of the continent surface and make up 25% of the forests of the world (FOREST-EUROPE et al., 2011). However, only 10% thereof are protected with the objective of conserving biodiversity (FOREST-EUROPE et al., 2011), and only 1% is allowed to develop without human intervention (class 1.1, MCPFE, 2007; Sabatini et al., 2018). The majority (91%) is subjected to multi-purpose forestry with "near-natural forest management" as dominant sivlicultural system in Central Europe (FOREST-EUROPE et al., 2011). This management regime is based on permanent forest cover with mixed stands of predominantly native tree species (Bauhus et al., 2013), and has been introduced in replacement of even-aged forest management with clearcutting (Messier et al., 2015) so as to integrate ecological and societal demands in the process of wood production (Bollmann and Braunisch, 2013). Such multi-functional forests, however, have been altered by humans for centuries and lack the structural heterogeneity and habitat continuity of natural forests (Peterken, 1996): While clearcutting systems, focusing on economically valuable tree species at optimized tree growth (Zlonis and

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Niemi, 2014), produce a landscape-scale mosaic of different age-classes which lack structural heterogeneity at the stand-level, near-natural forest management promotes uneven-aged, vertically structured stands, but leads to structural homogeneisation at the landscape-scale, by emphasizing the continuity of forest cover (Bauhus et al., 2013). Moreover, as logging usually takes place at the end of the "optimal phase", when timber stock is at its maximum (Commarmot and Brang, 2011), managed forests represent only the first part of the natural successional cycle, i.e. lack late seral stages, senescent trees. Natural or unmanaged forests, in contrast, resemble a heterogeneous mosaic of all developmental phases at different spatial scales (Franklin and Van Pelt, 2004; Mikoláš et al., 2017), including late successional phases with large amounts of deadwood (Spies and Franklin, 1991; Spies and Turner, 1999) of different decay stages (Commarmot and Brang, 2011) and with abundant tree-micro-habitats (Paillet et al., 2017, e.g. holes, crevices, loose bark, epiphytes), which provide habitat for a large number of species (Larrieu et al., 2018).

Natural disturbances, such as fire, wind-storms, hill-slides, avalanches, insect outbreaks and beaver activity, are important drivers of forest dynamics, maintaining structural complexity and promote a diverse species composition in both managed and unmanaged forest ecosystems (Spies and Turner, 1999). However, minimizing the risk and extent of natural disturbances – and thus the economic loss – is a primary goal of forest management, which changes disturbance regimes in scale, structure and rate and alters natural gap dynamics (Cada et al., 2016; Korpel, 1995). Although forest management can mimic natural disturbances by creating small (selective cutting) or large (clear-cutting) gaps, managed forests are more homogeneous in terms of tree composition, vertical stratification, age structure and successional dynamics which can strongly affect biodiversity (Paillet et al., 2010). While various species and species groups were found to benefit from the broad spectrum of structures that can be provided by forest management (Schall et al., 2017), with especially logged areas and small clearcuts and the associated ecotone structures providing valuable habitat for species of early-successional habitats (Schulte and Niemi, 1998), almost all forests in temperate Europe are impoverished in indicator species for structural complexity, late successional stages and habitat continuity (Lange et al., 2014).

Increasing the proportion of unmanaged forest reserves is therefore a central goal of international and national conservation strategies (e.g. Convention on Biological Diversity CBD (www.cbd.int), EU-Biodiversity strategy (EU-Commission, 2011) (Bücking, 2007; Parviainen et al., 2000), with many countries having even set quantitative targets. The National Biodiversity Strategies of Germany and Switzerland, for example, aim at increasing the share of unmanaged forests from currently 1.9% and 2.5%, respectively, to 5% (BMU, 2007; Bolliger et al., 2012). Recently established "strict forest reserves" are expected to gradually acquire the structural complexity of secondary natural forests and develop towards primeval ecosystem references (Körner et al., 1997). However, the effectivity and efficiency of this conservation measure in supporting different components of forest biodiversity, as well as the minimum required reserve size and restoration time for supporting multiple conservation targets are largely unknown. The pace and magnitude at which this transition takes place strongly depends on the structural and seral stage of the forest at the time of management cessation, as well as the prevailing factors driving natural dynamics, such as the frequency of biotic and abiotic disturbances, site-specific properties like climate and soil conditions and the duration and intensity of previous management (Brang et al., 2011a). This makes exact predictions about the natural development of a forest after protection very difficult (Nagel et al., 2013). In addition, the various components of structural complexity may change differently: most forests are relatively "young" when they are released into natural development, i.e. most trees have maximally reached their optimal phase. At this phase, at least for the first decades after management cessation, timber stock is still expected to increase and forests will grow denser, until natural disturbances or decay take place (Scherzinger, 1996). This process might reduce the light availability for sub-canopy species, which was formerly periodically provided by logging. In absence of natural disturbances, management cessation can therefore lead to a reduction in light-demanding species (Nagel et al., 2013) and consequently a reduction in tree species richness (Heiri et al., 2009). Other structural components, in contrast, like old trees, coarse woody debris and standing deadwood are expected to increase continuously with the age of a reserve (Tyrrell and Crow, 1994; Vacek et al., 2015).

Abandonment of forest use may therefore favour or disadvantage different species and functional groups, depending on their competitive strength and key habitat requirements and alter the community composition. Although overall biodiversity was found to be higher in unmanaged forests, the effect of management cessation differed considerably between the investigated species groups and also between species of the same taxonomic group (Paillet et al., 2010). As a consequence, the designation of strictly protected forest reserves is controversially discussed, even among conservationists. While the long-term benefit of natural forest development for biodiversity is generally unchallenged, the abandonment of management might – at least temporarily – endanger some, particularly photophilic species.

In this study, we focused on the effect of management cessation on the habitat suitability for indicator species of structural complexity in mountain forest habitats. We selected four forest bird species, indicative of different forest structural characteristics, for which, based on their habitat requirements, diverging response patterns to reserve designation could be expected: Capercaillie (*Tetrao urogallus*), Hazel grouse (*Bonasa bonasia*), Three-toed woodpecker (*Picoides tridactylus*) and Pygmy owl (*Glaucidium passerinum*). All these indicator species are hypothesized to benefit from management cessation in the long run. However, in the absence of disturbing agents, we expect forest closure and homogeneisation the first period after reserve designation causing a decrease in habitat suitability for the two forest grouse species, in contrast to a continuous increase in habitat suitability for the deadwood-associated woodpecker and an intermediate or even indifferent response for the Pygmy owl, a predator and secondary cavity breeder. To test our hypotheses, we compared species-specific habitat suitability – as well as key habitat structures – in managed and unmanaged forests and assessed their state in relation to the time since reserve designation. The results are expected to contribute to objectifying the debate around the effects of strict forest protection on mountain forest biodiversity, and to inform systematic reserve selection processes.

2. Material and methods

2.1. Study area

The study was conducted in four mountain regions in Switzerland and Southwestern Germany with sympatric occurrence of the four model species but different environmental and altitudinal profiles: the lowest and northernmost region, the Black Forest, expands over 7000 km^2 in Southwestern Germany, with elevations ranging from 120 to 1493 m a.s.l (mean: 663). The Swiss Jura in Western Switzerland, 4200 km^2 in size, covers an altitudinal range between 500 and 1718 m a.s.l (mean: 817). The Swiss Alps were represented by two climatically and geographically distinct regions: the Northern Prealps with altitudes between 370 and 3227 m a.s.l. (mean 1391), and the Eastern Central Alps, with altitudes from 560 to 4010 m a.s.l. (mean: 2112) (Gonseth et al., 2001) (Fig. 1). While in the two lower-altitude regions the forests are patchily distributed and interspersed with pastureland, the forests in the two Alpine regions surround treeless mountain tops. Forest composition also varies along the altitudinal gradient, with decreasing proportions of European beech (*Fagus sylvatica*) and silver fir (*Abies alba*) and an increasing share of Norway spruce (*Picea abies*) when moving from the submontane to the subalpine belt.

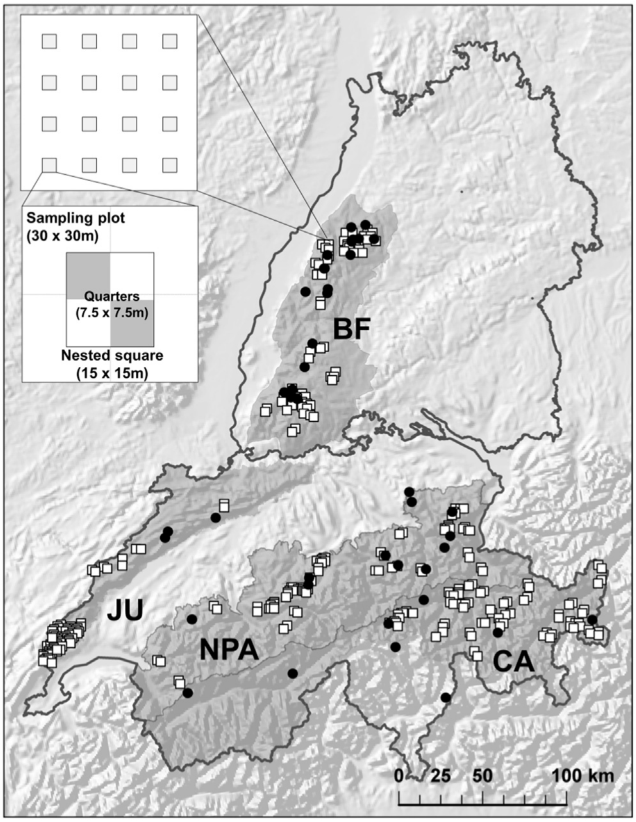

Fig. 1. Study regions in Switzerland and Southwestern Germany (BF: Black Forest, JU: Swiss Jura, NPA: Northern Prealps, CA: Central Alps) with the location of 1 km^2 grid cell-pairs with either presence or absence of the model species (white squares) and unmanaged forest reserves (black dots). The insert illustrates the sampling scheme for recording forest vegetation and structure at regularly distributed sampling plots: Whereas some variables were mapped across the whole plot (30 × 30 m) others were mapped within a nested square (15 × 15 m) the two diagonal corners of which were used to record the ground vegetation. Lying deadwood was counted along a 4x15m long transect representing the outline of the nested square according to the method described in Braunisch et al. (2014).

Moreover, larger proportions of larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) can be found in the Eastern Central Alps.

2.2. Model species and hypothesized response to management cessation

The four model species were selected as they are all strongly associated to different structural components in boreal and mountaineous forests of Europe and are – singly and in combination – considered as good indicators for forest structural complexity (Magg et al., 2019). Their sympatric occurrence and narrow ecoclimatic niche (Braunisch et al., 2013) makes them suitable for studying responses to forest structural developments under similar environmental conditions.

The Capercaillie is a species of old, open, coniferous and mixed forests (Graf et al., 2007) with a rich field layer, ideally dominated by bilberry (*Vaccinium myrtillus*) (Storch, 1993). The species is declining throughout its Central European range, with habitat deterioration, human disturbance, increasing predator abundance and climate warming considered as the main factors (Storch, 2001). Especially in the lower mountain ranges, Capercaillie had strongly benefitted from the forest-overexploitation in the second half of the 19th century (Suchant and Braunisch, 2004) and suffers now from the change from rotation forestry to selective cutting, associated with increasing canopy closure, a lack of clearings and forest structural homogenization at the landscape scale (Graf et al., 2007; Suchant and Braunisch, 2004). We therefore hypothesize this species to suffer in the first decades after management cessation due to canopy closure and a decrease in ground vegetation cover. Once reserves reach older seral stages and disturbance events (Kortmann et al., 2018; Mikoláš et al., 2017) or natural decay processes create a mosaic of different successional stages, we expect habitat suitability to increase again.

The Hazel grouse prefers early successional stages and small regeneration areas in old-growth forests, and is very sensitive to forest structure (Bergmann et al., 1996; Schäublin and Bollmann, 2011). In old-growth forest suitable conditions can be maintained by small-scale disturbances, like wind throw, snow break or insect infestations (Kortmann et al., 2018) or created by management (Hofstetter et al., 2015). Buds and catkins of softwood trees are the key winter food, and the removal of these species under earlier forest management regimes is considered a main driver of the dramatic declines in most Central European mountain regions (Bergmann et al., 1996). As the species depends on early successional stages, we expect a similar response pattern to management cessation as Capercaillie, i.e. disappearance from homogeneously structured reserves in the optimal phase and a later return with structural heterogenization and the return of pioneer trees.

The Three-toed woodpecker is a widespread keystone species in boreal and alpine coniferous, particularly spruce-dominated forests (Wesolowski et al., 2005). The species strongly depends on the abundance of dead and decaying trees (Bütler et al., 2004; Zielewska-Büttner et al., 2018), which are essential for excavating breeding cavities and foraging on bark beetles and other saproxylic insects (Pakkala et al., 2002; Wesolowski et al., 2005). We expect the Three-toed woodpecker to strongly benefit from reserve creation, as the amount of deadwood is expected to increase, either gradually, due to local insect infestations, or rapidly, when mass infestations follow natural disturbance events.

The Eurasian Pygmy owl is distributed from Central and Northern Europe to eastern Siberia (König et al., 2008), where it inhabits well-structured, semi-open boreal and montane coniferous and mixed forests (Schönn, 1995) with mature trees and clearings (König et al., 2008). Pygmy owls hunt in different successional stages and along inner forest edges (Strom and Sonerud, 2001), which offer elevated perches and a greater availability and accessibility of prey (Strom and Sonerud, 2001). The secondary cavity breeder (Piorecky and Prescott, 2006) is often limited by a shortage and strong intra- and interspecific competition for woodpecker holes (Newton, 1994), which are used for nesting, roosting and prey storage (Strom and Sonerud, 2001). We expect Pygmy owl to generally benefit from reserve designation due to an increasing amount of snags. However, especially in the first phase after reserve designation, this benefit might be blurred by structural homogenization, a decrease of edges and seral stage mosaics, which may only occur in old forest reserves.

2.3. Study sites

2.3.1. Forest sites with species presence or absence

In a first step we selected forest sites, independently of their management status, with either presence or absence of the respective study species (in the following referred to as “presence/absence grid cells”). Data of species presence were adopted from the Swiss Ornithological Institute, Sempach, Switzerland (http://www.ornitho.ch), and the Forest Research Institute of Baden-Württemberg (FVA), Germany (https://wimo.wildtiermonitoring.de). Both databases contain long-term observation data from ornithologists, foresters, hunters, and private birdwatchers at a minimum resolution of 1 km^2. In each of the four study regions we randomly selected at least ten 1 km^2 grid cells with presence per model species, i.e. with confirmed observations in at least three years between 2006 and 2010 (Table 1, Fig. 1). For each presence grid cell, a corresponding “absence” cell was selected, with “absence” defined as no species proof within the preceding ten years (2001–2010). To ensure that absence cells are reachable by the species,

Table 1
Number of grid cell pairs (1 km^2) with species presence or absence selected in each of the mountain regions across the study area (BF: Black Forest, J: Swiss Jura, NPA: Northern Prealps, CA: Central Alps). In each region, a minimum of 10 pairs were selected, except for Hazel grouse in the Black Forest, as it got extinct there. Due to species co-occurrence, several grid cells were included in the models of more than one species.

Species	BF	J	NPA	CA	Total
Capercaillie	23	21	16	11	71
Hazel grouse	0	28	27	13	68
Three-toed woodpecker	11	12	30	15	68
Pygmy owl	15	22	21	13	71

they were randomly selected within a minimum distance of one and maximum 5 km to the presence cell, from all cells that had at least 50% forest cover. We selected a similar number of grid cell-pairs for each species, yet, since some cells were occupied sympatrically by two or more species and some cells turned out to be inaccessible during fieldwork and were therefore dropped, the final number of sites used in the analyses differed between species and mountain regions (Table 1).

2.3.2. Forest reserves

In addition, we investigated 42 unmanaged forest reserves in the four study regions that were located in the same altitudinal range as the species presence or absence grid cells (i.e. 450–2350 m a.s.l.). With 88.1 ha (SD: 54.7) the average size of the reserves roughly corresponded the size of the presence/absence grid cells (100 ha), the minimal size of included reserves was set to 10 ha. In addition, of very large reserves (> 300 ha) only a part was sampled. As the reserves that met the selection criteria were unevenly distributed, their number differed between the study regions (Table S1).

2.4. Assessment of forest composition and structure

Forest structures were mapped at sampling plots of 30 × 30 m, regularly distributed across the study sites (Braunisch et al., 2014). In each of the 1 km^2 grid cells, 16 plots were placed (Fig. 1). In the forest reserves, we adopted the plot-raster of the respective reserve monitoring scheme (Brang et al., 2008). Depending on the reserve size, the distance between the plots varied between 50 and 200 m. First, plots within a 50 m buffer zone from the reserve boundaries and forest trails were discarded to avoid edge effects. Then, plots outside the forest and on inaccessible cliffs were omitted. Of the remaining plots, a minimum of 20 plots per 100 ha area (i.e. smaller reserves were also represented by at least 20 points) were selected in a systematic way so as to achieve a good spatial coverage of the whole reserve area.

Plot centers were located using a handheld GPS, and plots orientated parallel to the slope. At each plot we collected information on stand structure, vegetation cover, tree species and ground vegetation composition and special habitat features or resources relevant to the focal species (Table 2). For matter of precision, different variables were recorded at different reference areas around the plot center: tree species composition, successional stage, vertical and horizontal stand structure, the presence of ecotones and the abundance of selected species-relevant features (e.g., basal-branched trees or snags) were recorded within the whole 30 × 30 m plot, whereas special resources like the number of rowans (*Sorbus aucuparia*) were quantified within a nested square of 15 × 15 m, the two diagonal quarters of which (7.5 × 7.5 m) were used to assess ground vegetation composition and structure (Fig. 1). In addition, lying deadwood was counted along a transect that corresponded to the border of the nested square. The description of the variables and the reference scale at which they were measured are detailed in Table 2.

2.5. Statistical analysis

2.5.1. Habitat suitability

The relative probability of presence of each species (in the following termed "habitat suitability") was modelled as a function of forest structure recorded within the presence-absence grid cells. We used generalized linear mixed models (as implemented in the R-package *lme4*, Bates et al., 2014) with a binomial error distribution and the grid-cell pair included as a random effect. To select the variables that best explained species presence we identified the most parsimonious model using an information-theoretic approach based on Akaike's Information Criterion (AIC) (Burnham and Anderson, 2002; Johnson and Omland, 2004).

First, for each species, univariate models were run for each predictor variable, testing also the quadratic term for variables for which we expected a unimodal response. Of pairs of univariately significant but correlated variables (|Spearman's r| > 0.7) (Spearman, 1904) we discarded the least performing one based on the univariate AIC. Subsequently, we identified the "best", i.e. most parsimonious model from models including all possible combinations of the retained variables using the "*dredge*"-function of the R-package *MuMIn* (Bartón, 2014). AIC-ranking was performed using the function *aictab* of the R package *AICcmodavg* (Mazerolle, 2014). Finally, the models' fit was evaluated using the area under the receiver operating characteristics (ROC) curve (AUC).

2.5.2. Habitat suitability of managed and unmanaged forests

We used the best model for each species for predicting the habitat suitability at each sampling plot, both within the presence-absence-grids and the forest reserves and calculating the average suitability per site. We then regrouped the sites according to their management status and compared the species-specific habitat suitability, as well as key variables, of three site-categories: managed forest sites with either (1) species presence or (2) species absence and (3) unmanaged forest reserves using a Kruskal-Wallis-Test (Kruskal and Wallis, 1952) followed by a Wilcoxon-Mann-Whitney-Test (Wilcoxon, 1945) for pairwise assessment of differences.

2.5.3. Effect of reserve age on habitat suitability and key structural variables

Finally, the species-specific habitat suitability of each reserve was related to the age of the reserve, which was defined as the time since reserve designation. We used generalized additive models with a Gaussian error distribution, first accounting for potential regional effects by including the study region as a random factor (package *gamm4*) but changing to simple generalized additive models (package *gam*) (Wood, 2017) as no regional effect was found. Similarly, we modelled canopy cover, as the main indicator of light availability, the amount of standing deadwood, as well as species-specific key variables as a function of reserve age (i.e. time since reserve designation). Model fit was evaluated calculating a pseudo *R*-squared with the explained deviance. All analysis were done with R version 3.3.1 (R-Core-Team, 2014).

3. Results

3.1. Habitat selection

Despite using only vegetation variables, the presence of all four model species was predicted with a good level of accurracy (AUC-values > 0.7, Hosmer et al., 2013). The main predictors (Table 3) largely corresponded with previous results. Capercaillie presence-probability was highest in coniferous mixed forests with abundant and patchy ground vegetation dominated by bilberry. The presence of other berries, rowans and basal branched trees also had a positive effect on this species, whereas outer forest edges were avoided by both Capercaillie

Table 2
Variables recorded in the sampling plots, with the variable code, description and unit. Reference surface indicates the part of the plot at which the variable was mapped (see Fig. 1).

Category/Variable	Code	Description	Unit	Reference surface
Stand structure				
Successional stage	SUCC	1 = regeneration (< 1.3 m height) 2 = thicket (< 10 cm DBH*) 3 = pole stage (< 30 cm DBH) 4 = tree stage (< 60 cm DBH) 5 = “old” forest (≥3tr. > 60 cm DBH) 6 = multi-age	Categorical	30 × 30 m
Stand structure	STANDSTRU	1 = one layered 2 = two layered 3 = multi layered	Categorical	30 × 30 m
Inner forest edge	E_INNER	Presence of inner forest edge	1/0	30 × 30 m
Outer forest edge	E_OUTER	Presence of outer forest edge	1/0	30 × 30 m
Vegetation cover				
Canopy cover	CANCOV	Canopy (≥5m) cover	%	30 × 30 m
Shrub cover	SHRUBCOV	Shrub (≥1.3 m < 5 m) cover	%	30 × 30 m
Ground vegetation cover	GVCOV	Ground vegetation (< 1.3 m) cover	%	30 × 30 m
Ground vegetation distribution	GVDIS	The pattern of ground vegetation was classified into 3 categories: 1 = homogeneous, 2 = patchy, 3 = clumped	categorical	30 × 30 m
Tree species composition (estimated for shrub layer: SHR_, canopy layer: CAN_, and both combined: ALL_)				
Beech	BEE	Percent of beech (*Fagus sylvatica*)	%	30 × 30 m
Spruce	SPR	Percent of spruce (*Picea abies*)	%	30 × 30 m
Pine	PIN	Percent of pine (*Pinus* spp.)	%	30 × 30 m
Fir	FIR	Percent of fir (*Abies alba*)	%	30 × 30 m
Ressource trees	RESTREE	Percent of resource trees (*Sorbus* spp., *Salix* spp., *Betula* spp., *Alnus* spp., *Corylus* spp. and *Sambucus* spp.)	%	30 × 30 m
Ground vegetation				
Ground vegetation height	GVHEI	Height of ground vegetation	cm	7.5 × 7.5 m
Herbs	HERB	Percent of herbs	%	7.5 × 7.5 m
Ferns	FERN	Percent of ferns	%	7.5 × 7.5 m
Grasses	GRASS	Percent of fir grass	%	7.5 × 7.5 m
Vaccinium	VAC	Percent of bilberry (*Vaccinium* spp.)	%	7.5 × 7.5 m
Berries	BERRY	Percent of berries (other than *Vaccinium* spp.)	%	7.5 × 7.5 m
Coniferous regeneration	CON	Percent of coniferous regeneration	%	7.5 × 7.5 m
Deciduous regeneration	DEC	Percent of deciduous regeneration	%	7.5 × 7.5 m
Special features				
Standing deadwood	STANDDEAD	Standing dead trees (snags) > 12 cm	number	30 × 30 m
Basal-branched trees	BBTREE	Trees with branches < 50 cm above ground	number	30 × 30 m
Rowans	ROWAN	Rowans > 3 m	number	15 × 15 m
Ant hills	ANTHILL	Anthills	number	15 × 15 m
Hard stumps	HSTUMP	Hard stumps > 12 cm	number	15 × 15 m
Soft stumps	SSTUMP	Soft stumps > 12 cm	number	15 × 15 m
Lying deadwood	LDEAD	Deadwood > 7 cm diameter, > 1 m length	number	4 × 15 m transect

and Hazel grouse. The latter species selected forest stands where coniferous tree species (spruce, pine and fir) were intermixed with a high share of softwood trees and rowans. Positive effects were also found for basal-branched trees and abundant, patchily distributed ground vegetation with bilberry. Three-toed woodpecker habitats were characterized by spruce-dominated forests with a high amount of standing dead trees. Hard stumps, a sign for recent logging, were negatively correlated with woodpecker presence. Pygmy owl presence was highest in spruce- and pine-dominated forests with a high abundance of inner forest edges. The positive association with basal-branched trees and an abundant ground vegetation cover indicates the species preference for structurally heterogeneous forests. Detailed model results are presented in Table 3.

3.2. *Habitat suitability of managed and unmanaged forests*

Habitat suitability of all model species differed between the three forest categories (Kruskal-Wallis-Test (KW), p-value: < 0.001 in all cases). For all species except Pygmy owl, unmanaged forest sites were of similar habitat quality to managed forest sites with species presence, and both differed significantly from managed forest sites with species absence (Fig. 2a–c, for details see Table 4). For Pygmy owl, the predicted habitat suitability of unmanaged forest sites did not differ from that of managed forests with species absence, both being significantly less suitable than managed sites with species presence (Fig. 2d, Table 4). For all four species, the between-site variance in habitat suitability was much higher in unmanaged forests than in the two other forest categories (Fig. 2, Table 4).

3.3. *Key habitat variables in managed and unmanaged forests*

Key habitat variables, selected for the four model species based on literature, were bilberry cover for Capercaillie, the share of resource trees for Hazel grouse, standing dead wood for the Three-toed woodpecker and the relative amount of inner forest edge presence for Pygmy owl. According to their contribution to the AIC, all variables also revealed a high relative importance in the respective species models (Table 3). In addition, we also investigated canopy cover, as an indicator of canopy openness.

Bilberry cover (KW: $p < 0.001$) was significantly higher in managed sites with Capercaillie presence (mean: 20.4%) than absence (mean: 8.2%) (post-hoc Wilcoxon-Mann-Whitney test (WMW): $p < 0.001$). Forest reserves (mean: 16.5%) showed significantly lower bilberry cover than presence sites (WMW: $p = 0.045$) but higher than absence sites (WMW: $p = 0\ 0.017$) (Fig. S1a). In managed Hazel grouse presence sites, the share of resource trees (KW: $p = 0.004$) was higher

Table 3

Results of the habitat selection models of the four model species. The relative importance of each variable is indicated by the increase in AIC (Δ AIC) when omitting the respective variable from the full model. Model fit is indicated by the Area under the ROC-curve (AUC). For variable codes see Table 2.

Variable	Estimate	SE	z-value	p-value	Δ AIC
Capercaillie (AUC: 0.752, SD: 0.012)					
(Intercept)	−1.061	0.389	−2.727	0.006	
GVDIS_2	0.537	0.269	1.994	0.046	22.7
GVDIS_3	−0.340	0.254	−1.340	0.180	
GVCOV	0.011	0.003	3.633	< 0.001	11.4
VAC	0.034	0.004	7.640	< 0.001	64.2
BERRY	−0.019	0.008	−2.459	0.014	4.3
ALL_SPR	0.029	0.008	3.644	< 0.001	11.5
ALL_SPRˆ2	−0.0002	0.000	−2.641	0.008	
ALL_PIN	0.019	0.006	3.185	0.001	8.9
ALL_BEE	−0.051	0.009	−5.570	< 0.001	24.0
ALL_BEEˆ2	0.001	0.000	5.261	0.000	
HSTUMP	−0.114	0.050	−2.266	0.023	3.5
ROWAN	0.090	0.029	3.147	0.002	9.9
BBTREE	0.129	0.035	3.722	< 0.001	13.2
E_OUTER	−0.709	0.269	−2.633	0.008	5.0
Hazel grouse (AUC: 0.758, SD: 0.013)					
(Intercept)	−2.157	0.453	−4.757	< 0.001	
STANDSTRU_2	−0.394	0.194	−2.032	0.042	0.1
STANDSTRU_3	−0.178	0.174	−1.027	0.304	
GVDIS_2	0.888	0.323	2.752	0.006	12.5
GVDIS_3	0.011	0.271	0.040	0.968	
GVCOV	0.011	0.003	3.173	0.002	8.2
GVHEI	0.020	0.011	1.916	0.055	2.2
GVHEIˆ2	−0.0002	0.000	−2.356	0.018	
VAC	0.028	0.006	5.085	< 0.001	26.8
DEC	−0.034	0.010	−3.494	< 0.001	11.2
ALL_SPR	0.016	0.004	4.264	< 0.001	17.7
ALL_PIN	0.029	0.007	4.426	< 0.001	20.4
ALL_FIR	0.012	0.006	2.003	0.045	2.0
ALL_RESTREE	0.035	0.007	4.889	< 0.001	24.6
ROWAN	0.070	0.034	2.097	0.036	3.0
BBTREE	0.219	0.041	5.405	< 0.001	32.2
E_OUTER	−0.754	0.244	−3.090	0.002	7.6
Three-toed woodpecker (AUC: 0.724, SD: 0.014)					
(Intercept)	−0.927	0.409	−2.264	0.024	
CANCOV	−0.009	0.004	−2.342	0.019	3.6
SHRUBCOV	−0.016	0.004	−3.670	< 0.001	12.0
GVCOV	0.006	0.003	2.109	0.035	2.5
CAN_SPR	0.020	0.003	7.979	< 0.001	74.5
CAN_PIN	0.022	0.006	4.023	< 0.001	17.4
HSTUMP	−0.134	0.046	−2.944	0.003	7.9
STANDDEAD	0.099	0.020	4.880	< 0.001	29.9
Pygmy owl (AUC: 0.708, SD: 0.014)					
(Intercept)	−2.729	0.371	−7.347	< 0.001	
GVDIS_2	0.833	0.313	2.661	0.008	7.0
GVDIS_3	0.326	0.296	1.103	0.270	
GVCOV	0.019	0.003	6.303	< 0.001	39.8
CAN_SPR	0.019	0.003	7.487	< 0.001	61.7
ALL_PIN	0.025	0.005	5.010	< 0.001	27.2
BBTREE	0.388	0.065	6.013	< 0.001	46.8
E_INNER	0.893	0.265	3.366	0.001	10.0

(mean: 12.3%) than in absence sites, (mean: 7.8%, WMW: $p = 0.007$). Forest reserves had similar shares (mean: 7.2%, WMW: $p = 0.285$) which were lower than in presence sites (WMW: $p = 0.005$) (Fig. S1b). The number of dead trees per plot (KW, $p < 0.001$), by contrast, was highest in forest reserves (mean: 6.4), followed by managed forests with Three-toed woodpecker presence (mean: 3.1) and absence (mean: 1.6) (WMW: $p < 0.001$ for all pairwise comparisons). (Fig. S1c). Inner forest edges differed in abundance (KW: $p = 0.016$) between managed forests with Pygmy owl presence (mean: 0.14) and absence (mean: 0.05) (WMW: $p = 0.007$). Forest reserves, showed intermediate values (mean: 0.06), which neither differed from presence (WMW: $p = 0.094$) nor from absence sites (WMW: $p = 0.180$) (Fig. S1d).

3.4. *Effect of reserve age on habitat suitability and key structural variables*

For Capercaillie, Hazel grouse and Pygmy owl habitat suitability in the unmanged forest reserves was significantly related to the time after reserve designation (Table 5). The deviance explained by the models ranged between 35.8% (Pygmy owl) and 37.9% (Hazel grouse).

In line with our key assumption, habitat suitability of the two grouse species first dropped markedly with reserve age and was lowest in “young” reserves with three decades of management cessation, thereafter it increased again and leveled off in reserves of about 70 years and older (Fig. 3a, b). For the Pygmy owl, we found a similar pattern (Fig. 3d), however habitat suitability continued to increase with reserve age up to 104 years, the age of our oldest reserve. No significant relationship was found for habitat suitability of the Tree-toed woodpecker (Fig. 3c).

The species-specific response could be well explained by key structural variables: whereas canopy cover was significantly related to reserve age, with a high cover in young and lower cover in the older reserves (Fig. 3e, Table 5), the amount of standing deadwood, the key resource for the Three-toed woodpecker, showed no significant pattern (Fig. 3f, Table 5). In addition, no other of the key habitat variables showed any clear trend in relation to time since reserve designation.

4. Discussion

Our results confirm that strict forest reserves can – on average – provide suitable habitat for different mountain forest bird species of conservation concern. However, independently of the species or study region, habitat suitability as well as structural characteristics varied greatly between reserves. In support of our hypothesis we show that this variance can be partly explained by the reserve age. For the three species associated with heterogeneous and open forest structures, habitat suitability was markedly lower in reserves undergoing the first decades of secondary forest succession and increased afterwards to or above former levels in older reserves. This pattern was paralleled by an opposite trend in canopy closure, supporting the often discussed concern that open structures and associated light availability might temporarily limit open forest species in the initial transition phase after management cessation. Canopy cover influences the subcanopy light regime and was strongly correlated with ground vegetation cover (Ford and Newbould, 1977), a key habitat variable for all species. Such a temporal pattern was found for none of the other key structural variables, even not for the abundance of standing deadwood, which was significantly higher in forest reserves than in managed forests, but independent of the reserve age. This finding is in line with other studies demonstrating a fast and substantial increase in deadwood volume after management cessation (Meyer and Schmidt, 2011; Vacek et al., 2015; Vandekerkhove et al., 2009). Nevertheless, apart from the management regime, our models do not account for variance in abiotic factors such as soil conditions, climate and topography. Despite all sites being selected from mixed coniferous forests in the montane and high-montane zone, these factors are likely to cause additional variance in the system.

4.1. *Habitat suitability, variability and development*

Forest reserves provided suitable structures for bird species indicative of different structural characteristics, but open structures were found to be limiting in the first decades after designation. This is mainly due to the fact that almost all strict forest reserves are still relatively young (< 100 years since designation) and originate from formerly managed forests of 80–150 years. Although we have no information about the reserves' exact age structure and habitat suitability at the time of designation, they were all still in the optimal phase and hence expected to first grow denser before starting to accumulate typical attributes of natural stand dynamics and disturbance patterns (Brang et al., 2011b). Age structure at the start of the non-intervention phase

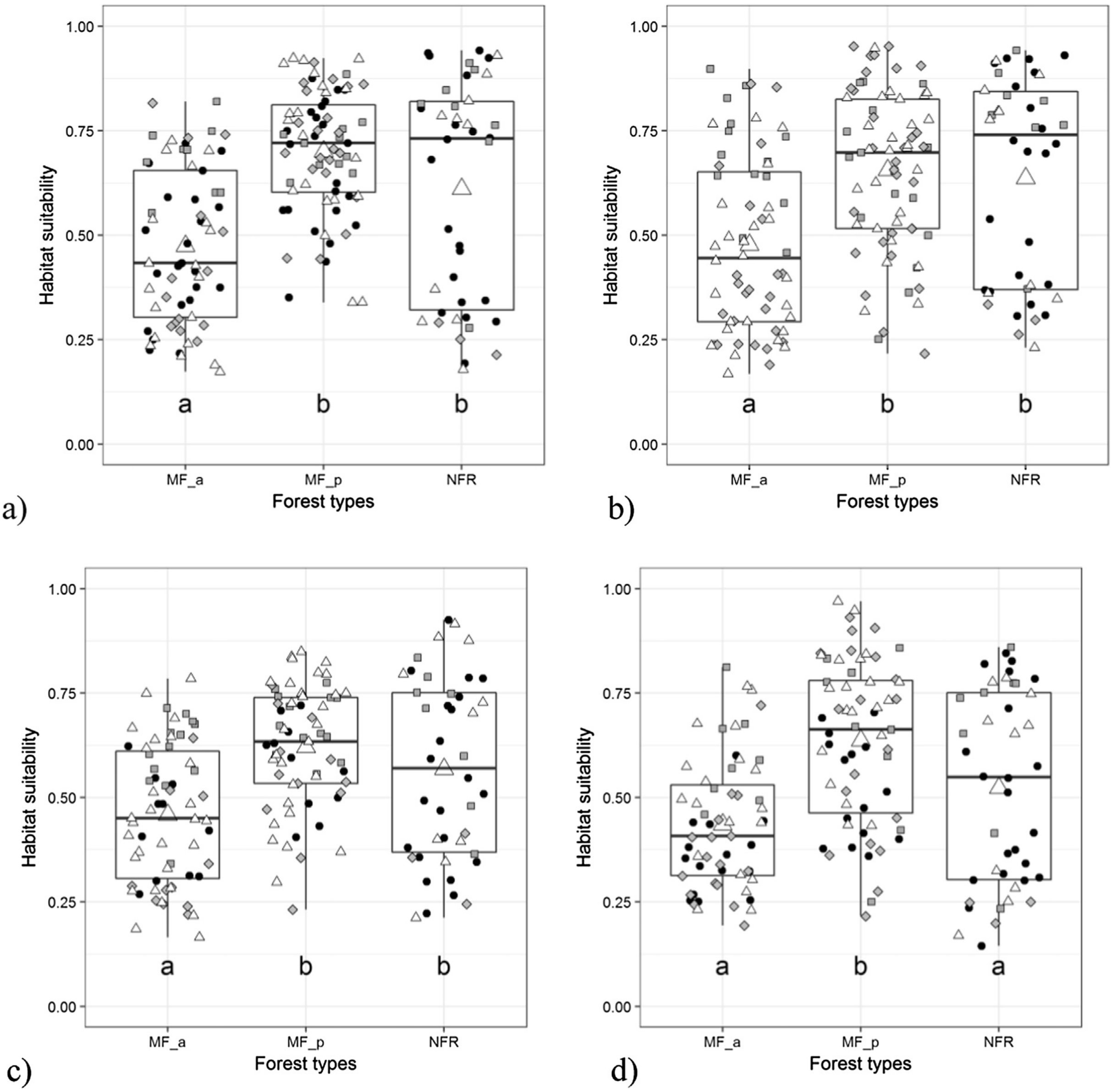

Fig. 2. Habitat suitability of managed forests with species absence (MF_a) or presence (MF_p) in comparison to unmanaged strict forest reserves (NFR) for Capercaillie (a), Hazel grouse (b), Three-toed woodpecker (c) and Pygmy owl (d). Symbols indicate the mean suitability per forest site in the Black Forest (black points), Swiss Jura (grey diamonds), Northern Prealps (white triangles) or Central Alps (grey squares). Different letters below the boxplots indicate significant differences between management types, details are shown in Table 4.

Table 4
Species-specific habitat suitability (mean and standard deviation SD) in managed forests with species presence (MF_p) or absence (MF_a) and unmanaged natural forest reserves (NFR) as shown in Fig. 2a–d. Significant differences in habitat suitability between the three site categories were found for all species (Kruskal-Wallis (KW) test, with pairwise differences assessed using on a post-hoc Wilcoxon Man-Whitney (WMW)).

Category	Habitat suitability						KW-test		Pairwise differences (WMW-test)					
	MF_a		MF_p		NFR				MF_a - MF_p		MF_p - NFR		MF_a - NFR	
	mean	SD	mean	SD	mean	SD	chi2	*p*	W	p	W	p	W	*p*-value
Capercaillie	0.474	0.184	0.701	0.147	0.610	0.266	38.967	< 0.001	4077	< 0.001	1415	0.310	1821	0.004
Hazel grouse	0.477	0.209	0.655	0.189	0.637	0.245	24.007	< 0.001	1244	< 0.001	1528	0.979	1878	< 0.001
T-t woodpecker	0.458	0.165	0.620	0.143	0.568	0.219	25.118	< 0.001	959	< 0.001	1191	0.268	1722	0.009
Pygmy owl	0.435	0.156	0.636	0.192	0.522	0.233	27.813	< 0.001	793	< 0.001	945	0.014	1487	0.088

Table 5
Generalized additive models showing the relationship between the habitat suitability (HS) of the four model species, as well as two key habitat parameters (canopy cover and standing deadwood) with the time since reserve designation (reserve age). The model fit is indicated by the adjusted *R*-squared as well as the explained deviance.

	Parametric coefficients (Intercept)				Smooth term (Reserve age)				Model fit	
Dependent variable	Estimate	SE	*t*-value	*p*-value	edf	Ref.df	*F*	*p*-value	R^2(adj)	Expl.Dev. (%)
HS Capercaillie	0.610	0.035	17.600	< 0.001	4.282	5.163	3.395	0.011	0.285	35.90
HS Hazel grouse	0.637	0.031	20.220	< 0.001	4.394	5.285	3.606	0.007	0.305	37.9
HS Three toed woodpecker	0.568	0.031	18.620	< 0.001	3.825	4.655	2.331	0.068	0.185	26.1
HS Pygmy owl	0.522	0.030	17.230	< 0.001	3.866	4.701	3.867	0.008	0.292	35.8
Canopy cover	51.449	2.517	20.440	< 0.001	4.866	5.797	2.264	0.050	0.217	31.0
Standing deadwood	6.388	0.929	6.876	< 0.001	1.000	1.000	0.257	0.615	−0.019	0.6

plays a crucial role because tree mortality and deadwood accumulation rate increase with tree maturation (Peterken, 1996). This influences gap dynamics which is crucial for forest species such as Hazel grouse and Capercaillie which are obligate to open areas and regeneration stages in early and late successional forest habitats, respectively (Bollmann et al., 2005; Braunisch et al., 2014; Schäublin and Bollmann, 2011), and have been shown to benefit substantially from large-scale disturbances (Kortmann et al., 2018; Rosner et al., 2014).

There is good evidence for the temporal dependence of ecosystem processes after land use abandonment (Freschet et al., 2014), particularly the recovery of old-growth attributes such as large ancient trees and deadwood (Paillet et al., 2015) is considered to take very long time (Burrascano et al., 2013; Silver et al., 2013) until reaching the expected values of pristine mixed mountain forests (Müller and Bütler, 2010). However, deadwood accumulation is only partly a continuous process and depends also on the frequency and magnitude of natural disturbances (Kulakowski et al., 2017) which are common in montane and high-montane conifer-dominated forests (Kurz et al., 2008). This may explain why we did not find the expected, continual increase in deadwood amounts and associated habitat suitability for the Three-toed woodpecker with reserve age. While forest reserves offered on average much higher deadwood amounts than managed forests, the highest amounts were even found in the youngest reserves (Fig. 3f) which had undergone disturbance events. Moreover, our study only refers to standing deadwood without considering deadwood quality. Whereas natural disturbances such as windthrow and insect outbreaks can rapidly produce high amounts of deadwood also in young seral stages, senescent and naturally decaying trees only slowly accumulate with reserve age (Peterken, 1996). The Three-toed woodpecker, mainly depending on bark beetles attacking freshly dying spruce trees (Balasso, 2016), thus responds differently than old-growth obligates such as epiphytic bryophytes (Ódor et al., 2013; Ódor and van Hees, 2004), lichens (Dymytrova et al., 2014) or heart-rot agent fungi (Heilmann-Clausen and Christensen, 2004) which often rely on large, downed trunks and old decay stages and should continually benefit from the process of forest maturation (Dittrich et al., 2013; Hilmers et al., 2018). The data in our study originate from a climatically and regionally representative set of mountain forest reserves of Central Europe, and our species represent different seral stages and nutritional guilds as well as being complementary indicators for structural complexity in mountain forests (Magg et al., 2019). We therefore consider our results also applicable for large parts of the mountain forest species community which rely on similar key structures, particularly on open and structurally heterogeneous forest stands.

4.2. Management cessation and long-term effects

While the impact of human forest use in biodiversity conservation is relatively well understood, we know little about how management cessation as restoration measure will modify ecosystem properties and functioning in the medium and long term. Our study provides some evidence that even mid-term transition processes have the potential to drive the forest along alternative trajectories mainly determined by maturation and disturbance.

The high inter-reserve variability in habitat suitability and deadwood abundance in our study is likely resulting from differences in the silvicultural legacy between forest reserves as well as in their exposure to natural disturbances. Moreover, our study could consider only the first 100 years after management cessation with only few old reserves available to represent the right tail of the gradient. A stronger focus on long-term (> 200 yr) consequences of secondary succession would be necessary to better predict ecosystem trajectories after land use abandonment. However, it should be noted that time since reserve designation must not necessarily equal the time of management cessation. Many forest reserves have been designated in remote and economically unviable areas, which were only extensively managed before they were selected as natural forest reserves (Brang et al., 2011b). Only for very few reserves information about their “true age”, i.e. the actual time since the last harvesting event, was known, and no information was available about the type and intensity of past management or about the initial structural condition of the reserve. The “reserve age” in our analysis therefore represents an approximation for the true period of secondary natural forest development. Nevertheless, we still found the expected relationships with age, which should be even clearer if the above information could be integrated (Heiri et al., 2012).

4.3. Strict forest reserves as conservation management tools

The primacy of timber production as the dominant objective of silviculture has given way to a multifunctional view of forests and the goal of setting aside 5–10 percent of forests as strict reserves is the related measure to trigger long-term, natural processes in forest landscapes with multi-purpose management (Bollmann and Braunisch, 2013). Since these processes take place on the area of former production forests, secondary natural forests lack the habitat continuity of primeval forests and the associated species (Eckelt et al., 2018), even after a long restoration time. In our study, structural features in strict forest reserves did not differ significantly from those in managed forests, except for deadwood abundance, and – especially for species reliant on open structures – habitat suitability could also be supported by targeted management interventions. Given the relatively small size of the reserves in our study region, which correspond on average to a small territoriy size of our target species, enhancing the species-relevant key structures in the managed forest matrix is essential for supporting viable populations. Yet, while mobile organisms with extensive spatial requirements can use suitable reserves as “resource-hotspots” and spatially avoid unfavourable development stages, our results have stronger implications for less mobile, site-dependent and dispersal limited species: On the one hand, spatial targets with regard to reserve size, spatial configuration and connectivity have to be oriented towards the requirements of such species critically depending on unmanaged forest conditions (e.g. fungi or primeval forest relict beetles, Eckelt

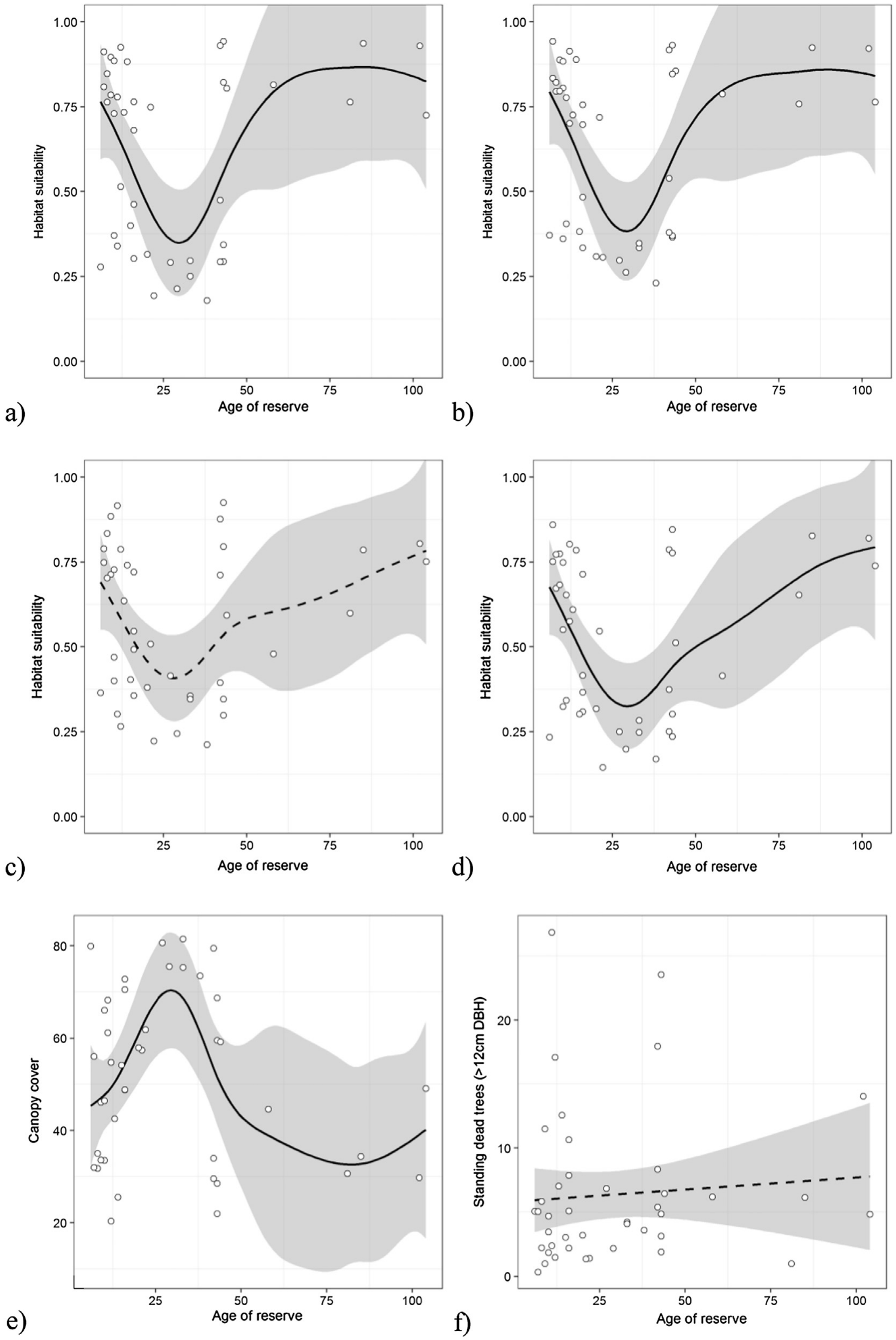

Fig. 3. Habitat suitability for Capercaillie (a), Hazel grouse (b), Three-toed woodpecker (c) and Pygmy owl (d), as well as the two key variables canopy cover (e) and the amount of standing deadwood (f) in strict forest reserves as a function of time since reserve designation (age of reserve) as modelled using generalized additive models. Dashed lines indicate non-significant relationships. Model results are shown in Table 5.

et al., 2018; Heilmann-Clausen and Christensen, 2004). On the other hand, for sedentary or immobile open-forest species, temporary habitat management before or within the first decades after reserve designation may be required to bridge the critical phase. Our results also suggest that temporal management cessation, as often promoted in contractual nature conservation frameworks to enhance structural and biological diversity in private-owned or communal forests, may even be harmful for these species, except if based on long-term contracts. However, the development of structural and functional properties of strict forest reserves depends not only on time since management cessation, but also on the duration and intensity of former forest practices, the regional species pool and the exposure to natural disturbances. Disturbance regimes are climate-sensitive (Seidl et al., 2011), have intensified during the last decades and are expected to further intensify (i.e. increase in frequency, extent and severity) in the future (Seidl et al., 2014; Thom et al., 2017). Especially in forest areas where the average volume of growing stock and stand age increased considerably, forests are expected to be more vulnerable to disturbances (Schelhaas et al., 2003). This may favour and accelerate the development of structural heterogeneity and gap dynamics in both managed and unmanaged forests. We therefore recommend focusing on old, near-natural and structurally diverse forests when designating new reserves. Yet, how, and how fast and how strong natural processes and anthropogenic legacies will shape the reserves' structural composition and associated species community has to be the subject of future investigations.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.06.007.

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