Habitat selection of an old-growth forest specialist in managed forests

A. Ettwein[1], P. Korner[1], M. Lanz[1], T. Lachat[2,3] (iD), H. Kokko[4] (iD) & G. Pasinelli[1,4] (iD)

1 Swiss Ornithological Institute, Sempach, Switzerland
2 School of Agricultural, Forest and Food Sciences HAFL, Zollikofen, Switzerland
3 Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland
4 Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

Abstract

Old-growth forest specialists are among the species most affected by commercial forestry. However, it is often unclear whether such species can persist and what their habitat needs are in managed forests. We investigated habitat selection of one such old-growth forest specialist, the white-backed woodpecker *Dendrocopos leucotos*, a species highly dependent on dead wood and typically found in primeval forests. Our aim was to understand factors affecting occupancy probability in managed forests in Central Europe, based on detection/non-detection data in 62 squares of 1 km^2 in 2015 and 2016. We used occupancy models to compare *a priori* expectations about the relationships between occupancy and habitat characteristics at two spatial scales while accounting for imperfect detection. Occupancy was best explained by a proxy for food availability at a large (1 km^2) scale and increased with the abundance of emergence holes produced by saproxylic beetles on standing and lying dead wood. Furthermore, occupancy was positively related to the mean diameter at breast height of live trees and standing dead wood at a small scale (0.25 km^2 with high amounts of dead wood). Detection probability was negatively related to time of day, date and number of accessible survey points, and positively related to the number of observers. Our results demonstrate that detailed knowledge about a species' foraging ecology is important for its effective conservation as surrogate criteria such as dead wood availability might not reflect the key factors required. For white-backed woodpeckers, it is important that the available dead wood is sufficiently colonized by saproxylic beetles, and for the conservation of the species, the habitat requirements of saproxylic beetles thus have to be taken into account as well.

Introduction

A long history of human land-use has altered forests in many parts of the world. In Central Europe, most forests are characterized by homogeneous tree species composition, vertical stratification and age structure, as well as by low amounts of habitat trees (live or dead trees providing ecological niches, Bütler *et al.*, 2013) and dead wood (Kuuluvainen *et al.*, 1996; Commarmot *et al.*, 2005; Merino *et al.*, 2007; Müller, Hothorn & Pretzsch, 2007; Brumelis *et al.*, 2011). As a consequence, wildlife communities have also changed – often at the expense of specialist species which are sensitive to changes in their environment because of their narrow ecological niche and other characteristics, such as low population size, population growth rate, competitive ability or dispersal ability (Grove, 2002; Henle *et al.*, 2004; Devictor, Julliard & Jiguet, 2008; Clavel, Julliard & Devictor, 2010). Old-growth forest specialists are

among the species most affected by commercial forestry (Bengtsson *et al.*, 2000; Fraixedas, Lindén & Lehikoinen, 2015) in which short rotation periods usually inhibit the occurrence of late successional stages. The decline of many old-growth species (Fraixedas *et al.*, 2015) highlights the need to increase our understanding of these species' biological requirements to develop effective measures for their conservation. This particularly applies if old-growth species occur in managed forests. While knowledge of the factors affecting habitat selection is important for the conservation of any species, it is crucial for the conservation of specialized species in managed habitats, as such habitats are prone to becoming unsuitable for the specialists if key resources are removed.

We examined habitat selection of the white-backed woodpecker *Dendrocopos leucotos leucotos* in managed forests in the Eastern Alps (western Austria, eastern Switzerland, Liechtenstein) during the mating and breeding season (end

of February to mid-May). The white-backed woodpecker is a resident bird species found in old-growth and mature deciduous and mixed forests (Aulén, 1988; Hogstad & Stenberg, 1994). As it is considered a species with high demands in terms of its ecological requirements (Scherzinger, 1989), the white-backed woodpecker has been proposed as an umbrella species for communities associated with old deciduous-dominated forests rich in dead wood (Roberge, Mikusiński & Svensson, 1982) and an indicator of forest biodiversity (Mikusiński, Gromadzki & Chylarecki, 2001). Its preference for forests rich in dead wood is due to its foraging ecology: the white-backed woodpecker is a food specialist feeding mainly on the larvae of saproxylic beetles (beetles that are dependent on dead or dying wood, wood inhabiting fungi, or the presence of other saproxylics, Speight, 2004), where it prefers large larvae such as those of *Cerambycidae* (Aulén, 1988; Glutz von Blotzheim & Bauer, 1994). Due to intensive forest management, many European populations have massively declined (Virkkala *et al.*, 1993; Carlson, 2000; Czeszczewik & Walankiewicz, 2006). As a consequence, the species is considered threatened in the red lists of several European countries and is listed in the Annex I of the European Union's Birds Directive.

Contrary to the generally rather negative population trends in Europe, the species has colonized western Austria, eastern Switzerland and Liechtenstein since the 1970s (Mollet, Zbinden & Schmid, 2009). Forests in western Austria, eastern Switzerland and Liechtenstein are mostly managed, while most previous studies on habitat selection or habitat use of the white-backed woodpecker have been conducted in regions containing large areas of forest not commercially used or even relicts of primeval forest (Scherzinger, 1989; Hogstad & Stenberg, 1994; Frank, 2002; Czeszczewik, 2009). The expansion of the species' range to regions dominated by managed forests raises the question as to which factors enable the occurrence of an old-growth habitat specialist in this type of landscape. We built a set of candidate models, each of which representing a hypothesis to examine whether forest structure [hypothesis (1) 'Old mixed and deciduous forests'], volume or diameter of dead wood [hypotheses (2) 'Dead wood volume' and (3) 'Large pieces of dead wood'], nest site availability [hypothesis (4) 'Abundance of suitable nesting trees'], saproxylic beetle abundance [hypothesis (5) 'Food availability'] or topography [hypotheses (6–8) 'South-exposed slopes in intermediate elevation'] best explain white-backed woodpecker occupancy (see Table 1 for candidate models and *a priori* expectations). Each candidate model was evaluated at two spatial scales (1 km^2 and 0.25 km^2). The key aim was to understand the habitat needs of this old-growth forest specialist to develop measures for the conservation of the species in managed forests.

Materials and methods

Study area

The study presented here was conducted in the Eastern Alps in western Austria (province Vorarlberg), eastern Switzerland

(cantons Grisons and St. Gallen) and the Principality of Liechtenstein. The study region is characterized by human settlements and agricultural land in the valley bottoms and less intensive land use in the mountainous area, which is mostly covered with forest up to the timber line at *c.* 1600–1800 m. The dominating tree species are Norway spruce *Picea abies*, silver fir *Abies alba* and European beech *Fagus sylvatica*. The natural vegetation are beech-dominated forests in the submontane belt, mixed forests in the montane belt and pure coniferous forests in the subalpine belt (Ellenberg & Strutt, 2009). Forests easily accessible from the valley bottoms are typically intensively managed (except for protection forests), whereas forests at remote or inaccessible locations in the mountains tend to be used less intensively or sometimes not at all for timber production.

Within the study region, we selected 62 squares of 1 km^2 (Fig. 1) in which we recorded detection/non-detection of white-backed woodpeckers, habitat structure and a measure of saproxylic beetle abundance. The white-backed woodpecker occurs at low density in the study area, thus to avoid having a vast majority of squares not occupied, half of the 62 squares included locations at which the species had been observed since 1975 (based on data from the Swiss Ornithological Institute, inatura Dornbirn and BirdLife Vorarlberg). The rest of the squares were placed at a distance of 2–5 km to the next square with a previous observation, but without any previously known white-backed woodpecker observations in the square itself. This distance was chosen because it was large enough to avoid attracting individuals from nearby squares to an unoccupied square during the white-backed woodpecker surveys on the one hand; on the other hand, the distance was small enough to ensure that all squares could have potentially been reached by white-backed woodpeckers (i.e. the unoccupied squares were not isolated from occupied ones). We selected only squares without previous observations which could potentially contain suitable white-backed woodpecker habitat: squares without previous observations had a forest cover at least as high as squares with observations (≥45%) and were situated at the same elevation (635–1520 m above sea level), resulting in a mean (means are reported with ± SD throughout the whole text) forest cover of 75.0 ± 15.3% for squares with and 75.1 ± 17.3% for squares without observations, and a mean elevation of 958 ± 242 m and 1074 ± 239 m, respectively. It is important to note that the non-random selection of squares on the one hand led to a higher occupancy probability in our results than generally found in the study area, and probably weakened the effect of forest area and elevation in our models on the other hand. Our approach was, however, necessary to obtain enough white-backed woodpecker observations to be able to model occupancy in the first place, and to proceed beyond results which are already well-known (e.g. that the species occupies forested areas).

White-backed woodpecker surveys

Data on the detection/non-detection history of each square were collected with up to two replicate surveys in 2015 and

Table 1. Covariates used for modeling white-backed woodpecker occupancy (ψ) and detection (P) probabilities according to different hypotheses (*a priori* models)

Hypothesis	Covariate name	Description	Pred. effect P	$\psi/\varepsilon/\gamma$	1-km² square Without WBW	With WBW	0.25 km² with the most dw Without WBW	With WBW
(1) Old mixed deciduous forests	dbh	Mean DBH of live trees (cm)	+	+/−/+	32.3 ± 5.0	33.2 ± 4.2	29.9 ± 6.1	34.1 ± 7.0
	forest	Area (ha) of forest per 1-km² square per quarter of the square		+/−/+	76.6 ± 12.8	77.2 ± 14.4	19.3 ± 4.1	20.4 ± 4.5
	deadbr	Number of live trees with dead branches per ha		+/−/+	12.9 ± 11.9	20.7 ± 19.6	9.0 ± 12.9	17.1 ± 24.3
	dec	Proportion of deciduous trees	+	+/−/+	41.5 ± 28.4	45.7 ± 20.0	40.8 ± 31.6	46.2 ± 24.2
(2) Dead wood volume	vollog	Volume of lying dead wood (m³)		+/−/+	36.4 ± 33.7	38.2 ± 40.5	69.3 ± 70.5	79.1 ± 82.2
	volsnag	Volume of snags (m³)		+/−/+	19.4 ± 10.9	16.5 ± 7.5	34.0 ± 29.8	26.1 ± 17.5
(3) Large pieces of dead wood	dlog	Mean diameter of lying dead wood		+/−/+	15.4 ± 6.1	15.2 ± 5.1	16.9 ± 12.8	19.5 ± 11.8
	dsnag	Mean DBH of snags		+/−/+	18.5 ± 8.5	19.0 ± 9.1	18.9 ± 17.6	20.7 ± 13.6
(4) Abundance of suitable nesting trees	snag30	Number of snags with a DBH > 30 cm		+/−/+	4.2 ± 4.6	4.6 ± 3.5	6.6 ± 9.4	6.8 ± 6.7
(5) Food availability	beetlel	Number of beetle emergence holes in lying dead wood per m²		+/−/+	457 ± 582	599 ± 545	346 ± 357	580 ± 539
	beetles	Number of beetle emergence holes in snags per m²		+/−/+	254 ± 136	291 ± 101	252 ± 177	274 ± 183
(6–8) South-exposed, steep slopes in intermediate elevation	northness	Aspect computed as cosinus (aspect[°] × pi/180)		−/+/−	−0.2 ± 0.52	−0.28 ± 0.48	−0.21 ± 0.71	−0.36 ± 0.72
	eastness	Aspect computed as sinus (aspect[°] × pi/180)		X	−0.09 ± 0.58	−0.04 ± 0.57	−0.06 ± 0.69	−0.1 ± 0.61
	slope	Slope (%), linear and quadratic effects	X	+/−/+	54.8 ± 16.5	53.0 ± 11.9	57.5 ± 20.6	55.2 ± 24.9
	elev	Elevation above sea level (m), linear and quadratic effects		^/+/^	1008 ± 260	978 ± 189	999 ± 269	998 ± 229
Survey-specific covariates	time	Time of day, linear and quadratic effects	−					
	date	Day of year, linear and quadratic effects	−					
	accessible	Number of accessible survey points (2, 3, 4)	+					
	obs	Number of observers during white-backed woodpecker survey (1, 2)	X					
	year	Year of white-backed woodpecker survey (2015, 2016)	X					

Each hypothesis was represented by one model containing the corresponding listed covariates. Predicted (pred.) effects are the *a priori* expectations: +, positive correlation between parameter and covariate was predicted; −, negative correlation predicted; x, no prediction, but correlation could be present; ^, quadratic effect predicted. Mean ± SD of the covariates are reported for squares with and for squares without white-backed woodpecker (WBW) observations at the 1 km² scale as well as for the 0.25 km² with the highest amount of dead wood. DBH, diameter at breast height.

2016 (i.e. with a total of four surveys per square for most squares). White-backed woodpeckers were searched for at four predefined survey points per square (Fig. 1). Each survey point was situated at a distance of 300 m from the edges of the square to ensure that only white-backed woodpeckers within the square were recorded. At each survey point, one or two field workers used playbacks of white-backed woodpeckers to stimulate responses of individuals. We used a series of drumming (available in Schulze *et al.*, 2018), two different calls (the first call can be found in

Schulze et al., 2018, the second one in Stübing & Bergmann, 2019), and the imitation of foraging pecking sounds by knocking on a tree with a stick in a manner that mimics (to the human ear at least) the typical behavior of woodpeckers. The sounds were played back/produced for a minute each in a random order. After 1 min of playback/knocking, we waited for a reaction for 3 min. If no woodpecker responded, the next 1 min series was played back and responses observed during the following 3 min, etc. If no woodpecker was detected after a total of 16 min of playback, knocking and waiting, the field workers proceeded to the next point. On the other hand, as soon as a white-backed woodpecker reacted, the playback was stopped to minimize disturbance, and the species was considered to be present at that point. The white-backed woodpeckers usually responded by approaching the playback tape while calling, or by drumming at a nearby tree. In some cases, the woodpeckers did not approach the playback but were drumming in some distance. The species can be distinguished from other woodpecker species by its drumming as well as its calls, and both visual and acoustic detections were recorded.

When the species had been detected at one of the first points, the other survey points within a square were also checked for white-backed woodpeckers in 2015, but not in 2016, because preliminary analyses of the 2015 data suggested that the playback influenced the location of response by the woodpeckers within a square (Ettwein, 2016). Consequently, the species was considered detected in a square if a white-backed woodpecker responded at one of the four survey points per square.

In 2015, all squares were surveyed twice between the beginning of March and mid-May. In 2016, not all of the 62 squares could be surveyed twice due to high amounts of snow in April, leading to time constraints in May: 48 squares were surveyed twice, 11 randomly selected squares once, and three squares were not surveyed at all.

Habitat measurements

Habitat structure was mapped in the summer of 2015 in two circular sample plots of 500 m² (radius of 12.62 m) per survey point (i.e. eight sample plots per square). The centers of these plots were located 50 m to the west and to the east of the survey point (Fig. 1). We mapped live trees, snags (standing dead wood with a height > 1.30 m), stumps (standing dead wood with a height ≤ 1.30 m) and lying dead wood (logs, pieces of branches). We measured diameter at breast height (DBH) of all live trees with a DBH ≥ 12 cm, recorded tree species and whether dead branches with a diameter ≥ 10 cm were present or not. Snags and stumps were mapped when their diameter exceeded 5 cm, and height and diameter (DBH for snags, diameter in the middle for stumps) were recorded. We used the formula for a cylinder to calculate the volume of snags and stumps. Lying dead wood was recorded along three transects with a method used in the Swiss National Forest Inventory when the diameter at the intersection with the transect was ≥7 cm (for details see Böhl & Brändli, 2007; Keller, 2011).

To estimate the abundance of saproxylic beetles (a measure of relative food availability), we counted all emergence holes of saproxylic beetles within a 20-cm wide strip around each mapped piece of dead wood (for logs lying on the ground, the inaccessible part was excluded). The strip was situated at the same place at which the diameter was measured. The number of emergence holes within this strip was then used to calculate the density of holes per m² on the surface of the piece of dead wood, and the mean density of holes on standing and lying dead wood was taken as the relative abundance of saproxylic beetles per sample plot.

Aspect [°] was determined with a compass, elevation above sea level with a hand-held GPS device (Garmin eTrex 20, Olathe, KS, USA), and slope inclination with a hypsometer (Haglöf Vertex IV, Långsele, Sweden).
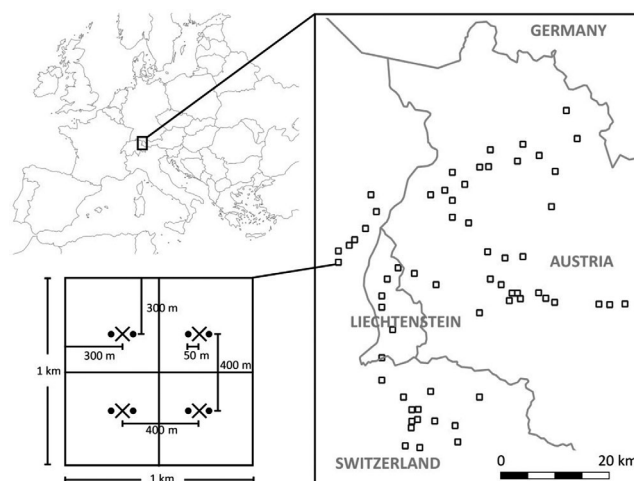

Figure 1 Overview of study area and study design. Detection/non-detection of white-backed woodpeckers was recorded in 62 1-km² squares at four survey points (cross) per square. Habitat structure and saproxylic beetle abundance were mapped in eight circular sample plots (dots) with a size of 500 m² each per square.

Statistical analyses

We analyzed the detection/non-detection data of the white-backed woodpecker surveys using occupancy models to account for imperfect detection (MacKenzie *et al.*, 2002). To relate the occupancy and detection probabilities to predictors, we used the logit-link-function. For intercepts and slopes we used normal priors with mean zero and standard deviation 1.5 and 5, respectively. For a simple prior sensitivity analysis, we rerun the best models using a narrower prior (SD 2) for the slopes of the occupancy part of the model, which yielded the same model ranking. Also, effect plots changed very little using the narrower prior (see Supporting Information, Appendix S1). Models were fitted in a Bayesian framework using Hamiltonian Monte Carlo as implemented in the open-source software Stan via R (R Core Team, 2018; R-package *rstan*, Stan Development Team, 2006). This technique allows for sampling from the posterior distribution of the model parameters, hence, with enough samples, the posterior distribution can be approximated. The posterior distribution can be used to predict detection and occupancy probability for any combination of the predictors (as e.g. done for the effect plots we present), or to report the estimate of a parameter together with a 95% credible interval (median and 95%-interquantile range of the marginal posterior distribution).

Model convergence was confirmed using the $\hat{R}$ statistics and diagnostic plots (package *shinystan*, Gabry, 2018). We used 2000 after 8000 warm-up samples from each of four Markovian chains. To ease model convergence, all linear predictors were centered and scaled to one standard deviation. Highly correlated covariates ($|r| > 0.7$, see Supporting Information, Appendix S2 for a correlation matrix) were not used in the same model. For quadratic effects, we used orthogonal polynomials. For model ranking, we used the package *loo* (Vehtari *et al.*, 2018) which produces a leave-one-out cross-validation score (LooCVS) for each model [a measure that is approximated by the well-known Akaike's information criterion (AIC)].

Initially, we attempted to fit dynamic occupancy models (MacKenzie *et al.*, 2003) which estimate first-year occupancy, a yearly colonization and extinction probability, and detection probability (package *unmarked*, Fiske & Chandler, 2011, function *colext*) or single-season occupancy models using a frequentist approach (and AIC model ranking). However, many models did not converge. Similarly, occupancy models with square as random factor could not be fitted successfully in the Stan framework as the detection/non-detection data from only 2 years apparently did not contain enough information to fit such complex models. Hence, we treated each square-year combination as a separate square, resulting in a sample size of 121 (2×62 minus the three squares that were not surveyed in 2016) instead of 62 squares. We are aware of the pseudoreplication in our analyses by not including the square as random effect in the models. However, using data from 1 year only yielded the same best models, and effect plots based on the data from single years (Supporting Information, Appendix S3) show similar effects.

We are also aware of the risk of having single false positive errors (individuals that had been attracted into unoccupied squares due to the use of playbacks) in our data, which would violate an assumption of occupancy models (Royle & Link, 2003); even so, we feel confident that our results are reliable, and false positives should be rare as the range of the playbacks which depended on terrain and background noise was usually <300 m.

Model selection procedure

As we had a large number of covariates, we used a multistep process to build models following Kéry & Royle (2015) (Fig. 2; Tables 2 and 3). At a given step, we compared models based on LooCVS and used the model with the lowest value to proceed to the next step.

The model selection procedure was conducted as follows. In step 1, we compared models containing covariates describing detection probability P while holding ψ constant: In step 1.1, year and the following survey-specific predictors were included (see Table 2): time, date, number of observers and number of accessible survey points (2 to 4 as at least 2 survey points were accessible in all squares; 31 of the 248 points were inaccessible due to steep terrain, barriers such as rock ledges, or high amounts of snow). Time and date were tested as both linear and quadratic effects. Then, in step 1.2, we considered models adding *a priori* selected habitat covariates on P (see Table 2). Note that P was modeled at the 1 km^2 scale only.

In step 2, we selected covariates describing occupancy probability ψ by comparing a set of *a priori* models (Table 1) and including the covariates selected in step 1 for P. To evaluate whether the mean habitat structure of the whole square or the habitat structure of the supposedly most suitable part of the square explained occupancy best, we included habitat data at two spatial scales in our analyses and ran each model twice (once for each spatial scale): in step (2.1a), each covariate in the occupancy part of the models was represented by the mean across the eight habitat sample plots per square (1 km^2 scale). In step (2.1b), the values of the quarter with the highest amount of dead wood were used for each covariate (0.25 km^2 scale), an approach that ignores the other three quarters of each square. For (b), values for the covariates were calculated as means of the two respective habitat sample plots. In step 2.2, we included interactions (see Table 3). Interactions were not included in the *a priori* models due to the high number of covariates for ψ but all possible two-way interactions were evaluated in step 2.2 with the covariates of the best model from step 2.1.

Results

White-backed woodpeckers were found in 20 of 62 squares in 2015 and in 18 of 59 squares in 2016. In 10 squares, white-backed woodpeckers were observed in both years. In 8 squares, the species was found in 2016 but not in 2015; in 10 squares, it was found in 2015 but not in 2016.

When modeling detection probability, the best-supported model included time of day, date, number of observers and
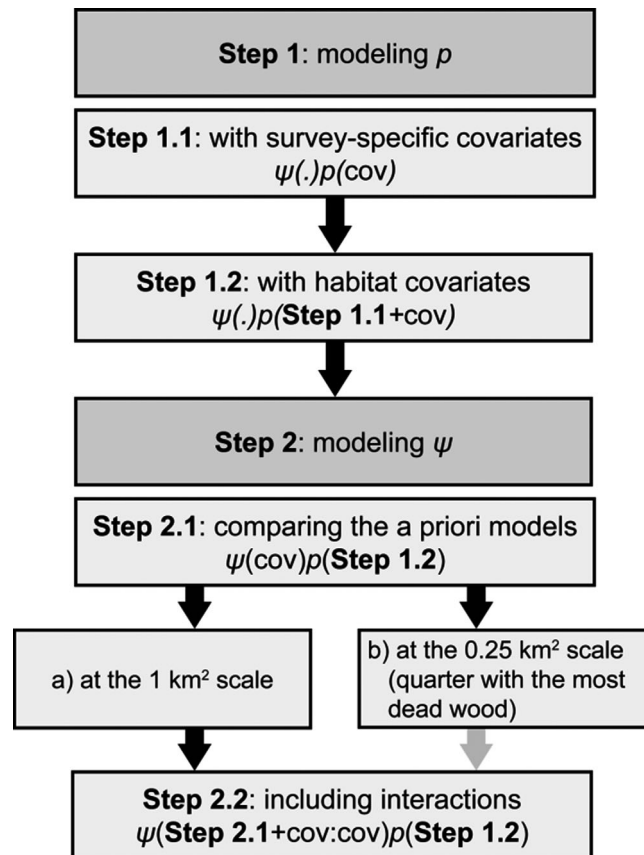
Figure 2 Model selection procedure for modeling white-backed woodpecker detection (*P*) and occupancy probabilities (*ψ*).

the number of accessible survey points. Detection probability decreased with time, date and number of accessible survey points, and increased with the number of observers (Table 4; Fig. 3).

When modeling occupancy probability, the model including the covariates abundance of beetle emergence holes on standing and lying dead wood (representing the food availability hypothesis) had the lowest LooCVS value at both spatial scales, with the model at the 1 km² scale having a remarkably lower LooCVS value than all other models at both spatial scales (ΔLooCVS to the next model at the 1 km² scale = 16.2, ΔLooCVS to the top-ranked model at the 0.25 km² scale = 10.6; Table 3). Occupancy was positively related to the abundances of beetle emergence holes on standing and lying dead wood at each spatial scale. In general, models describing forest structure yielded lower LooCVSs than models describing topography. Two covariates not included in the top-ranked model, mean DBH of live trees and of snags, were also strongly related to occupancy (95% credible interval did not include 0) at the 0.25 km² scale (Table 5; Fig. 4).

Discussion

By using occupancy modeling with habitat data at two spatial scales, we demonstrated that food availability at a large

scale (1 km²) appears to be more important for occupancy probability of the white-backed woodpecker in a landscape dominated by managed forests than forest structure characteristics or geographical aspects (food availability hypothesis supported). While most approaches for the conservation of old-growth forest species focus on quantitative targets of structural elements such as the volume of dead wood, our results indicate that detailed knowledge about how a species uses these structural elements is required for its effective conservation. Here, the preference for saproxylic beetle larvae turned out to be the key to understand why a proxy for food availability explained occupancy much better than more general habitat factors.

Habitat factors related to occupancy probability

At both spatial scales, the model including the abundances of saproxylic beetles on lying and standing dead wood performed best; however, the LooCVS of this model was much lower at the 1 km² scale than at the 0.25 km² scale, indicating that saproxylic beetles should ideally be available in high densities over a large area. Consistent with this result, the white-backed woodpecker is considered a food specialist with relatively large area requirements (e.g. Scherzinger, 1989). Both the observations of foraging

Table 2. Results of model selection for modeling white-backed woodpecker detection (*P*) probability

Model	n_p	LooCVS	ΔLooCVS
Step 1.1: including survey-specific covariates			
ψ(.)p(time+date+obs+accessible)	**5**	**220.2**	**0**
ψ(.)p(time+date+accessible)	5	220.6	0.4
ψ(.)p(time+date)	4	222	1.8
ψ(.)p(time+date+obs)	5	222.9	2.7
ψ(.)p(time+date+year)	5	223.2	3
ψ(.)p(time)	3	224.3	4.1
ψ(.)p(time+time²)	4	225.6	5.4
ψ(.)p(date)	3	229.1	8.9
ψ(.)p(accessible)	3	229.4	9.2
ψ(.)p(.)	2	230.2	10
ψ(.)p(accessible+obs)	4	231.2	11
ψ(.)p(year)	3	231.8	11.6
ψ(.)p(obs)	3	231.8	11.6
ψ(.)p(date+date²)	4	231.8	11.6
ψ(.)p(obs+accessible+year)	5	232.8	12.6
Step 1.2: including habitat covariates			
ψ(.)p(time+date+obs+accessible)	**6**	**220.2**	**0**
ψ(.)p(time+date+obs+accessible+dec)	7	222	1.8
ψ(.)p(time+date+obs+accessible+dbh)	7	223.4	3.2
ψ(.)p(time+date+obs+accessible+forest)	7	223.4	3.2
ψ(.)p(time+date+obs+accessible+slope)	7	226.5	6.3

Model selection was performed based on the leave-one-out cross-validation score (LooCVS). n_p, number of estimated parameters; ΔLooCVS, difference between a model's LooCVS and the LooCVS of the top-ranked model of the respective section. Models printed bold were selected for further modeling. Abbreviations of covariate names are given in Table 1.

Table 3. Results of model selection for modeling white-backed woodpecker occupancy (ψ) probability

Model	n_p	LooCVS	ΔLooCVS
Step 2.1a: testing the *a priori* hypotheses at the 1 km² scale			
ψ(beetlel+beetles)p (time+date+obs+accessible)	**8**	**202.4**	**0**
ψ(snag30)p(time+date+obs+accessible)	7	218.6	16.2
ψ(.)p(time+date+obs+accessible)	6	220	17.6
ψ(vollog+volsnag)p (time+date+obs+accessible)	8	221.2	18.8
ψ(dbh+forest+deadbr+dec)p (time+date+obs+accessible)	10	223.3	20.9
ψ(dlog+dsnag)p (time+date+obs+accessible)	8	223.3	20.9
ψ(northness+eastness+slope+slope²+elev) p(time+date+obs+accessible)	11	224.7	22.3
ψ(northness+eastness+slope+elev+elev²)p (time+date+obs+accessible)	11	227.1	24.7
ψ(northness+eastness+slope+elev)p (time+date+obs+accessible)	10	227.7	25.3
Step 2.1b: testing the *a priori* hypotheses at the 0.25 km² scale			
ψ(beetlel+beetles)p (time+date+obs+accessible)	8	213	0
ψ(dbh+forest+deadbr+dec)p (time+date+obs+accessible)	10	216.5	3.5
ψ(dlog+dsnag)p (time+date+obs+accessible)	8	219.5	6.5
ψ(.)p(time+date+obs+accessible)	6	220	7
ψ(snag30)p(time+date+obs+accessible)	7	220.1	7.1
ψ(vollog+volsnag)p (time+date+obs+accessible)	8	225.1	12.1
ψ(northness+eastness+slope+elev)p (time+date+obs+accessible)	10	226.1	13.1
ψ(northness+eastness+slope+slope²+elev) p(time+date+obs+accessible)	9	226.4	13.4
ψ(northness+eastness+slope+elev+elev²)p (time+date+obs+accessible)	11	228.9	15.9
Step 2.2: testing the effect of year			
ψ(beetlel+beetles)p (time+date+obs+accessible)	**8**	**202.4**	**0**
ψ(beetlel+beetles+year)p (time+date+obs+accessible)	9	204.6	2.2
Step 2.3: including interactions			
ψ(beetlel+beetles)p (time+date+obs+accessible)	**8**	**202.4**	**0**
ψ(beetlel+beetles+beetlel:beetlex)p (time+date+obs+accessible)	9	215.7	13.3

Model selection was performed based on the leave-one-out cross-validation score (LooCVS). n_p, number of estimated parameters; ΔLooCVS, difference between a model's LooCVS and the LooCVS of the top-ranked model of the respective section. Models printed bold were selected for further modeling. Abbreviations of covariate names are given in Table 1.

individuals and of individuals feeding their nestlings have revealed that the larvae of saproxylic beetles, particularly large larvae such as those of *Cerambycidae*, make up the majority of the species' prey (Aulén, 1988; Hogstad & Stenberg, 1997).

Contrary to our expectations, volume of dead wood, the habitat of saproxylic beetles, was not included in well-supported models, which could have two reasons. The first might be related to our approach for processing the field data for dead wood for the models. At the 1 km² scale, we calculated the mean volume of standing and lying dead wood from the eight sample plots. Because of the often high heterogeneity of forests within the squares, this approach probably failed to discern forest stands relevant to white-backed woodpeckers. At the 0.25 km² scale, we used only the quarter with the highest amount of dead wood in squares with and without white-backed woodpecker observations. This approach resulted in dead wood volumes comparable to those found in old forest reserves or primeval forests (e.g. Christensen *et al.*, 2005; Drößler, 2006; Holeksa *et al.*, 2007; Motta *et al.*, 2010) and white-backed woodpecker habitats elsewhere (Frank, 2002; Bühler, 2009; Czeszczewik, 2009) in squares with and without white-backed woodpecker observations (Table 1). Focusing on the 0.25 km² with the highest dead wood volume may thus have removed the

potential effect of this covariate in the models. Second, high amounts of dead wood are not necessarily equal to high abundances of saproxylic beetles. Several studies have shown that other factors such as the diameter, decomposition or
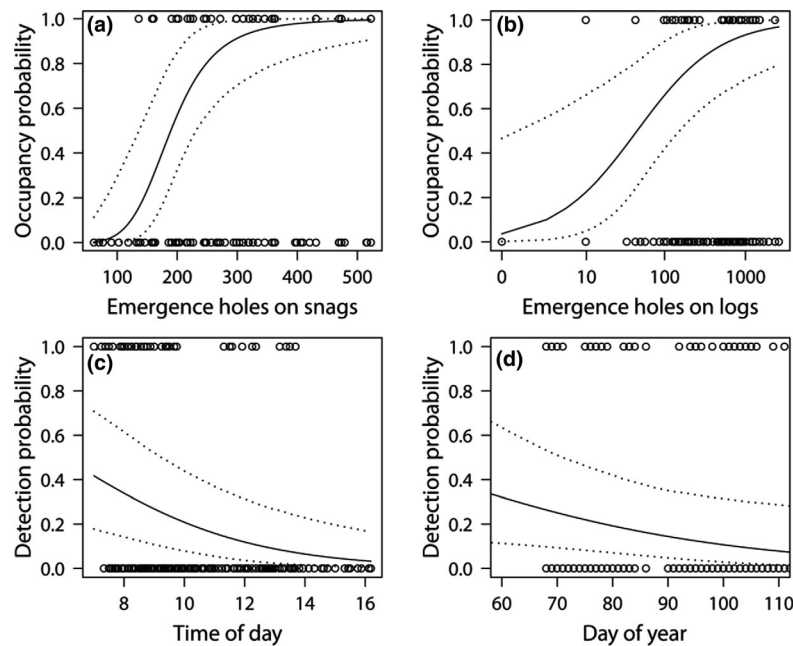
Figure 3 Relationships between white-backed woodpecker occupancy probability within surveyed squares at the 1 km² scale and abundance of beetle emergence holes on standing (a) and lying (b) deadwood (note the logarithmic *x*-axis), and between detection probability and (c) time of day and (d) day of year based on the top-ranked model from step 2.2 (Table 4). The solid lines are fitted values, calculated with the values for other covariates set to their means. Dotted line = 95% credible interval, circles = raw data. *n* = 121.

type (standing, lying, stump) of dead wood can play a more important role for saproxylic beetle abundance (Redolfi DeZan, Battisti & Carpaneto, 2006; Procházka & Schlaghamerský, 2019) and diversity (see review by Lassauce *et al.*, 2011) than dead wood volume alone, and the correlation between dead wood volume and saproxylic beetle abundance was also weak in our study system (Supporting Information, Appendix S2). Besides the characteristics of dead wood, the spatial and temporal habitat continuity may influence saproxylic beetle communities (Sverdrup-Thygeson, Gustafsson & Kouki, 1993). Consequently, dead wood varies in quality as foraging substrate for woodpeckers (Lõhmus, Kinks & Soon, 2010). Although the high importance of dead wood for white-backed woodpeckers has consistently been pointed out, it is important to keep in mind that dead wood is mainly necessary because it contains saproxylic beetle larvae and its quality is probably at least as important as its quantity.

Previous studies on the habitat requirements of this species have revealed a preference for stands with high amounts of lying deadwood (Czeszczewik, 2009), a high number of dying trees and a low density of forest roads (Kajtoch, Figarski & Pelka, 2013), and for old stands with a high density of dead and dying trees (Hogstad & Stenberg, 1994). In contrast, covariates describing forest structure are not included in our top-ranked model. However, none of the studies above has considered food availability in their analyses. The few studies on food specialist woodpeckers, in which this important covariate was included in habitat models, have also highlighted its high importance compared to forest structure characteristics. For instance, Bonnot, Millspaugh &

Rumble (2009) found that availability and distribution of food explained territory selection of black-backed woodpeckers *Picoides arcticus* better than nest site availability. Similarly, American three-toed woodpecker *Picoides dorsalis* occupancy was positively related to the number of trees infested by bark beetles, whereas no relationship to the density of old snags or the diameter of healthy or infested trees was found (Kelly *et al.*, 2019).

That our models describing food availability received overwhelming support compared with the other models does not imply that other factors do not affect occupancy. Accordingly, the covariates mean DBH of live trees and snags also showed strong positive relationships to occupancy at the 0.25 km² scale (Fig. 4; Table 5). A high mean DBH of live trees represents stands with large old trees which are often considered as habitat trees because they might offer various microhabitats such as crown dead wood or bark injuries to arthropods (Bütler *et al.*, 2013; Larrieu *et al.*, 2018), and may therefore be important for foraging. Snags are also known to be important as foraging substrate for white-backed woodpeckers, with all diameter classes being used (Scherzinger, 1989; Aulén, 1988; Aulén & Lundberg, 1991; Frank & Hochebner, 2001; Stenberg & Hogstad, 2014; Bühler, 2009). The positive relationship between occupancy and mean DBH of snags might be due to the higher availability of large larvae (preferred by the white-backed woodpecker) in forest stands with large-diameter dead wood: the mean body size of saproxylic beetles has been shown to increase with the diameter of dead wood (Brin *et al.*, 2011) and the availability of large snags (Janssen *et al.*, 2017).

Table 4. Medians and credible intervals (2.5% and 97.5% quantiles) of the marginal posterior distribution of the covariates included in each *a priori* occupancy model attempting to predict white-backed woodpecker occupancy and detection probability at the 1 km² scale

Covariate	Hypothesis (5)	(2)	(4)	(1)	(3)	(6)	(7)	(8)
Occupancy probability								
intercept	1.24 [0.17;3.10]	1.97 [0.23;4.40]	1.01 [−0.08;2.98]	1.27 [−0.05;3.86]	1.41 [0.06;3.69]	2.85 [0.55;5.16]	2.98 [1.02;5.15]	2.97 [0.86;5.32]
dbh	–	–	–	0.49 [−6.45;7.21]	–	–	–	–
forest	–	–	–	0.35 [−6.47;7.25]	–	–	–	–
deadbr	–	–	–	0.56 [−0.48;1.56]	–	–	–	–
dec	–	–	–	0.36 [−1.42;2.22]	–	–	–	–
vollog	–	−0.31 [−1.74;0.99]	–	–	–	–	–	–
volsnag	–	1.18 [−1.64;3.41]	–	–	–	–	–	–
dlog	–	–	–	–	−0.13 [−1.38;1.16]	–	–	–
dsnag	–	–	–	–	0.95 [−0.56;2.98]	–	–	–
snag30	–	–	0.98 [−0.01;2.21]	–	–	–	–	–
beetlel	1.76 [0.54;3.51]	–	–	–	–	–	–	–
beetles	2.61 [1.12;4.92]	–	–	–	–	–	–	–
northness	–	–	–	–	–	−0.70 [−2.87;1.40]	0.00 [−2.20;1.82]	0.07 [−2.28;1.97]
eastness	–	–	–	–	–	1.45 [−0.71;3.71]	0.81 [−1.41;3.20]	0.52 [−2.29;3.47]
slope	–	–	–	–	–	1.53 [−0.65;3.60]	0.71 [−2.26;2.75]	0.15 [−2.25;2.32]
slope_q	–	–	–	–	–	–	–	−1.31 [−3.50;0.88]
elev	–	–	–	–	–	−1.48 [−4.43;1.26]	0.09 [−3.78;3.17]	0.50 [−3.28;3.49]
elev_q	–	–	–	–	–	−1.62 [−3.31;−0.11]	–	–
Detection probability (only given for the top-ranked model)								
intercept	−1.59 [−2.75;−0.47]							
time	−0.73 [−1.22;−0.31]							
date	−0.47 [−0.99;0.00]							
obs	0.44 [−0.27;1.18]							
accessible	−0.72 [−1.26;−0.24]							

Models are ordered according to their leave-one-out cross-validation score, from lowest on the left to highest on the right. Explanations of covariate names and hypothesis (i.e. *a priori* model) numbers are given in Table 1.

Table 5. Medians and credible intervals (2.5% and 97.5% quantiles) of the marginal posterior distribution of the covariates included in each a priori occupancy model attempting to predict white-backed woodpecker occupancy and detection probability at the 0.25 km² scale

Covariate	Hypothesis							
	(5)	(1)	(3)	(4)	(2)	(6)	(7)	(8)
Occupancy probability								
intercept	1.03 [−0.08;3.09]	0.89 [−0.23;3.19]	0.74 [−0.20;2.78]	1.10 [−0.06;3.33]	1.32 [−0.02;4.08]	2.74 [0.72;5.09]	2.53 [0.70;4.88]	2.62 [0.96;4.91]
dbh	–	1.42 [0.41;3.00]	–	–	–	–	–	–
forest	–	0.76 [−0.35;2.03]	–	–	–	–	–	–
deadbr	–	0.82 [−0.21;2.40]	–	–	–	–	–	–
dec	–	0.77 [−0.42;2.41]	–	–	–	–	–	–
vollog	–	–	–	–	0.09 [−1.43;1.28]	–	–	–
volsnag	–	–	–	–	0.31 [−2.65;1.58]	–	–	–
dlog	–	–	0.45 [−0.73;1.48]	–	–	–	–	–
dsnag	–	–	0.94 [0.22;1.97]	–	–	–	–	–
snag30	–	–	–	0.86 [−0.15;2.86]	–	–	–	–
beetel	1.27 [0.41;2.56]	–	–	–	–	–	–	–
beetles	1.22 [0.27;2.75]	–	–	–	–	–	–	–
northness	–	–	–	–	–	0.67 [−1.33;2.73]	0.62 [−1.47;2.73]	−0.04 [−1.76;2.10]
eastness	–	–	–	–	–	−0.73 [−3.41;1.92]	−0.50 [−2.70;1.97]	−0.14 [−2.21;2.31]
slope	–	–	–	–	–	0.20 [−1.34;1.72]	0.02 [−1.37;1.21]	1.12 [−1.11;3.26]
slope_q	–	–	–	–	–	–	–	2.16 [−0.16;5.36]
elev	–	–	–	–	–	1.13 [−1.69;4.18]	1.31 [−1.92;3.39]	1.03 [−2.13;3.35]
elev_q	–	–	–	–	–	−0.44 [−2.09;1.98]	–	–
detection probability (only given for the top-ranked model)								
intercept	−1.63 [−2.81;−0.52]							
time	−0.73 [−1.22;−0.31]							
date	−0.56 [−1.08;−0.09]							
obs	0.40 [−0.28;1.15]							
accessible	−0.58 [−1.10;−0.14]							

Models are ordered according to their leave-one-out cross-validation score, from lowest on the left to highest on the right. Explanations of covariate names and hypothesis (i.e. a priori model) numbers are given in Table 1.
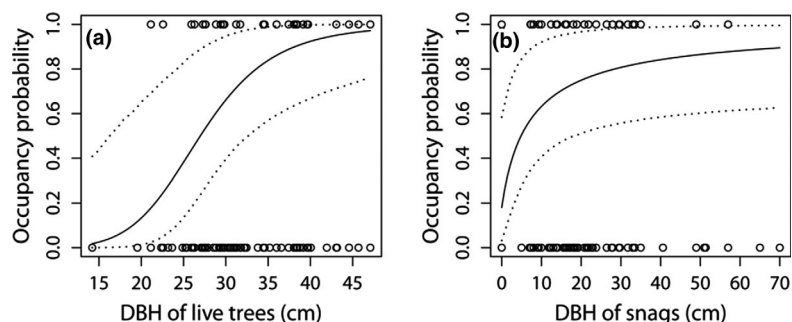
Figure 4 Relationships between white-backed woodpecker occupancy probability within surveyed squares at the 0.25 km² scale and (a) mean diameter at breast height (DBH) of live trees and (b) mean DBH of standing dead wood. The solid lines are fitted values, calculated with the values for other covariates set to their means. Dotted line = 95% credible interval, circles = raw data. *n* = 121.

Detection probability

An important aspect of our study was the explicit modeling of the presence/absence measurement error. Consistent with the known general decrease in acoustic activity of birds over the day (Bibby *et al.*, 2000), detection probability decreased with time of day, even though we used playbacks to stimulate responses of woodpeckers. Detection probability was also negatively related to date. White-backed woodpeckers are known to have the highest drumming activity during the pre-breeding season from the end of February to the beginning of April as well as shortly before the chicks fledge at the end of May/beginning of June, while they behave inconspicuously during the breeding and early nestling periods (Scherzinger, 1989). As we finished our surveys in mid-May, the linear relationship between detection probability and date met our expectations. Contrary to our expectation, detection probability decreased when more survey points were accessible within the square. This result might be explained by the fact that most of the skipped survey points were inaccessible due to the steepness of the terrain and thus probably situated in forest stands with low management intensity. Lastly, detection probability was slightly higher when two observers conducted the survey, which might be due to a higher chance of hearing drumming individuals that did not approach the playback/survey point. However, the credible interval included zero, indicating that the effect is relatively unimportant.

It is generally accepted that accounting for detection probability provides more reliable and less biased estimates of the biological parameters related to the occupancy of a site by a species (Kéry, Guillera-Arroita, & Lahoz-Monfort, 2013). Our study emphasizes that detection probability should also be accounted for when using playbacks.

Conservation implications

The occurrence of the white-backed woodpecker in western Austria, eastern Switzerland and Liechtenstein in managed forests shows that this old-growth specialist is not restricted to primeval forests or large conservation areas without (ongoing) forest management. However, it is important to note that the management intensity of the forests considered in the present study is generally rather low, as shown by the relatively high amounts of dead wood: the mean volume of dead wood was *c.* 55 m³ ha⁻¹ in both squares with and without white-backed woodpecker observations (Table 1), which is much higher than the mean dead wood volumes reported for all European countries, where the values range between 8 m³ ha⁻¹ in North Europe and 20 m³ ha⁻¹ in Central-West Europe (Forest Europe, 2015). In addition, patches with amounts of dead wood comparable to those found in primeval forests (on average 79 m³ ha⁻¹ of lying and 26 m³ ha⁻¹ of standing dead wood) were found in our study area. Occupancy was positively related to the mean DBH of live trees and standing dead wood in these patches, indicating that large-diameter trees and snags in stands rich in dead wood should be present and retained for the conservation of the species.

More important than covariates describing forest structure, however, was food availability at a large (1 km²) scale. This result is particularly interesting in the context of approaches currently applied for biodiversity conservation in forests. Forest management often focuses on reaching thresholds in dead wood quantity although it is well-known that the diversity of saproxylic species at the stand level is also linked to dead wood diversity (Lassauce *et al.*, 2011). Likewise, present recommendations for the conservation of specialized woodpecker species such as the white-backed and three-toed woodpecker *Picoides tridactylus* are mainly based on quantitative targets regarding dead wood (e.g. Bütler *et al.*, 2004; Kajtoch *et al.*, 2013). Although factors such as volume of dead wood or number of habitat trees per hectare are valuable criteria for forest management guidelines because they are relatively easy to assess and implement in the field, quantitative targets alone might not be the appropriate criteria for the conservation of dead wood specialists in managed forests. For example, dead wood in managed forests is often composed of a high proportion of stumps and small-diameter dead wood compared to old-growth forests (Keren & Diaci, 2018). Even when high amounts of dead wood with these characteristics are retained, only a certain proportion of the saproxylic species will benefit from

this measure, whereas the habitat might remain unsuitable for species preferring large-diameter snags or logs (Gossner *et al.*, 2013). Similarly, white-backed woodpeckers are unlikely to occur where dead wood is available but not sufficiently colonized by saproxylic beetles. Thus, we recommend that the existing knowledge about saproxylic species and dead wood management (e.g. Vítková *et al.*, 2018), particularly the promotion of large-diameter dead wood, be taken into account when implementing conservation measures in managed forests. For developing conservation measures specifically directed at white-backed woodpeckers in temperate managed forest, however, more knowledge about their preferred prey species and foraging substrates is needed.

Acknowledgements

References

Aulén, G. (1988). *Ecology and distribution of the white-backed woodpecker Dendrocopos leucotos in Sweden*. Dissertation, Swedish University of Agricultural Sciences, Uppsala.

Aulén, G. & Lundberg, A. (1991). Sexual dimorphism and patterns of territory use by the white-backed woodpecker *Dendrocopus leucotos*. *Ornis Scand. Scand. J. Ornithol.* **22**, 60–64.

Bengtsson, J., Nilsson, S.G., Franc, A. & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manag.* **132**, 39–50.

Bibby, C.J., Burgess, N.D., Hill, D.A., & Mustoe, S. (2000). *Bird census techniques*. 2nd edn. London: Academic Press.

Böhl, J. & Brändli, U.-B. (2007). Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. *Eur. J. For. Res.* **126**, 449–457.

Bonnot, T., Millspaugh, J. & Rumble, M. (2009). Multi-scale nest-site selection by black-backed woodpeckers in outbreaks of mountain pine beetles. *For. Ecol. Manag.* **259**, 220–228.

Brin, A., Bouget, C., Brustel, H. & Jactel, H. (2011). Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. *J. Insect Conserv.* **15**, 653–669.

Brumelis, G., Jonsson, B.G., Kouki, J., Kuuluvainen, T. & Shorohova, E. (2011). Forest naturalness in northern Europe: perspectives on processes, structures and species diversity. *Silva Fenn.* **45**, 807–821.

Bühler, U. (2009). Totholz – existenziell für den Weissrückenspecht in Nordbünden | Dead wood – a vital necessity for the white-backed woodpecker in the Grisons. *Schweiz. Z. Forstwes.* **160**, 210–217.

Bütler, R., Angelstam, P., Ekelund, P. & Schlaepfer, R. (2004). Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. *Biol. Conserv.* **119**, 305–318.

Bütler, R., Lachat, T., Larrieu, L., & Paillet, Y. (2013). Habitat trees: key elements for forest biodiversity. In *Integrative approaches as an opportunity for the conservation of forest biodiversity*: 84–91. Kraus, D. & Krumm, F. (Eds). Freiburg: European Forest Institute.

Carlson, A. (2000). The effect of habitat loss on a deciduous forest specialist species: the white-backed woodpecker (*Dendrocopos leucotos*). *For. Ecol. Manag.* **131**, 215–221.

Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. (2005). Dead wood in European beech (*Fagus sylvatica*) forest reserves. *For. Ecol. Manag.* **210**, 267–282.

Clavel, J., Julliard, R. & Devictor, V. (2010). Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Env.* **8**, 222–228.

Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R. & Zingg, A. (2005). Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *For. Snow Landsc. Res.* **79**, 45–56.

Czeszczewik, D. (2009). Marginal differences between random plots and plots used by foraging white-backed woodpeckers demonstrates supreme primeval quality of the Białowieża National Park, Poland. *Ornis Fenn.* **86**, 30–37.

Czeszczewik, D. & Walankiewicz, W. (2006). Logging affects the white-backed woodpecker *Dendrocopos leucotos* distribution in the Białowieza Forest. *Ann. Zool. Fenn.* **43**, 221–227.

Devictor, V., Julliard, R. & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* **117**, 507–514.

Drößler, L. (2006). *Struktur und Dynamik von zwei Buchenurwäldern in der Slowakei*. Dissertation, Georg-August-Universität Göttingen, Göttingen.

Ellenberg, H. & Strutt, G.K. (2009). *Vegetation ecology of Central Europe*. 4th edn. Cambridge: Cambridge University Press.

Ettwein, A. (2016). *Habitatwahl des Weißrückenspechts (Dendrocopos leucotos) in Vorarlberg, der Ostschweiz und dem Fürstentum Liechtenstein*. Master's thesis, Universität für Bodenkultur Wien, Wien.

Fiske, I.J. & Chandler, R.B. (2011). Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* **43**, 1–23.

Forest Europe. (2015). State of Europe's Forests 2015. Ministerial Conference on the Protection of Forests in Europe. Available at http://foresteurope.org/state-europes-forests-2015-report/

Fraixedas, S., Lindén, A. & Lehikoinen, A. (2015). Population trends of common breeding forest birds in sourthern Finland are consistent with trends in forest management and climate change. *Ornis Fenn.* **92**, 187–203.

Frank, G. (2002). Brutzeitliche Einnischung des Weissrückenspechtes *Dendrocopos leucotos* im Vergleich zum Buntspecht *Dendrocopos major* in montanen Mischwaldern der nordlichen Kalkalpen. *Vogelwelt* **123**, 225–239.

Frank, G. & Hochebner, T. (2001). Erfassung der Spechte – insbesondere des Weißrückenspechtes Picoides leucotos – im Rhmen des LIFE-Projektes Wildnisgebiet Dürrenstein. In *LIFE- Projekt Wildnisgebiet Dürrenstein*: 116–148. Amt der Niederösterreichischen Landesregierung (Ed.). St. Pölten: Amt der Niederösterreichischen Landesregierung.

Gabry, J. (2018). *shinystan: interactive visual and numerical diagnostics and posterior analysis for bayesian models. R package version 2.5.0*. Available at https://CRAN.R-project.org/package=shinystan

Glutz von Blotzheim, U.N. & Bauer, K. (1994). *Handbuch der Vögel Mitteleuropas. Band 9: Columbiformes – Piciformes*. 2nd edn. Wiesbaden: Aula-Verlag.

Gossner, M.M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W.W. & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conserv. Biol.* **27**, 605–614.

Grove, S.J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* **33**, 1–23.

Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004). Predictors of species sensitivity to fragmentation. *Biodivers. Conserv.* **13**, 207–251.

Hogstad, O. & Stenberg, I. (1994). Habitat selection of a viable population of white-backed woodpeckers *Dendrocopos leucotos*. *Fauna Nor. Ser. C Cinclus* **17**, 75–94.

Hogstad, O. & Stenberg, I. (1997). Breeding success, nestling diet and parental care in the white-backed woodpecker *Dendrocopos leucotos*. *J. Für. Ornithol.* **138**, 25–38.

Holeksa, J., Saniga, M., Szwagrzyk, J., Dziedzic, T., Ferenc, S. & Wodka, M. (2007). Altitudinal variability of stand structure and regeneration in the subalpine spruce forests of the Pol'ana biosphere reserve, Central Slovakia. *Eur. J. For. Res.* **126**, 303–313.

Janssen, P., Fuhr, M., Cateau, E., Nusillard, B. & Bouget, C. (2017). Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biol. Conserv.* **205**, 1–10.

Kajtoch, L., Figarski, T. & Pelka, J. (2013). The role of forest structural elements in determining the occurrence of two specialist woodpecker species in the Carpathians, Poland. *Ornis Fenn.* **90**, 23–40.

Keller, M. (2011). *Swiss National Forest Inventory. Manual of the field survey 2004–2007*. Birmensdorf: Swiss Federal Research Institute WSL.

Kelly, J.J., Latif, Q.S., Saab, V.A. & Veblen, T.T. (2019). Spruce beetle outbreaks guide American three-toed woodpecker *Picoides dorsalis* occupancy patterns in subalpine forests. *The Ibis* **161**, 172–183.

Keren, S. & Diaci, J. (2018). Comparing the quantity and structure of deadwood in selection managed and old-growth forests in south-east Europe. *Forests* **9**, 76.

Kéry, M., Guillera-Arroita, G. & Lahoz-Monfort, J.J. (2013). Analysing and mapping species range dynamics using occupancy models. *J. Biogeogr.* **40**, 1463–1474.

Kéry, M. & Royle, J.A. (2015). *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Vol. 1: Prelude and static models*. 1st edn. Cambridge: Academic Press.

Kuuluvainen, T., Penttinen, A., Leinonen, K. & Nygren, M. (1996). Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. *Silva Fenn.* **30**, 315–328.

Larrieu, L., Paillet, Y., Winter, S., Bütler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B. & Vandekerkhove, K. (2018). Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* **84**, 194–207.

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* **11**, 1027–1039.

Lõhmus, A., Kinks, R. & Soon, M. (2010). The importance of dead-wood supply for woodpeckers in Estonia. *Balt. For.* **16**, 76–86.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**, 2200–2207.

Merino, A., Real, C., Álvarez-González, J.G. & Rodríguez-Guitián, M.A. (2007). Forest structure and C stocks in natural *Fagus sylvatica* forest in southern Europe: the effects of past management. *For. Ecol. Manag.* **250**, 206–214.

Mikusiński, G., Gromadzki, M. & Chylarecki, P. (2001). Woodpeckers as indicators of forest bird diversity. *Conserv. Biol.* **15**, 208–217.

Mollet, P., Zbinden, N. & Schmid, H. (2009). Steigende Bestandszahlen bei Spechten und anderen Vogelwarten dank Zunahme von Totholz? *Schweiz. Z. Forstwes.* **160**, 334–340.

Motta, R., Berretti, R., Castagneri, D., Lingua, E., Nola, P. & Vacchiano, G. (2010). Stand and coarse woody debris dynamics in subalpine Norway spruce forests withdrawn from regular management. *Ann. For. Sci.* **67**, 803.

Müller, J., Hothorn, T. & Pretzsch, H. (2007). Long-term effects of logging intensity on structures, birds, saproxylic beetles and wood-inhabiting fungi in stands of European beech *Fagus sylvatica L. For. Ecol. Manag.* **242**, 297–305.

Procházka, J. & Schlaghamerský, J. (2019). Does dead wood volume affect saproxylic beetles in montane beech-fir forests of Central Europe? *J. Insect Conserv.* **23**, 157–173.

R Core Team (2018). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Redolfi DeZan, L., Battisti, C. & Carpaneto, G.M. (2014). Bird and beetle assemblages in relict beech forests of central Italy: a multi-taxa approach to assess the importance of dead wood in biodiversity conservation. *Community Ecol.* **15**, 235–245.

Roberge, J.-M., Mikusiński, G. & Svensson, S. (2008). The white-backed woodpecker: umbrella species for forest conservation planning? *Biodivers. Conserv.* **17**, 2479–2494.

Royle, J.A. & Link, W.A. (2006). Generalized site occupancy models allowing for false positive and false negative errors. *Ecology* **87**, 835–841.

Scherzinger, W. (1982). *Die Spechte im Nationalpark Bayerischer Wald. Vol. Heft 9*. Grafenau: Nationalparkverwaltung Bayerischer Wald.

Schulze, A., Roché, J.C., Chappuis, C., Dingler, K.H. & Werle, A. (2003). *Die Vogelstimmen Europas, Nordafrikas und Vorderasiens*. Germering: Ample Edition.

Speight, M.C.D. (1989). *Saproxylic invertebrates and their conservation*. Strasbourg: Council of Europe.

Stan Development Team. (2018). *RStan: the R interface to Stan. R package version 2.18.2*. Available at http://mc-stan.org/

Stenberg, I. & Hogstad, O. (2004). Sexual dimorphism in relation to winter foraging in the white-backed woodpecker (*Dendrocopos leucotos*). *J. Ornithol.* **145**, 321–326.

Stübing, S. & Bergmann, H.H. (2006). *Methodenstandards zur Erfassung der Brutvögel Deutschlands: Klangattrappen*. 1st edn. Radolfzell: Verein Sächsischer Ornithologen.

Sverdrup-Thygeson, A., Gustafsson, L. & Kouki, J. (2014). Spatial and temporal scales relevant for conservation of dead-wood associated species: current status and perspectives. *Biodivers. Conserv.* **23**, 513–535.

Vehtari, A., Gabry, J., Yao, Y. & Gelman, A. (2019). *Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 2.1.0*. Available at https://CRAN.R-project.org/package=loo

Virkkala, R., Alanko, T., Laine, T. & Tiainen, J. (1993). Population contraction of the white-backed woodpecker *Dendrocopos leucotos* in Finland as a consequence of habitat alteration. *Biol. Conserv.* **66**, 47–53.

Vítková, L., Bače, R., Kjučukov, P. & Svoboda, M. (2018). Deadwood management in Central European forests: key considerations for practical implementation. *For. Ecol. Manag.* **429**, 394–405.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Fitted values and 95% credible intervals of relationships between white-backed woodpecker occupancy probability and abundance of beetle emergence holes on (a) standing and (b) lying deadwood (note the logarithmic *x*-axis) modeled with two different priors (solid lines = used prior, dotted lines = alternative prior).

Appendix S2. Correlations between the covariates used for occupancy modeling (Pearson correlation coefficient).

Appendix S3. Relationships between white-backed woodpecker occupancy probability and abundance of beetle emergence holes on standing and lying deadwood (note the logarithmic *x*-axis) modeled separately for the years 2015 and 2016.