



Landscape context plays an important role for the occurrence of the white-backed woodpecker *Dendrocopos leucotos*

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Received: 19 December 2025 / Accepted: 4 May 2026
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Abstract

Context Habitat models typically relate the occurrence of a species to environmental predictors measured within study sites or home ranges (“local habitat”). However, sites with high local habitat quality might be unoccupied when the composition and configuration of the surrounding landscape hamper their colonization.

Objectives We examined the occurrence of the white-backed woodpecker, an umbrella species of European conservation concern, in relation to local habitat and landscape context (habitat amount, habitat fragmentation, and matrix quality).

Methods The study was conducted in Western Austria, Eastern Switzerland, and the Principality of Liechtenstein. Variables describing local habitat and landscape context were compared between 30 sites with and 30 sites without white-backed woodpecker presence.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-026-02380-5>.

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Results Landscape context explained 2.5 times more of the variance in occurrence probability than local habitat. Occurrence probability increased with the volume of lying deadwood and abundance of trees with dead branches at the local scale. It also increased with the proportion and fragmentation of old deciduous forests (representing habitat amount and habitat fragmentation, respectively) and increasing proportion of coniferous and young deciduous forest (representing matrix quality) at spatial scales ranging from 20 to 64 km² (i.e., 6 to 20 times the annual home range size).

Conclusions Conservation measures for the white-backed woodpecker might be ineffective in landscapes with low forest cover, even if high-quality habitat at the local scale is abundant. Conservation of and habitat improvements in areas with a high proportion of old deciduous forest and of coniferous and young deciduous forests are thus key.

Keywords *Dendrocopos leucotos* · Fragmentation threshold · Habitat specialist · Habitat amount · Habitat fragmentation · Matrix quality · Spatial scale · Forest structure · Landscape composition · Remote sensing · CORINE · LIDAR · Picidae

Introduction

Habitat models typically relate the occurrence or abundance of a species to environmental predictors

and are an important basis for various conservation applications such as adapting forest management or agricultural practices (Bütler et al. 2004; Franco and Sutherland 2004) or planning habitat networks (Angelstam et al. 2004). The quality and outcome of the model may vary depending on the spatial scale, i.e., the extent (area or radius), at which the environmental predictors included were measured (de Knecht et al. 2010; Jackson and Fahrig 2015), which in turn may affect the effectiveness of conservation measures derived from the model. Although the importance of scale in species-environment relationships has long been acknowledged (e.g., Wiens 1989), most habitat selection studies are based on environmental data recorded at rather small spatial scales, e.g., within study sites or home ranges of the studied species (“local habitat”), and scale optimization for environmental predictors is rarely done (McGarigal et al. 2016). Local habitat quality undoubtedly affects the occurrence and abundance of species. However, a site with high local habitat quality might be unoccupied by a species if the amount of suitable habitat at the landscape level is too low to sustain a population or if the colonization of the site is impeded by the spatial configuration of suitable habitat patches and/or poor quality of the matrix (the area between patches of the habitat type relevant to a species). Incorporating landscape context, that is, the configuration and composition of the landscape surrounding a given site, into habitat models may thus be crucial to better understand the processes affecting the occurrence or abundance of a species.

Despite decades of research into the influences of landscape context mainly on community-level responses such as species richness, there is no general consent about the relative importance of landscape composition (habitat amount; “habitat” meaning “habitat suitable for the species”) versus landscape configuration (spatial distribution of habitat, e.g. fragmentation) (Banks-Leite et al. 2022). This is partly due to the confounded effects of habitat amount and habitat fragmentation; fragmentation does not only change the spatial configuration of a habitat type but often causes habitat loss at the same time, which complicates our ability to disentangle these two processes (Fahrig 2019). While habitat amount has consistently positive effects on biodiversity (Fahrig 2003), the role of habitat fragmentation is still heavily debated (Fahrig 2013, 2017; Hanski 2015; Fletcher et al.

2018; Saura 2021; Gonçalves-Souza et al. 2025). Simulation studies and empirical research suggest that habitat fragmentation may have either negative, positive, or no effects on species’ responses, which has led to several competing hypotheses.

According to the *habitat fragmentation hypothesis*, the occurrence of a species is affected by habitat fragmentation, independent of the effect of habitat amount. In the context of the present study, we define fragmentation as spatial pattern rather than as process (Fahrig 2019) and use the term habitat fragmentation for both negative and positive predicted effects of fragmentation. Negative effects may arise due to reduced dispersal (Schtickzelle and Baguette 2003) or negative edge effects (Deng and Gao 2005). Positive fragmentation effects may arise from small inter-patch distances in landscapes with many small instead of few large patches, positive edge effects (e.g., because of higher productivity and structural diversity of edges than of habitat interiors), or reduced competition (Fahrig 2017). By contrast, the *habitat amount hypothesis* proposed by Fahrig (2013) states that the occurrence of a species in equal-sized sample sites located in habitat patches is unaffected by habitat configuration within an ecologically meaningful distance to the site; rather, occurrence is driven by one single factor, the amount of habitat within this distance. The hypothesis posits that the effects of local habitat patch size and isolation are both contained within the effect of habitat amount and that there is no effect of habitat fragmentation per se. This hypothesis has received support by some empirical studies (e.g. meta-analysis by Watling et al. 2020) but has also been criticized, particularly for its inability to predict effects of habitat fragmentation at scales larger than the study sites (Hanski 2015; Saura 2021). While the habitat fragmentation and habitat amount hypotheses state that there either are effects or no effects of habitat fragmentation, the *fragmentation threshold hypothesis* (Andrén, 1994; Fahrig 1998; Flather and Bevers 2002) posits that fragmentation effects only occur below a certain threshold of habitat amount. Such thresholds have been found for some species (e.g., Betts et al. 2006; Bosco et al. 2021) but appear generally to be rare (Fahrig 2017). Lastly, while the three hypotheses presented so far assume a binary landscape consisting of the focal habitat type and the matrix (which comprises all other habitat types), the *matrix quality hypothesis* states that

the quality of the intervening landscape influences the occurrence of a species in habitat patches. For instance, high matrix quality may increase survival during dispersal (Schtickzelle and Baguette 2003) or movement rates (Eycott et al. 2012) and thus facilitate patch colonization.

Here, we examined the occurrence of the white-backed woodpecker *Dendrocopos leucotos* ssp. *leucotos* in relation to local habitat and landscape context in Western Austria, Eastern Switzerland and Liechtenstein, where the subspecies reaches its western range edge in Central Europe. The white-backed woodpecker prefers old-growth deciduous or mixed forests with abundant deadwood (Aulén, 1988; Scherzinger 1982; Czeszczewik 2009a), mainly because its diet largely consists of wood-boring larvae (Aulén, 1988; Hogstad and Stenberg 1997). The species is distributed over the entire Palearctic but has a disjunct distribution in Europe as a result of deforestation and intensive forest management (Virkkala et al. 1993). Accordingly, the occurrence of the species in Europe is limited to regions with generally low forest management intensity, and within a population, the presence and abundance of the species is associated with factors typically found in old-growth forests (Walankiewicz et al. 2011; Kajtoch et al. 2013; Ettwein et al. 2020). Today, the white-backed woodpecker is of high conservation concern in many European countries (e.g., it is listed in Annex 1 of the European Union's Birds Directive). Current conservation recommendations and action plans focus on the maintenance and creation of old forest stands with abundant deadwood and deciduous trees within areas of the size of a home range (Löhmus et al. 2010; Nagel et al. 2017), or without reference to the spatial extent at which the measures should be implemented (Ettwein et al. 2020). While it is known that habitat amount at the landscape level determines population persistence (Carlson 2000; Angelstam et al. 2004), it is unknown how suitable habitats should be spatially distributed or how the landscape surrounding habitat patches, i.e. the matrix, should be composed.

The aims of the study were (1) to evaluate occurrence probability of the white-backed woodpecker in relation to local habitat and to landscape context (habitat fragmentation hypothesis, habitat amount hypothesis, fragmentation threshold hypothesis, matrix quality hypothesis); (2) to assess the relative importance of local habitat and landscape context for

modeling white-backed woodpecker occurrence probability; and (3) to complement existing conservation recommendations for this species by addressing how suitable habitats should be embedded in the surrounding landscape.

Methods

Study area and study sites

The study area was located in the Eastern Alps in Austria (State of Vorarlberg), Eastern Switzerland (Cantons of Grisons and St Gallen), and the Principality of Liechtenstein (46.8 – 47.5°N, 9.3 – 10°E). Forest cover is naturally limited by the partly high elevation (ranging from 400 to 3000 m a.s.l., tree line at approximately 1600 – 1800 m) and has been additionally reduced by deforestation, particularly in the bottoms of larger valleys. Today, about 40% of the study area is covered with forest. Deciduous and mixed forests, dominated by European beech *Fagus sylvatica*, Norway spruce *Picea abies*, and silver fir *Abies alba*, comprise about 10 to 43% of the forested area and are found in lower elevations. Coniferous forests naturally occur in higher elevations up to the tree line but are also found as spruce plantations in lower elevations. Forest management intensity in the study area varies with accessibility of the terrain and landownership; it ranges from intensive management for timber production in easily accessible stands to the occasional logging of single trees or management abandonment in steep protection forests or some privately owned stands.

We selected 30 sites with and 30 sites without known white-backed woodpecker presence. Presence sites corresponded to the breeding home ranges of white-backed woodpeckers radio-tracked between 2016 and 2019 (see Ettwein et al. 2025 for details regarding capturing and tracking). We used minimum convex polygons based on all locations collected between egg-laying and fledging to compute these breeding home ranges. We selected only home ranges that did not overlap with another breeding home range from the same or another year and used only one breeding home range per individual for the analyses. Absence sites were selected in 2018 using the following procedure (see Online Resource 1 for an explanatory map). We first created a 550×550 m

grid to obtain potential absence sites (=30.25 ha, $n=1488$) corresponding in size to a white-backed woodpecker breeding home range (mean breeding home range size of 12 individuals tracked in 2016 and 2017 was 29 ha). Next, we calculated the proportions of deciduous or mixed forest area and of total forest area from CORINE Land Cover data (European Environment Agency 2019, CORINE Land Cover (CLC) 2018, Version 20, Copenhagen, Denmark) for the breeding home ranges of birds tracked in 2016 and 2017 and for all potential absence sites. We then calculated the 25% quantiles of the proportions of deciduous or mixed forest and of total forest area, respectively, in the breeding home ranges. To obtain absence sites that contain at least some potential white-backed woodpecker habitat, we omitted all potential absence sites in which the proportion of deciduous or mixed forest and of total forest was below these 25% quantiles. Since 1100 m represented the maximum elevation of observed breeding territories, potential absence sites above this threshold were excluded as well. Moreover, we omitted potential absence sites that were closer than 1000 m to a previous white-backed woodpecker observation. These observations were mainly made while searching individuals for the telemetry study (Ettwein et al. 2026) and were complemented by citizen science data from ornitho.ch, inatura Dornbirn, and BirdLife Vorarlberg. Finally, we selected all potential absence sites that overlapped with absence sites used by Ettwein et al. (2020; $n=8$; only sites in which no white-backed woodpecker was detected in both years of the study were used), and randomly 22 of the remaining potential absence sites that were considered accessible based on the inspection of topographic maps. We checked whether white-backed woodpeckers were present in the 30 absence sites in two surveys between February and April 2018. During each survey, a field worker used playbacks of drumming and calls (1 min of drumming, 1 min of calls, and again 1 min of drumming; 1 min of waiting for a reaction of a white-backed woodpecker after playing each sound) every 200 m. In two absence sites, white-backed woodpeckers were detected during the first survey. These sites were replaced by two new randomly chosen potential absence sites, in which absence of white-backed woodpeckers was confirmed in two surveys. Thus, it is highly probable that all 30 absence sites were truly unoccupied; white-backed woodpeckers

typically respond readily to the playback used. Even if a few sites were misidentified, such errors would likely decrease the power to detect effects and lead to more conservative effect size estimates. While false absences could undermine claims of "no effect", we recognize that any such statements are inherently limited by our sample size ($n=60$).

Habitat data

Local habitat

We selected similar variables describing local habitat (habitat within the presence and absence sites) as in previous studies addressing white-backed woodpecker habitat preferences (e.g., Hogstad and Stenberg 1994; Frank and Hochebner 2001; Ettwein et al. 2020; Kajtoch et al. 2013). We recorded forest structure characteristics in the field within circular 500 m² sampling plots whose centers were situated at the intersections of a 200×200 m grid placed over the presence and absence sites, respectively (Online Resource 1). We recorded diameter at breast height (DBH) and tree species of all live trees with a DBH ≥ 30 cm, and whether a live tree had dead branches with a diameter ≥ 10 cm. We further recorded diameter in the middle and length of all pieces of lying deadwood (=logs) with a diameter ≥ 7 cm, and DBH and height of all pieces of standing deadwood (=snags) with DBH ≥ 5 cm and height ≥ 130 cm. We used the formula of a cylinder to calculate the volume of individual snags and logs. The variables derived from these data and used for the analyses are shown in Table 1. We additionally computed the mean potential annual insolation for each site based on digital elevation models using SAGA 2.1.4 (Conrad et al. 2015), as white-backed woodpeckers have been shown to prefer sun-exposed slopes (Hogstad and Stenberg 1994; Scherzinger 1982; Frank 2002). Lastly, we calculated the proportion of old deciduous or mixed forest, the habitat type preferred by white-backed woodpeckers during the breeding season (Ettwein 2024; see "Landscape context" for the definition of this habitat type) in 500 m buffers around the site centroids. We did not calculate this variable within the sites because the home ranges varied in size. 500 m buffers resulted in areas of 78 ha, which approximately corresponded to the size of the largest breeding home range.

Table 1 Variables used for modeling white-backed woodpecker occurrence probability based on data recorded for presence sites (breeding season home ranges) and absence sites (550×550 m squares without white-backed woodpeckers). Local habitat was recorded within the study sites apart from

dec_old_500, which was recorded in a 500 m buffer around the site centroid; landscape context was recorded within circular buffers around the site centroid ranging from 1000 to 5000 m radii in 500 m increments (i.e., 9 variables per landscape metric)

Variable name	Description	Represented aspect of landscape context
Local habitat		
logs	Mean volume of lying deadwood ha ⁻¹	–
snags	Mean volume of standing deadwood ha ⁻¹	–
basallive	Mean basal area of live trees with DBH > 30 cm ha ⁻¹	–
deadbr	Mean number of trees with dead branches ha ⁻¹	–
beech50 ¹	Mean number of beech trees with DBH > 50 cm ha ⁻¹	–
sun	Mean potential annual insolation (kWh/m ²)	–
dec_old_500	Proportion of old deciduous/mixed forest	–
Landscape context		
dec_old	Proportion of old deciduous/mixed forest (proportion of deciduous trees > 25%, maximum tree height ≥ 40 m)	Habitat amount
clumpy	Clumpiness index for old deciduous/mixed forest (deviation of the proportion of adjacent old deciduous forest cell pairs from that expected under a spatially random distribution)	Habitat fragmentation
con_dec_young	Proportion of young and old coniferous forest and young deciduous/mixed forest (proportion of forest minus dec_old)	Matrix quality
dec_young	Proportion of young deciduous/mixed forest (proportion of deciduous trees > 25%, maximum tree height < 40 m)	Matrix quality
con_old	Proportion of old coniferous forest (proportion of deciduous trees ≤ 25%, maximum tree height ≥ 40 m)	Matrix quality

¹Used because the white-backed woodpecker prefers old deciduous forests and beech is the dominating deciduous tree species in the study area

Landscape context

We used remote sensing data to create variables representing landscape context because mapping forest characteristics in the field was not feasible at the landscape scale. We used Corine Land Cover data and LiDAR-based digital surface models (provided in a 0.5 m resolution by the responsible authorities in Austria and Liechtenstein and by the Federal Institute for Forest, Snow and Landscape Research WLS in Switzerland as terrain-normalized heights, i.e., the height of the vegetation relative to the ground) to create a 50×50 m raster with five habitat types: old deciduous or mixed deciduous/coniferous forest (proportion of deciduous trees > 25%, maximum tree height ≥ 40 m), young deciduous or mixed deciduous/coniferous forest (proportion of deciduous trees > 25%, maximum tree height < 40 m), old coniferous forest (proportion of deciduous trees ≤ 25%, maximum tree height ≥ 40 m), young coniferous forest (proportion of

deciduous trees ≤ 25%, maximum tree height < 40 m), and unforested (unforested area in the alpine zone, alpine pastures, and the deforested bottoms of larger valleys, cliffs, slopes > 60°). This way, the relevant information is provided rather referring readers to Ettwein 2024, cliffs, slopes > 60°). The 40-m threshold was chosen because the dominant tree species (beech) in our study area typically reaches this height in mature and old-growth stands (Commarmot et al 2005). We used tree height as a proxy of tree age because positive correlations between tree age and height have been found both for individual trees based on heights measured in the field (Kuuluvainen et al 2002) and at the stand scale based on parameters obtained from LiDAR data (Maltamo et al 2020).

We then calculated five landscape metrics describing habitat amount, habitat fragmentation, and matrix quality (see below) at nine spatial scales ranging from 1000 to 5000 m radii (in increments of 500 m) around the site centroids. The smallest radius (1000 m)

resulted in an area of 314 ha, which approximately corresponded to the annual minimum convex polygon home range size of a white-backed woodpecker (Ettwein et al. 2025), while the largest radius (5000 m) corresponded to an area 25 times the annual home range size. Based on the well-known preference for old-growth deciduous and mixed forest as breeding habitat (e.g., Hogstad and Stenberg 1994; Scherzinger 1982; Wesołowski 1995), we considered old deciduous or mixed forests (henceforward referred to as “old deciduous forest”) as focal habitat type to calculate metrics representing habitat amount and habitat fragmentation and considered all other habitat types as matrix. We used the R package *landscapemetrics* v1.5.5 (Hesselbarth et al. 2019) to calculate the five landscape metrics at each spatial scale. First, we calculated the proportion of old deciduous forest as metric representing habitat amount. Next, we used a clumpiness index for old deciduous forest as metric representing habitat fragmentation. This metric describes the deviation of the proportion of adjacent old deciduous forest cell pairs from that expected under a spatially random distribution and ranges from -1 when the habitat type is maximally disaggregated (i.e., maximally fragmented) to 1 when it is maximally clumped (McGarigal et al. 2012). Lastly, we calculated the proportions of coniferous and young deciduous forest (that is, the proportion of forest minus old deciduous forest), of young deciduous/mixed forest, and of old coniferous forest as three metrics representing matrix quality (Table 1), assuming that forest habitat types are associated with higher matrix quality for a forest specialist than unforested area (Brotons et al. 2003). We considered the three metrics as separate variables in our analyses to evaluate which one(s) might reflect high matrix quality.

Statistical analyses

We modeled white-backed woodpecker occurrence probability in three steps to select relevant local habitat variables (step 1), to evaluate the most relevant spatial scale(s) for each landscape metric (step 2), and to evaluate the hypotheses stated in the introduction (step 3; see Online Resource 2 for a summary of the three steps). As our response variable (presence/absence) was binary, we used binomial generalized linear mixed models with a logit-link function. We fitted the models in a Bayesian framework

using *rstanarm* v.2.21.3 (Goodrich et al. 2020) and performed model selection in each step. All variables were centered to mean=0 and scaled to standard deviation=1 prior to the analyses. As the sites were partly spatially clustered (e.g., several breeding home ranges close to each other), we created the variable *cluster_id* using the DBSCAN clustering tool in QGIS 3.22.8, which resulted in 17 site clusters being at least 5 km apart from each other. We included a random intercept for *cluster_id* in each model to account for spatial autocorrelation. We used the mean of the marginal posterior distribution as point estimate for a coefficient, and the 2.5% and 97.5% as bounds of 95% uncertainty interval.

In step 1, we first fitted a model including all seven local habitat variables. We then fitted four additional models with different combinations of *dec_old_500* (which was kept in all models to account for varying habitat amount at the local scale) and variables that had coefficient estimate > 0.5 in the first model (see “local habitat” in Table 3) and compared the five models via the information criterion for approximate leave-one-out cross-validation (LOOIC, Vehtari et al. 2019; results given in Online Resource 3). Variables from the top-ranked model were used below in further analyses. To select the most relevant spatial scale per landscape metric (step 2), we applied a ridge regression, a form of regularized linear regression that shrinks the regression coefficients towards zero by constraining the sum of the squared values of the coefficients (Hooten and Hobbs 2015). Ridge regression is particularly useful when multicollinearity among the covariates is present or when fewer observations than variables are available (Brown et al. 2002). This approach allowed us to include all (partly highly correlated) landscape metrics at all spatial scales in one model and hence to control for effects of other potentially relevant variables while evaluating the most relevant spatial scale for each metric. As we had no a priori information to select a specific scale, we applied this formal approach to identify the scale that was the most relevant according to our data. We constructed a model with the local habitat variables of the top-ranked model from step 1 and the five landscape metrics at all spatial scales (i.e., 45 landscape context variables). We then performed the ridge regression in a Bayesian framework by gradually increasing the width of the priors on the coefficients of the landscape context variables

(Hooten and Hobbs 2015). We used normal priors with mean=0 and standard deviation (SD)=0.1 to 2.5 (in increments of 0.05, i.e., 49 different priors and models) for the landscape context variables and with mean=0 and SD=2.5 for the local habitat variables (same priors in all models), with wide prior distributions resulting in weak regularization and narrow prior distributions in strong regularization. We compared the 49 models via the k-fold cross-validation information criterion (KFOLDIC; Online Resource 4). Using the top-ranked model, we selected for each landscape metric the spatial scale at which it had the largest absolute coefficient estimate for step 3. If the absolute coefficient estimates were similar at two spatial scales, we kept both variables. In step 3, we used the landscape context variables at the spatial scales selected in step 2 to build models representing the hypotheses presented in the introduction (see Table 2 for an overview of the predictions of each hypothesis and the corresponding models) and performed model selection via LOOIC. If a landscape metric was equally important at two scales according to the top-ranked model of step 2, we ran two models, using one of the two spatial scales per model. Each model also included the variables selected in step 1 to control for effects of local habitat, as well as a random intercept for cluster_id. Patterns of white-backed woodpecker occurrence probability at the landscape level were interpreted based on variables from the top-ranked model. Variables from lower-ranked models were additionally considered when their 95% credible intervals did not include zero.

To assess the relative importance of local habitat and landscape context for modeling white-backed woodpecker occurrence probability, we used the top-ranked model from step 3 as model representing both local habitat and landscape context (*m.full*). We also fitted one model (*m.local*) including only the local habitat variables from step 1 and cluster_id, and one model (*m.landscape*) including only the important landscape context variables from step 3 and cluster_id. We then calculated 1) the LOOIC for each of the three models, 2) the proportion of sites for which white-backed woodpecker presence/absence was correctly predicted (estimated presence probability > 0.5 vs. < 0.5) by each of the three models, and 3) the proportion of variance explained a) by local habitat and landscape context while controlling for cluster_id, b) by local habitat while controlling for landscape

context and cluster_id, and c) by landscape context while controlling for local habitat and cluster_id. We additionally fitted a model including only cluster_id as random effect (*m.ranef*) and calculated the proportion of explained variance following Gelman and Pardoe (2006):

$$R^2(\text{local habitat} + \text{landscape context}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{ranef}}$$

$$R^2(\text{local habitat}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{landscape}}$$

$$R^2(\text{landscape context}) = 1 - \frac{\text{residual variance under } m.\text{full}}{\text{residual variance under } m.\text{local}}$$

Hence, with this definition, R^2 (local habitat) is the variance explained by the local habitat variables that is not also explained by the landscape variables, and vice versa for R^2 (landscape context).

Results

According to our local habitat models (step 1), white-backed woodpecker occurrence probability was positively associated with the volume of lying deadwood and the number of live trees with dead branches (Fig. 1, Table 3a, Table 4a). Occurrence probability was also positively related to the proportion of old deciduous forest, which was used in all models. None of the credible intervals in this model included zero (Table 4a).

The top-ranked model from the Bayesian ridge regression (step 2) showed that habitat amount best explained white-backed woodpecker occurrence at relatively small spatial scales of 1000 to 2500 m (highest coefficient estimate at the 2500 m scale, Fig. 2a). White-backed woodpecker occurrence probability was negatively related to the clumpiness index (i.e., it was positively related to habitat fragmentation) across all spatial scales (largest absolute coefficient estimates at the 1500 and 4500 m scales) except for the 1000 m scale (Fig. 2b). The coefficient

Table 2 Models at the landscape level, examined for evaluating predictions of the habitat fragmentation hypothesis (HF), fragmentation threshold hypothesis (FT), habitat amount hypothesis (HA), and matrix quality hypothesis (MQ1: high

importance of coniferous and young deciduous forest as matrix habitat; MQ2: high importance of young deciduous forest as matrix habitat; MQ3: high importance of old coniferous forest as matrix habitat)

Hypothesis	Predictions	Models
Habitat fragmentation (HF)	a) Occurrence probability is positively or negatively related to clumpiness index	clumpy
	b) Occurrence probability is positively related to habitat amount and positively or negatively related to clumpiness index	dec_old + clumpy
Fragmentation threshold (FT)	a) Occurrence probability is positively related to clumpiness index (i.e., negative effect of habitat fragmentation) when habitat amount is low; model including interaction between dec_old and clumpy performs better than model without interaction	dec_old + clumpy + dec_old:clumpy
Habitat amount (HA)	a) Occurrence probability is positively related to habitat amount at the landscape level (after accounting for habitat amount at the local scale) and not related to clumpiness index; model including only dec_old performs better than model additionally including clumpy	dec_old
Matrix quality 1 (MQ1)	a) Occurrence probability is positively related to proportion of coniferous and young deciduous forest	con_dec_young
	b) Occurrence probability is positively related to habitat amount and to proportion of coniferous and young deciduous forest	dec_old + con_dec_young
	c) The effect of matrix quality (proportion of coniferous and young deciduous forest) may be stronger when habitat amount is low	dec_old + con_dec_young + dec_old:con_dec_young
Matrix quality 2 (MQ2)	a) Occurrence probability is positively related to proportion of young deciduous forest	dec_young
	b) Occurrence probability is positively related to habitat amount and to proportion of young deciduous forest	dec_old + dec_young
	c) The effect of matrix quality (proportion of young deciduous forest) may be stronger when habitat amount is low	dec_old + dec_young + dec_old:dec_young
Matrix quality 3 (MQ3)	a) Occurrence probability is positively related to proportion of old coniferous forest	con_old
	b) Occurrence probability is positively related to habitat amount and to proportion of old coniferous forest	dec_old + con_old
	c) The effect of matrix quality (proportion of old coniferous forest) may be stronger when habitat amount is low	dec_old + con_old + dec_old:con_old

The column “Models” lists the variables used in models evaluating predictions (indicated by small letters a–c) of the respective hypotheses. All models also included dec_old_500, logs and deadbr. For definitions of the variables, see Table 1

estimates for proportion of coniferous and young deciduous forest were positive at all spatial scales (Fig. 2c), whereas those for the proportion of young

deciduous forest (Fig. 2d) were close to zero across almost all spatial scales, so we used a middle scale of 3000 m. Proportion of old coniferous forest showed

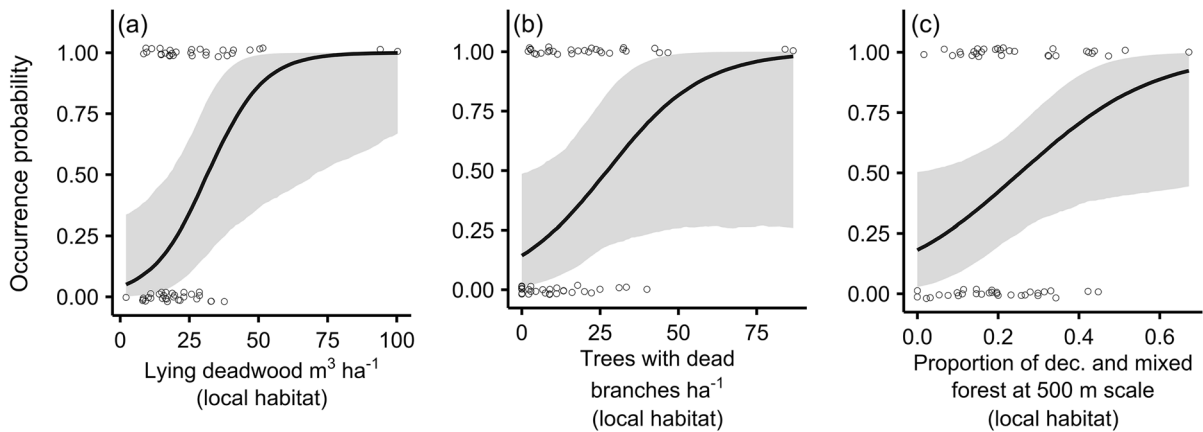


Fig. 1 Relationships between white-backed woodpecker occurrence probability and variables representing local habitat context. Shown are medians and 95% credible intervals

using the joint posterior distribution of the top-ranked model (Table 3a). Estimates were calculated with other variables set to their means. N = 60

Table 3 Models used to relate white-backed woodpecker occurrence to local habitat and to landscape context (represented by four hypotheses: HA = Habitat amount hypothesis; HF = Habitat fragmentation hypothesis; FT = Fragmentation

threshold hypothesis; MQ = Matrix quality hypothesis: 1: high importance of all non-old deciduous forest types, 2: high importance of young deciduous forest, 3: high importance of old coniferous forest as matrix habitat)

Hypothesis	Model	LOOIC	ΔLOOIC
a) Local habitat			
-	dec_old_500 + logs + deadbr	73.05	0
-	dec_old_500 + logs + deadbr + sun	74.42	1.37
-	dec_old_500 + deadbr + sun	75.19	2.14
-	dec_old_500 + logs + sun	78.57	5.52
-	dec_old_500 + logs + snags + basallive + deadbr + beech50 + sun	83.98	10.93
b) Local habitat + landscape context (all models also include dec_old_500 + logs + deadbr)			
MQ1 c	dec_old_2500 + con_dec_young_3000 + dec_old_2500:con_dec_young_3000	50.18	0
MQ1 b	dec_old_2500 + con_dec_young_3000	54.24	4.05
MQ3 b	dec_old_2500 + con_old_1500	56.81	6.63
HF b	dec_old_2500 + clumpy_4500	57.31	7.13
FT a	dec_old_2500 + clumpy_4500 + dec_old_2500:clumpy_4500	58.38	8.19
HA a	dec_old_2500	58.82	8.63
MQ1 a	con_dec_young_3000	59.72	9.54
MQ2 b	dec_old_2500 + dec_young_3000	60.81	10.62
MQ2 c	dec_old_2500 + dec_young_3000 + dec_old_2500:dec_young_3000	61.39	11.20
MQ3 c	dec_old_2500 + con_old_1500 + dec_old_2500:con_old_1500	61.48	11.30
HF a	clumpy_4500	69.09	18.90
MQ2 a	dec_young_3000	71.17	20.98
-	Only local habitat	73.05	22.87
MQ3 a	con_old_1500	74.94	24.75

In part b), small letters a–c following hypothesis abbreviations (HA, HF, MQ1–3) refer to different predictions and models evaluated per hypothesis (see Table 2). Model selection was performed based on the information criterion for approximate leave-one-out cross-validation (LOOIC). ΔLOOIC: Difference in LOOIC between a given model and the top-ranked model. Variables are defined in Table 1. The number at the end of a variable name refers to the spatial scale at which it was measured. If a landscape metric was used at two spatial scales, only the higher ranked model is presented (see Online Resource 5 for full list of models and Online Resources 6 and 7 for correlations between the variables). N = 60.

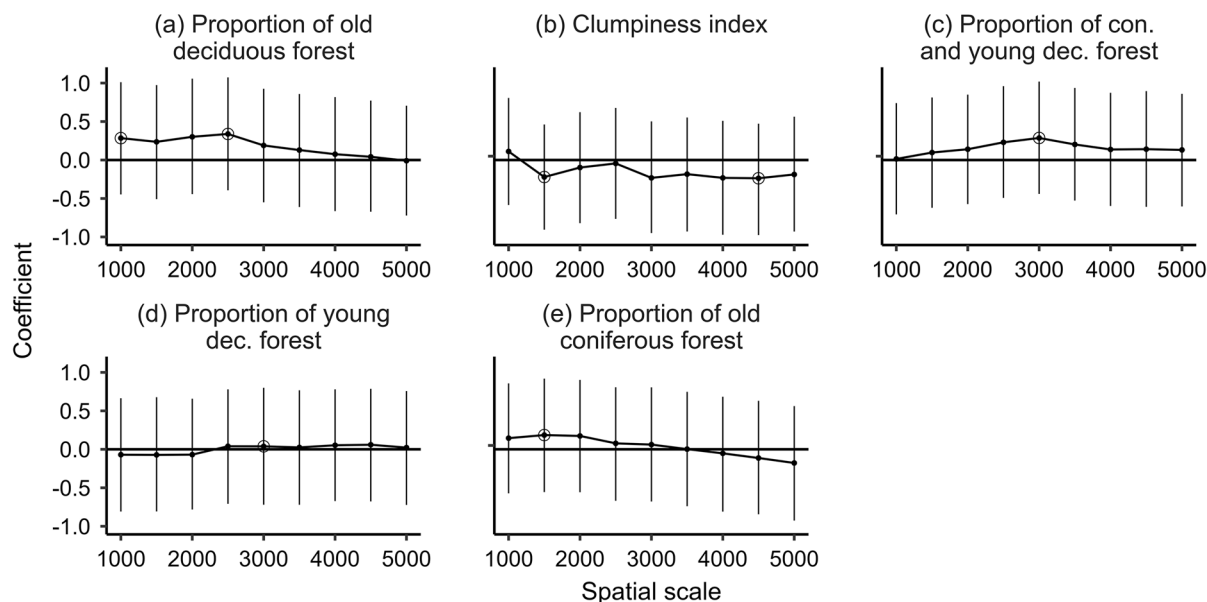
Table 4 Estimates of effects of variables on occurrence of the white-backed woodpecker in relation to local habitat and landscape context

Variable	a)	b)
(Intercept)	− 0.19 [− 1.30; 0.65]	− 0.67 [− 2.29; 0.71]
logs	0.80 [0.05; 1.72]	1.79 [0.39; 3.64]
deadbr	1.06 [0.30; 1.99]	1.21 [0.04; 2.84]
dec_old_500	0.84 [0.03; 1.88]	0.54 [− 0.83; 2.00]
dec_old_2500	–	2.40 [0.83; 4.84]
con_dec_	–	1.70 [0.38; 3.68]
young_3000	–	–
dec_old_2500:con_	–	2.35 [0.53; 4.66]
dec_young_3000	–	–
con_old_1500	–	–
clumpy_4500	–	–
Variance cluster_id	0.68 [0.00; 7.54]	1.72 [0.01; 13.79]

Shown are coefficient estimates and 95% credible intervals (medians and 2.5 and 97.5% quantiles of the marginal posterior distributions) of variables included in a) the top-ranked local habitat-only model (Table 3a), and b) the top-ranked model including local habitat and landscape context variables (Table 3b). Variables are defined in Table 1

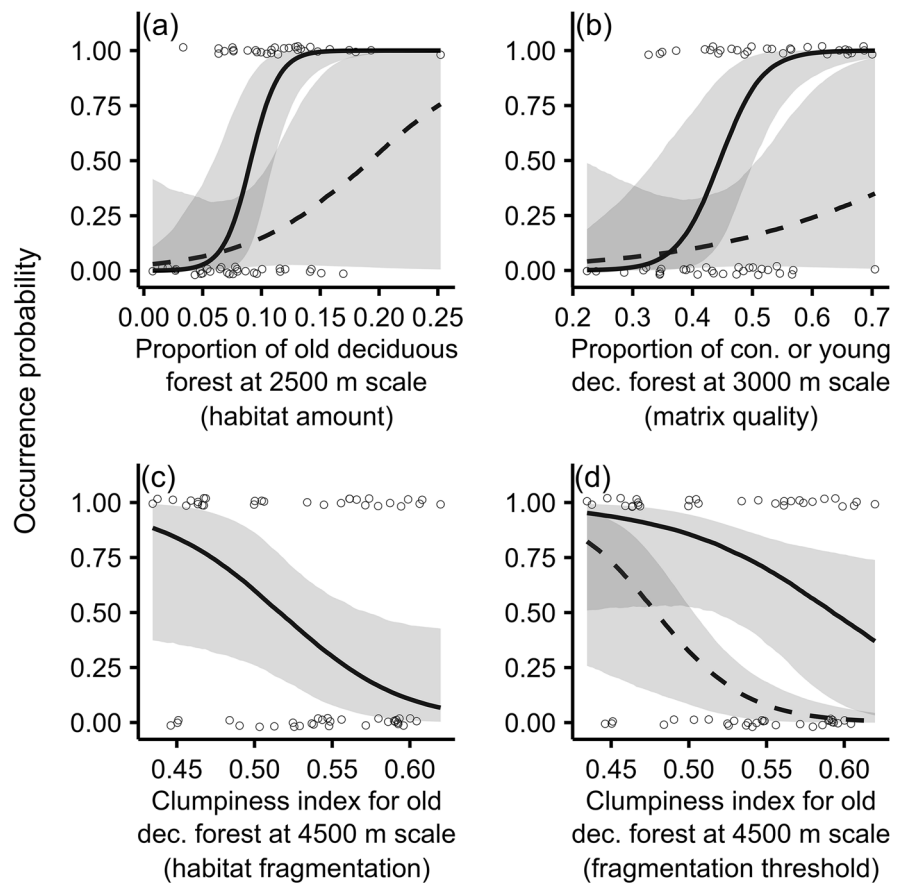
some preference for scales between 1000 and 2000 m (Fig. 2e).

Comparing the models representing the landscape context hypotheses (step 3) showed that white-backed woodpecker occurrence was best explained by a model including habitat amount and matrix quality variables and their interaction (model MQ1 c, Table 3b; for estimates and credible intervals see Table 4b). Occurrence probability increased with increasing proportion of old deciduous forest at the 2500 m scale and increasing proportion of coniferous and young deciduous forest at the 3000 m scale. The interaction between the two variables showed that occurrence probability was only high when both habitat amount and the proportion of coniferous and young deciduous forest (referring to matrix quality) were high (Fig. 3a, b). According to our top-ranked model (MQ1 c in Table 3b), at intermediate habitat amount (proportion of old deciduous forest) and matrix quality (proportion of coniferous and young deciduous forest) at the landscape scale, white-backed woodpecker occurrence probability exceeded 50% when in a site 31 m³ ha^{−1} of logs and 27 trees with dead branches ha^{−1} were locally available. However,

**Fig. 2** Results of the top-ranked model of a Bayesian ridge regression relating white-backed woodpecker occurrence probability to landscape metrics at spatial scales ranging from 1000 to 5000 m. Each dot is the coefficient estimate (median of the marginal posterior distribution) of one landscape metric at a

given spatial scale, with its 95% uncertainty interval. The ridge regression was used to evaluate the most relevant spatial scale per landscape metric, indicated by a circle (two scales used for proportion of old deciduous forest and for clumpiness index)

Fig. 3 Relationships between white-backed woodpecker occurrence probability and variables representing landscape context. Shown are medians and 95% credible intervals using the joint posterior distribution of (a,b) the top-ranked model (MQ1 c, Table 3b), c a high-ranked model representing the habitat fragmentation hypothesis (HF b, Table 3b), and (d) a model representing the fragmentation threshold hypothesis (FT a, Table 3b). Estimates were calculated with other variables set to their means, except when the variable on the x-axis was in interaction with another predictor (proportion of coniferous and young deciduous forest at the 3000 m scale in (a), proportion of old deciduous forest at the 2500 m scale in both (b) and (d)), where the 25% (dashed line) and 75% quantiles (solid line) of the interacting predictor were used. $N=60$



if a site with $31 \text{ m}^3 \text{ ha}^{-1}$ of logs and 27 trees with dead branches ha^{-1} was in a landscape with low habitat amount and low matrix quality at the landscape scale (25% quantiles), our model predicted an occurrence probability of only 30%. By contrast, when we set habitat amount and matrix quality to the respective 75% quantiles, occurrence probability exceeded 50% even at minimum local habitat quality (in our dataset $2 \text{ m}^3 \text{ ha}^{-1}$ of logs and no trees with dead branches; however, note that predicted values are associated with some uncertainty and all occupied sites in our study contained logs and trees with dead branches).

A model including habitat amount and old coniferous forest as matrix habitat also ranked relatively high (ΔLOOIC to the top-ranked model = 6.63, model MQ3 b in Table 3b), with a suggested positive effect of the proportion of old coniferous forest at the 1500 m scale on occurrence probability (estimate = 1.00, 95% credible interval = $-0.01 - 2.39$).

A similarly ranked model (ΔLOOIC to the top-ranked model = 7.13) included habitat amount and

habitat fragmentation variables (habitat fragmentation hypothesis model HF, model HF b in Table 3b), and the credible intervals of the respective landscape context variables did not include zero. According to this model, occurrence probability increased with increasing proportion of old deciduous forest at the 2500 m scale (estimate = 2.42, 95% credible interval = $1.06 - 4.07$) and decreased with increasing clumpiness index at the 4500 m scale (estimate = -1.39 , 95% credible interval = $-2.96 - 0.13$) (Fig. 3c). The model referring to the fragmentation threshold hypothesis and including the interaction between habitat amount and habitat fragmentation (model FT a, Table 3b) ranked lower than the model without the interaction (model HF b, Table 3b). In addition, occurrence probability decreased with increasing clumpiness index (i.e., decreasing fragmentation) regardless of habitat amount (i.e. old deciduous forest; Fig. 3d), which is in contrast to the predicted relationship for the fragmentation threshold hypothesis (Table 2).

Lastly, comparing the models including both local habitat and landscape context (*m.full*=MQ1 c, top-ranked model in Table 3b), or only local habitat (*m.local*=top-ranked model in Table 3a), or only landscape context (*m.landscape*=MQ1 c without local habitat variables) showed that the model with only landscape context variables (*m.landscape*) explained white-backed woodpecker occurrence substantially better than the model with only local habitat variables (*m.local*). The model including variables from both local habitat and landscape context (*m.full*) further decreased the LOOIC by about 8 points (Table 5).

Discussion

In the present study, we examined white-backed woodpecker occurrence probability in relation to local habitat and to four hypotheses describing potential effects of landscape context: the habitat fragmentation hypothesis, the habitat amount hypothesis, the fragmentation threshold hypothesis, and the matrix quality hypothesis. Landscape context explained 2.5 times more of the variance in occurrence probability than local habitat. The relationship between occurrence probability and landscape context was explained by the matrix quality hypothesis and, albeit with weaker support, the habitat fragmentation hypothesis.

White-backed woodpecker occurrence is related to local forest characteristics and to landscape composition and configuration

In accordance with previous studies addressing the white-backed woodpecker's habitat preferences (e.g., Hogstad and Stenberg 1994; Czeszczewik et al. 2013; Kajtoch et al. 2013; Ettwein et al. 2020), occurrence probability increased with the abundance of structural elements found in old(-growth) forests (lying deadwood and trees with dead branches) at the local scale. However, it is important to note that data on the abundance and spatial distribution of these structural elements at the landscape scale were not available and we thus do not know whether deadwood and trees with dead branches are important at larger spatial scales as well.

Complementing the existing knowledge about the white-backed woodpecker's breeding habitat preferences, we found that occurrence probability was also related to landscape composition and configuration at spatial scales beyond the home range scale. According to our top-ranked model in Table 3b, white-backed woodpecker occurrence probability increased with the proportion of old deciduous forest (representing habitat amount) at the 2500 m (=20 km²) scale, and, in line with the matrix quality hypothesis, the proportion of coniferous and young deciduous forest (at the 3000 m (=28 km²) scale). The positive sign of the interaction term between matrix quality and habitat amount showed that for high occurrence probabilities, both habitat amount and matrix quality needed to be high, with both variables exhibiting thresholds above which occurrence probability strongly increased. That the effects of habitat amount

Table 5 Performance of three models relating white-backed woodpecker occurrence to variables describing 1) both local habitat (those in the best model for local habitat, Table 3a) and landscape context (those in the best model for landscape

context in Table 3b, MQ1 c; *m.full*), 2) only local habitat (best model in Table 3a, *m.local*), or 3) only landscape context (best model in Table 3b, MQ1 c, but excluding local habitat variables, *m.landscape*)

Model	LOOIC	% of sites for which presence/absence was correctly predicted	Explained variance
1) Local habitat + landscape context (<i>m.full</i>)	50.2	90%	66%
3) Landscape context (<i>m.landscape</i>)	58.0	87%	50%
2) Local habitat (<i>m.local</i>)	73.1	78%	20%

LOOIC=information criterion for approximate leave one out cross-validation. All models also include a random intercept for cluster_id.

and matrix quality are larger, the larger the values of the other variable is (i.e., the interaction term is positive) relates to the slopes of the lines: in Fig. 3a the slope for the line with higher matrix quality (solid line) is steeper than the line for lower matrix quality (dashed), while in Fig. 3b the slope for the line with higher habitat amount (solid line) is steeper than the line for lower habitat amount (dashed line). Moreover, for a given relatively low proportion of old deciduous forest (e.g., 0.1 in Fig. 3a), occurrence probability is much higher if there is a higher proportion of coniferous and young deciduous forest at the 3000 m scale (75% vs. 25%). Thus, a combination of both habitat amount and matrix quality is key for the occurrence patterns of the white-backed woodpecker.

The proportion of old deciduous forest at the 500 m ($=0.8 \text{ km}^2$) scale, which we used in all models to account for varying habitat amount at the local scale and which was an important variable in the local habitat-only model, became unimportant once habitat amount at larger scales was also included (Table 4). That habitat amount is important at spatial scales beyond the home range scale is consistent with studies on the occurrence of many other species including forest birds (e.g., Betts et al. 2007, 2010; Smith et al. 2011), some of which also found thresholds for habitat amount (Betts et al. 2007, 2010). Considering that the annual home range size of the white-backed woodpecker is approximately 100–350 ha (Ettwein et al. 2025), the importance of habitat amount at a large spatial scale suggests that the individuals establish their home ranges in areas with enough habitat to sustain multiple breeding pairs. Indeed, in our study area usually at least three to five breeding territories were found next to each other.

Matrix quality was important at a similar spatial scale as habitat amount. This might either be because white-backed woodpeckers supplement their resource intake by foraging also in the matrix (“landscape supplementation hypothesis”, Dunning et al. 1992) or because forest as matrix habitat facilitates movement between habitat patches. It likely is a combination of both: On the one hand, white-backed woodpeckers are known to forage also in coniferous and young deciduous forests, particularly in the non-breeding season (Ettwein 2024), and high forest cover at large spatial scales thus provides additional foraging habitat. On the other hand, the species strongly avoids unfor-ested area (Ettwein 2024), and old deciduous stands

within larger forested areas are thus more likely to be reached than stands surrounded by unfor-ested area. The latter aspect may be particularly important for dispersal. Translocation experiments (Bélisle et al. 2001; Aben et al. 2012), tracking of dispersing juveniles (Cox and Kesler 2012), and studies addressing occupancy and abundance (Watling et al. 2011) have consistently concluded that matrix composition strongly influences movements and ultimately connectivity in many species. The importance of matrix composition for movement and connectivity tends to be stronger when the contrast between matrix types is high (Eycott et al. 2012). In our study area (see Methods for definition and spatial extent), where forest cover is relatively low (approximately 40% across the study area), matrix quality may thus be particularly important.

Lastly, in line with the habitat fragmentation hypothesis, white-backed woodpecker occurrence probability decreased with increasing clumpiness (i.e., decreasing fragmentation) of old deciduous forest at the 4500 m ($=64 \text{ km}^2$) scale. Conversely, our results provided no support for the fragmentation threshold hypothesis. The corresponding model ranked lower than the habitat fragmentation model, and occurrence probability decreased with an increasing clumpiness index (i.e., decreasing fragmentation) regardless of habitat amount. These results contradict our initial predictions. Similar to the positive effects of matrix quality, positive effects of habitat fragmentation may be related to enhanced connectivity fostering movements across the landscape (Fahrig 2017). That is, at the same habitat amount in the landscape, distances between habitat patches tend to be smaller in landscapes with many small instead of few large dispersed patches, and dispersed patches of old deciduous forest in a matrix of other forest types may serve as stepping stones between occupied sites. However, considering that the coefficient estimates of the clumpiness index were smaller than those of the proportions of old deciduous forest and of coniferous and young deciduous forest, respectively, and that the difference between the LOOIC values of the habitat fragmentation model and the matrix quality model was relatively large, habitat fragmentation appeared to be less important than habitat amount and matrix quality. Note that the observed clumpiness values were restricted to a narrow range (0.4 to 0.65), which reduces the statistical power to detect a correlation.

This lack of variance may have obscured a relationship that would only be apparent across a broader gradient of forest fragmentation.

Altogether, the relationships between white-backed woodpecker occurrence and landscape context suggest that occurrence probability within a study site is affected by the likelihood that the site is colonized by a dispersing bird. Dispersal of juvenile white-backed woodpeckers has not been studied yet, but studies on other woodpecker species avoiding unforested area also suggest that landscape context strongly affects site colonization through modifying dispersal. For instance, prospecting juvenile red-bellied woodpeckers (*Melanerpes carolinus*) chose foray paths and dispersal directions with high forest cover (Cox and Kesler 2012), suggesting a high importance of matrix composition for dispersal. Moreover, juvenile red-cockaded woodpeckers (*Picoides borealis*) and juvenile middle spotted woodpeckers (*Dendrocoptes medius*) dispersed across forests resembling the species' breeding habitat (Ciudad et al. 2009; Kesler and Walters 2012), supporting the idea that such habitat patches in the matrix may serve as stepping stones for dispersing birds.

Landscape context is more important than local habitat

According to our models including both local habitat and landscape context, landscape context explained about 2.5 times more of the variance in occurrence probability than local habitat. Moreover, the model including only landscape context variables performed substantially better than the local habitat-only model and almost as well as the model including both local habitat and landscape context variables. The high importance of landscape context in our models does not only show that the occurrence of the white-backed woodpecker in a given site may strongly depend on its surrounding landscape as discussed above but also illustrates that identifying important habitat factors requires consideration of variables at various spatial scales. Considering only local habitat may lead to the overemphasis of local habitat characteristics and ineffective conservation guidelines. We do not conclude that local habitat quality is generally unimportant for white-backed woodpeckers. Deadwood is used for foraging throughout the year (Czeszczewik 2009a, b, Ettwein 2024) and thus crucial for this species. The

relatively low importance of local habitat in our models was rather a result of the generally high habitat quality in most absence sites, which also contained deciduous or mixed mountain forest with relatively high amounts of deadwood. Moreover, the effect of the landscape context may differ between regions. For instance, Orme et al. (2019) showed that the negative effect of deforestation on the occurrence of forest birds was stronger near the range edge than in the range core, and the high importance of landscape context found in our study might be due to the study population being at the range edge. Similarly, our results may not be transferable to other species. In a similar study system as ours (spatially structured woodpecker population at the range edge), Robles and Ciudad (2012) found that local habitat was more important than landscape context for occupancy dynamics of the middle spotted woodpecker. More studies explicitly comparing the relative importance of local habitat and landscape context are needed to assess whether incorporating landscape context into habitat models is generally important for white-backed woodpeckers and other species.

Conservation implications

The high importance of landscape context for the occurrence of the white-backed woodpecker suggests that conservation measures for this species might be ineffective, if overall forest cover (that is, old deciduous forest, young and old coniferous forest as well as young deciduous/mixed forest) across large areas (up to 28 km² in our study) is low, even if sufficient habitat exists locally to support a single breeding pair. As afforesting currently unforested areas over large extents is not feasible in most of Europe, management measures for the white-backed woodpecker should focus on the conservation of and habitat improvements in large forested areas with known occurrence of the species or on unoccupied areas that contain enough forest to potentially sustain multiple breeding pairs. In our study region, a high proportion of old deciduous or mixed forest as well as of other forest types was important in areas of 20 to 28 km² surrounding a given occupied site. For example, occurrence probability exceeded 90% when 2.30 km² of old deciduous forest and 16 km² of other forest types were available within areas of

20 and 28 km², respectively. Therefore, conservation measures at the landscape level should focus on the protection or creation of old deciduous or mixed stands (e.g., by establishing forest reserves) embedded in large forested areas. The positive relationship between white-backed woodpecker occurrence probability and habitat fragmentation within 64 km² areas suggests that these forests large enough to sustain multiple breeding pairs should ideally be connected by dispersed patches of old deciduous or mixed forest. At the scale of the breeding home range (approximately 0.30 km²), logs and trees with dead branches appeared to be important and should thus be retained. However, as the yearly home ranges are larger than the breeding home ranges (Ettwein et al. 2025) and deadwood is the main foraging substrate not only within the home ranges but probably also during dispersal, white-backed woodpeckers will benefit from the availability of deadwood and old trees in much larger areas and in all forest types.

Acknowledgements We thank the many field assistants for their efforts during the data collection as well as the State Office for Land Surveying and Geoinformation, Vorarlberg, the Department for Civil Engineering and Geoinformation, Principality of Liechtenstein, and the Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland, for providing remote sensing data. We thank Thomas Püttner and two anonymous reviewers for their helpful comments to a previous draft. This work was financially supported by the Federal Office for the Environment, Switzerland, the Margarethe und Rudolf Gsell Foundation, and the Zigerli-Hegi Foundation.

Author contributions All authors contributed to the study conception and design. Material preparation and data collection were performed by Antonia Ettwein, Michael Lanz and Gilberto Pasinelli, and data analysis was done by Antonia Ettwein and Pius Korner. The first draft of the manuscript was written by Antonia Ettwein and all authors commented on various versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Swiss Ornithological Institute. This work was supported by the Federal Office for the Environment, Switzerland, the Margarethe und Rudolf Gsell Foundation, and the Zigerli-Hegi Foundation.

Data availability The datasets generated and/or analysed during the current study are available in the vogelwarte.ch Open Repository and Archive <https://zenodo.org/communities/vora/> hosted by Zenodo <https://doi.org/10.5281/zenodo.20552156>.

Declarations

Conflict of interest The authors declare no competing interests.

Research involving human and animal participants Capturing and tagging was permitted by the district commissions of Bludenz, Bregenz, Dornbirn and Feldkirch (Austria), the Office of Environment (Liechtenstein), the Federal Office for the Environment FOEN (Switzerland) and the Office for Food Safety and Animal Health, Canton of Grisons (Switzerland) and complied with the current laws of the respective countries.

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