Over the hills and far away: landscape factors affecting cavity digging by the Black woodpecker (*Dryocopus martius*, L. 1758)

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Abstract

The Black woodpecker (*Dryocopus martius*, L. 1758) is the largest primary cavity digger in western Europe. Its cavities represent an essential microhabitat for many other forest species but the landscape factors that influence the cavity digging by the Black woodpecker are poorly known and rarely been quantified at the scale of the vital range.

We used cavity maps by foresters and naturalists to build a large (2689 cavity bearing trees) database distributed over 11 sites in France. Based on this and on a set of pseudo-absence data, we analysed the effects of stand composition and landscape features at three different scales around each plot corresponding to a forest management unit (10ha), the core (100ha) and extended (250ha) vital range scales.

We showed that landscape shape index and forest composition (mixed forests) had significant effects but that the magnitude varied across the three scales. The Black woodpecker tend to avoid conifer-dominated stands to dig cavities, and also prefer homogeneous forest landscapes with low edge densities. These results vary with precipitation and slope with stronger effects of landscape in wetter climates and higher slopes.

Although forest management rarely modifies the landscape in western Europe, a better understanding of the features that influence cavity digging by the Black woodpecker may help to better integrate their conservation at the management planning scale. Our results also show the importance to maintain mixed broadleaf-conifer forests as well as connected forest landscapes to favour features that benefit forest biodiversity at the large scale.

Keywords: Black woodpecker, connectivity, landscape features, forest management, Tree-related microhabitat, cavity

Introduction

The conservation of forest biodiversity relies on an ensemble of methods including setting aside forest reserves, conservation islands and preserving, within managed forests, elements that favor the biodiversity of forest dwelling species (Bollmann and Braunisch 2013, Kraus and Krumm 2013). Tree-related microhabitats (hereafter microhabitats, sensu Larrieu *et al.* 2018), defined as tree-born singularities, are structural elements that support various species and communities. Among the different microhabitats, woodpecker cavities are, so far, the most documented regarding the biodiversity they harbor (Cockle *et al.* 2011, Larrieu *et al.* 2018). Black woodpecker (*Dryocopus martius* L. 1758) cavities are the largest cavities dug by a bird in Europe, and, as such, they have a crucial role for a large panel of secondary cavity nesters (Cockle *et al.* 2011). The Black woodpecker digs cavities for nesting, but also for roosting, and both cavity types may be used by other nesters. The Black woodpecker is qualified as an ecosystem engineer, because it significantly modifies its environment and thus allows species to live and reproduce (Pirovano and Zecca 2014): e.g. the Boreal owl (*Aegolius funereus*, L. 1758), the Stock dove (*Columba oenas*, L. 1758), the Greater Noctule (*Nyctalus lasiopterus*, S. 1780), the Pine marten (*Martes martes*, L. 1758), and numerous saproxylic beetles and fungi. The Black woodpecker is also considered as an umbrella species, because its presence conditions the presence of other species. This effect is accentuated by the fact that this bird has a large vital range (up to 500ha in Sweden and Norway, Tjernberg *et al.* 1993, Rolstad *et al.* 1998, 316ha in the Italian Alps, Bocca *et al.* 2007) and also needs forests in favorable conservation status to accomplish its life cycle (Olano 2015). As a consequence, understanding the factors that condition cavity digging by the Black woodpecker is essential to better integrate them in forest management at different scales. However, such knowledge often relies on expertise and has rarely been quantified using systematic approaches on large datasets (e.g. Cuisin 1967).

At the tree scale, several studies have shown that the Black woodpecker digs in less crowded environments, on trees devoid of low branches and trees with a diameter at breast height larger than the others in the vicinity (Puverel *et al.* 2019, Basile *et al.* 2020). At larger scales, several stand and landscape factors also seem to influence cavity digging (e.g. Gil-Tena *et al.* 2013, Brambilla and Saporetti 2014, Saporetti *et al.* 2016). As a forest specialist, the Black woodpecker depends on forest habitats to reproduce (Tjernberg *et al.* 1993, Angelstam *et al.* 2002, Mikusiński 2015), but also on more open habitats to feed (Dorresteijn *et al.* 2013, Brambilla and Saporetti 2014, Pirovano and Zecca

2014). Cavity digging may first be influenced by the forest cover, that would benefit both nesting and feeding of the species (Dorresteijn *et al.* 2013, Pirovano and Zecca 2014). This effect of forest cover would be stronger in heterogeneous (mixed mature stands combined with open habitats) and fragmented landscapes (Karimi *et al.* 2018). Then, landscape connectivity would positively influence the Black woodpecker presence and cavity digging, with higher probabilities in places where favorable patches are connected (Tobalske and Tobalske 1999, Gil-Tena *et al.* 2013).

In this context, we aimed to quantify the effects of intra- and extra- forest landscape factors on cavity digging by the Black woodpecker to better integrate its cavities in forest management and planning. We used a large database of Black woodpecker cavities maps provided by local managers and naturalists on nine different sites in France covering a wide range of ecological conditions (forest types, elevation, climate). We worked at three different scales to provide management and biologically relevant answers: (i) 10ha (0.1km2) scale that corresponds to a typical management unit in France; (ii) 100ha (1km2) scale that corresponds at the mean core vital range of the Black woodpecker where it defends its territory and breeds (Bocca *et al.* 2007); (iii) 250ha (2.5km2) scale that corresponds to the mean vital range over the year (Olano 2015). For each scale, we extracted the same landscape variables to assess those that were the most influential for cavity digging, and understand whether the landscape factors were the same across all scales. We hypothesized that:

(i) The presence of both broadleaf stands for nesting and conifer stands for feeding would positively influence the presence of cavities;

(ii) The presence of large, unfragmented, areas within its vital range would positively influence the presence of cavities. This would consist in zones with high forest cover and high values of connectivity between patches;

(iii) The landscape heterogeneity, measured as the size and distribution of the patches, would negatively influence the presence of cavities.

Materials and methods

Study sites and dataset

We worked on nine French forest sites where Black woodpecker cavities have been mapped by forest managers and naturalists (Figure 1).

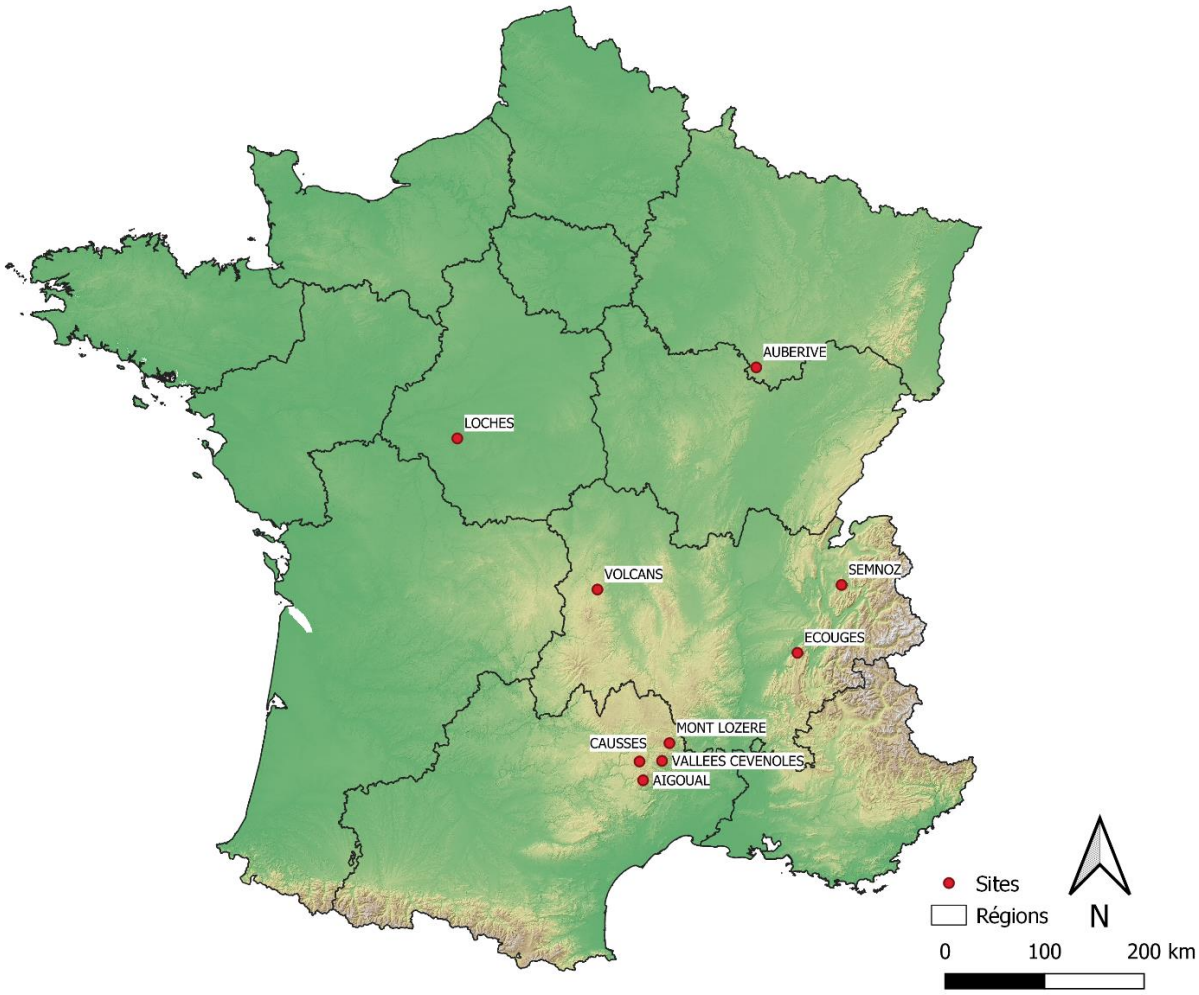

Figure 1: Map of the study sites.

The dataset has been compiled from different sources (National Forest Service, non-governmental organizations, local naturalists, National and Regional Parks) and is heterogeneous using different methods: trees identified during tree-marking operations in forest management or active prospections dedicated to these cavities. As such, we cannot assume that the maps are fully exhaustive, but we are confident that most cavities have been mapped at the site scale. Most cavities were observed from the ground, without relying on pole-cameras or other devices except binoculars (see discussion for the potential bias linked to this method of observation). We harmonized the different datasets and

selected data to control for dependence and heterogeneity. We first excluded observations made before 2010, since we considered that landscape (forest) variables could have changed significantly since then because of tree mortality and anthropogenic or natural disturbances (e.g. harvesting, tree dieback, storms). Cavities observed on dead trees and snags were also excluded since the conditions of digging may rely more on tree characteristics than landscape in this case (e.g. Puverel *et al.* 2019). Based on this first selection, we kept 2689 Black woodpecker cavities observations with spatial coordinates (Table 1). All locations were measured with commercial-grade GNSS receivers or directly plotted on maps. Precision is thus comprised between 10 m and 100 m, which is consistent with the minimum scale of analysis (10ha).

Site	Cavity number	Elevation (m)		Mean annual temperature (°C)		Mean annual precipitation (mm)		Slope (deg)	
		Min/Max	Mean	Min/Max	Mean	Min/Max	Mean	Min/Max	Mean
Aigoual	1819	796/1398	1218	5.6/10.2	7.3	774/979	900.9	1.1/51.4	16.4
Auberive	194	360/504	440	8.7/9.6	9.1	802/911	853	0/31.2	7.8
Causses	251	821/1400	1122	5.9/10.2	7.8	769/966	864.7	1.2/48.1	22.5
Ecouges	1	-	1218	5.7	5.7	1187	1187	16.4	16.4
Loches	111	91/141	124	11/11.3	11.1	690/716	703.8	0/9.7	1.9
Mont Lozère	14	941/1187	1107	6.8/8.7	7.5	787/898	857.8	10/33.3	17.2
Semnoz	37	1017/1500	1353	4.6/7.5	5.6	1154/1430	1335	4.3/28	12.2
Vallées Cévenoles	10	919/1248	1156	7.1/9.3	7.8	790/881	850.3	7.7/25.6	17.3
Volcans	252	685/1154	935	6.5/8.7	7.6	765/912	841	0.9/40.7	10.3

Table 1: Distribution and characteristics of Black woodpecker cavity locations selected for the study

The dataset is presence-only data and we chose to generate pseudo-absences to process statistical analyses. Random generated pseudo-absence is a powerful method to deal with presence-only data, notably because pseudo-absences are less time-consuming than true absence data to gather, even if they are sometimes less precise (e.g. Iturbide *et al.* 2015). We selected 5km radius areas around the presence locations and kept only forested areas around (from the satellite images derived layer OCSOL 2018, https://www.theia-land.fr/ceslist/ces-occupation-des-sols/, Inglada *et al.* 2017). Then, we excluded an area of 250m radius around each presence location to limit the spatial auto-correlation between presence and pseudo-absence locations. We then compiled 2689 presence data with 22326 pseudo-absence drawn at random in the envelopes described above, for a total of 25015 locations. To ensure spatial independence between the observations, we used spatial thinning to conserve presence data that were distant of at least 250m, and selected ten-times more pseudo-absence

locations within each of the nine sites (R package spThin, Aiello-Lammens *et al.* 2015). The training dataset finally comprises 7348 locations (668 presence and 6680 pseudo-absence). We also generated 10 datasets with different spatial thinning for model validation.

We then delineated the three buffer zones corresponding to our three study scales (radius 179m (10ha); radius 565m (100ha) and radius 879m (250ha) around each location) and extracted forest, landscape and biogeoclimatic variables (Table 2).

Group	Variable / Indices	Unit	Source
Topographic and climatic	Elevation	Meters	BD ALTI v.2.0: digital terrain model 25 m
	Slope	Percent	BD ALTI v.2.0: digital terrain model 25 m
	Cosinus(Aspect)		BD ALTI v.2.0: digital terrain model 25 m
	Sinus(Aspect)		BD ALTI v.2.0: digital terrain model 25 m
	Mean annual temperature	Celsius	Worldclim v2
	Mean annual precipitations	Millimeters	Worldclim v2
Forest composition	Proportion of broadleaves	Percent	BD Forêt v2
	Proportion of conifers	Percent	BD Forêt v2
	Proportion of mixed forests	Percent	BD Forêt v2
Forest diversity	Shannon diversity index for forest types		BD Forêt v2
	Simpson diversity index for forest types		BD Forêt v2
Forest cover	Proportion of forest cover	Percent	BD Forêt v2
Landscape connectivity (forest patches)	Contagion index	Percent	BD Forêt v2
	Cohesion index	Percent	BD Forêt v2
	Aggregation index	Percent	BD Forêt v2
Landscape heterogeneity	Landscape Shannon diversity index		Corine Land Cover
	Landscape Simpson diversity index		Corine Land Cover
Landscape fragmentation	Landscape shape index		OSO
	Edge density	Meters / hectares	OSO

Table 2: Explanatory variables and sources used to characterize the environment of Black woodpecker cavities

Forest variables

We used QGIS (version 3.16.6-Hannover) and R v 4.0.3 (R Core Team 2020) to extract forest characteristics in the different buffers around presence and pseudo-absence locations. We extracted stand composition summarized as the proportion of broadleaves, conifers and mixed forest types from the BD Forêt version 2.0 (National Forest Inventory, https://inventaire -forestier.ign.fr/IMG/pdf/dc_bdforet_2-0.pdf).

We then calculated Shannon and Simpson diversity indices based on the forest types issued from the BD Forêt v2. Both indices account for the number of types and their abundance within each buffer, they vary from 0 (only 1 type within the buffer) to plus infinite (types equitably distributed within each buffer). The Shannon index accounts more for rare elements than the Simpson does.

We finally calculated the proportion of forest within each buffer.

Landscape variables

Using the R package landscapemetrics (Hesselbarth *et al.* 2019), we calculated different landscape variables that account for the different approaches in landscape ecology: the patch characterizing a homogeneous unit, the class characterizing all patches within a given typology and the landscape characterizing all patches and classes within a given study window (Sertel *et al.* 2018). We first calculated landscape connectivity indices using the BD Forêt v2 taking into account forest cover only:

(i) the contagion index measures the probability that two patches belong to the same class. The index varies from 0 (a lot of dispersed patches) to 100 (large contiguous patches);

(ii) the patch cohesion index measures the connectivity of the patch type studied. The index also varies from 0 (when the studied class is fragmented) to 100% (when the studied class is aggregated);

(iii) the aggregation index is calculated using a contiguity matrix and measures, for each combination of patches, the frequency at which patches appear contiguous within a given window. The index varies from 0 (when the landscape is totally fragmented) to 100% (when the landscape is composed of fully contiguous patches, He *et al.* 2000).

Second, we calculated indices characterizing landscape heterogeneity: Shannon and Simpson indices measure the landscape diversity accounting for the number of patch classes and their abundance.

Both indices (H_DIV and D_DIV) were calculated from Corine Land Cover 2018 (https://land.copernicus.eu/pan-european/corine-land-cover/clc2018, Büttner *et al.* 2021).

Third, we calculated several landscape fragmentation indices based on the forest cover of BD Forêt V2:

(i) the landscape shape index measures the shape of the study class compared to a maximal level of aggregation within this class. The index varies from 1 (when the landscape is composed of only one patch) to the infinite;

(ii) the edge index measures edge length per surface unit (meters per hectare in our case). The index varies from 0 (no edge) to infinite.

<u>Biogeoclimatic variables</u>

We extracted biogeoclimatic variables to contextualize the relationships between stand and landscape variables and the occurrence of Black woodpecker cavities. For each location, we extracted the elevation, slope, aspect (cosinus and sinus transformed) based on the digital terrain model (BDAlti V2.0, resolution 25m) , mean annual temperature and precipitations issued of Worldclim 2 (Fick and Hijmans 2017, Table 2).

<u>Statistical analyses</u>

We used R v4.0.3 (R Core Team 2020) for all analyses. Following Zuur *et al.* (2010), we explored the data for variance homogeneity and unaccounted sources of variation, outliers, collinearity and interactions. We used linear mixed model to analyze the occurrence of Black woodpecker cavities as a function of the different explanatory variables listed above (Table 2). We fitted models using the function glmmTMB from the glmmTMB package (Magnusson *et al.* 2017) with binomial error distribution for occurrence data (presences and pseudo-absences), logit link and site as random effect to account for the fact that observations from the same site may be more similar than observations issued from two different sites. Before processing for model selection, we used the Variance Inflation factor (VIF, package car, Fox and Weisberg 2019) to detect multicollinearity amongst explanatory variables and excluded variables with a VIF higher than 5 points. We then processed a forward model selection based on Akaike Information Criterion (AIC, function stepAIC in the package MuMIn, Barton 2020), adding variables once at the time and limiting the interactions to first order. We standardized all

variables for the analyses to be able to compare the magnitudes of the effects. For each scale (10, 100, and 250ha), we added variables and interactions until the AIC did not changed by more than two points. We then validated the best model by fitting it on the 10 thinned datasets and comparing the estimates for each scale. The model was judged robust if the standard deviations of the mean estimates across the 10 datasets was not higher than the standard errors of the estimates of the training model.

Results

Model selection on the training dataset

At the 10ha scale, contagion index and proportion of broadleaves showed a VIF > 5 and were excluded. The best model comprised slope, mean annual precipitation, proportion of conifers, proportion of mixed forests, proportion of forest cover, landscape shape index and interactions between slope and mean annual precipitations and landscape shape index and mean annual precipitations (Table 3). All the effects were significant ($p<0.05$) or marginally significant ($p<0.1$). In terms of magnitude, the proportion of forest cover had the highest positive effect on the occurrence of Black woodpecker cavities (standardized estimate 1.56) followed by mean annual precipitation (positive effect, standardized estimate 1.49, Figure 2). Proportion of mixed forests and slope had a lesser positive effect (standardized estimates resp. 0.15 and 0.13, Figure 2). Conversely, proportion of conifers and landscape shape index had negative effects on the Black woodpecker cavities occurrence (standardized estimates resp. -018 and -0.17, Figure 2). Finally, the estimate of the interaction between slope and mean annual precipitation was negative (standardized estimate -0.12), while the estimate for the interaction between annual mean precipitation and landscape shape index was marginally positive (standardized estimate 0.08).

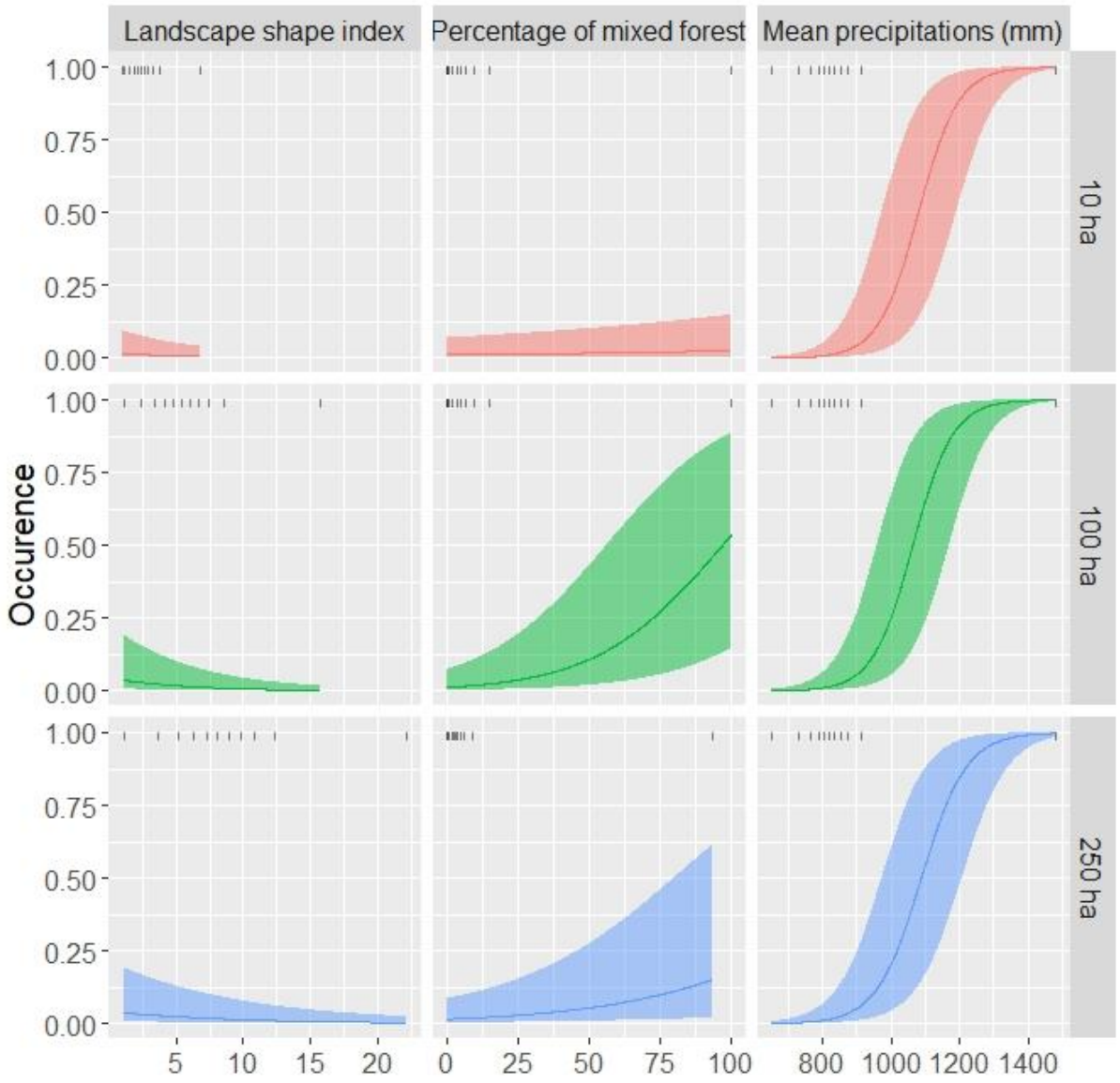

Figure 2: Effects of landscape shape index, proportion of mixed forest and mean precipitations on the occurrence of Black woodpecker cavities at three scales (n = 7348 locations). Plain line represents the mean estimation derived from a generalized linear mixed model with binomial error distribution and site as a random effect. Ribbons are 95% confidence intervals. All other variables were hold constant (mean) for the representation.

At the 100ha scale, contagion index showed a VIF > 5 and was excluded. The best model comprised slope, mean annual precipitations, proportion of broadleaves and mixed forests, edge density index, landscape shape index and Shannon landscape diversity index. In addition, it comprised the interactions between slope and mean annual precipitations, edge density index and landscape shape index, mean annual precipitations and landscape scale index, slope and proportion of broadleaves, proportion of broadleaves and mean annual precipitations, proportion of conifers and mean annual precipitations and Shannon landscape diversity index and slope (Table 3). All the effects were significant ($p<0.05$). In terms of magnitude, mean annual precipitations had the higher positive effect on Black woodpecker cavities occurrence (standardized estimate 1.49, Figure 2) followed by the edge density index (negative effect, standardized estimate -0.66). Other positive effects comprised the proportion of mixed forests (0.38, Figure 2), the slope (0.33), the Shannon landscape diversity index (0.15) and the proportion of broadleaves (0.14), as well as interactions between mean annual precipitations and landscape shape index (0.22). Landscape shape index (-0.44, Figure 2) and interactions between slope and mean annual precipitations (-0.17), edge density and landscape shape index (-0.20), proportion of broadleaves and slope (-0.21) and mean annual precipitations (-0.18), the proportion of mixed forests and mean annual precipitation (-0.11) and the Shannon index for forest types and slope (-0.12) all had negative effects.

At the 250ha scale, no variable was excluded based on VIF. The best model comprised the slope, the mean annual precipitations, the proportion of mixed forests, the edge density index, the proportions or broadleaves and mixed forests, the proportion of forest cover, the landscape shape index, the Shannon landscape diversity index, and the interactions between slope and mean annual precipitations, edge density and landscape shape index, mean annual precipitation and landscape shape index and proportion of broadleaves and slope. All the effects were significant ($p>0.05$). In terms of magnitude, mean annual temperatures had the strongest positive effect (standardized estimate 1.34, Figure 2) followed by the positive effect of the proportion of forest cover (positive effect, standardized estimate 0.94). Other positive effects comprised the Shannon landscape diversity index (0.33), the slope (0.29), the proportion of mixed forests (0.14, Figure 2) as well as the interactions between mean annual precipitation and landscape shape index (0.14). Landscape shape index (-0.39, Figure 2), the edge density (-0.36), the proportion of broadleaves (-0.11) as well as the interactions

between slope and mean annual precipitations (-0.16), the edge density index and the landscape shape index (-0.31) and the proportion of broadleaves and slope (-0.17) all had negative effects.

	10ha scale				100ha scale				250ha scale			
Variable	Estimate	SE	p		Estimate	SE	p		Estimate	SE	p	
Intercept	-4.346	0.937	<0.001	***	-4.075	0.921	<0.001	***	-4.035	0.905	<0.001	***
Slope	0.134	0.067	0.047	*	0.334	0.067	<0.001	***	0.286	0.067	<0.001	***
Mean annual precipitation	1.488	0.083	<0.001	***	1.491	0.089	<0.001	***	1.335	0.091	<0.001	***
%broadleaves					0.141	0.056	0.012	*	-0.110	0.054	0.043	*
%conifers	-0.182	0.052	0.000	***								
%mixed forests	0.152	0.038	<0.001	***	0.384	0.047	<0.001	***	0.138	0.044	0.002	**
Edge density					-0.661	0.076	<0.001	***	-0.364	0.082	<0.001	***
% forest cover	1.563	0.127	<0.001	***					0.938	0.099	<0.001	***
Landscape shape index	-0.170	0.068	0.012	*	-0.447	0.092	<0.001	***	-0.386	0.092	<0.001	***
Shannon landscape diversity					0.158	0.056	0.005	**	0.332	0.061	<0.001	***
Slope x Precipitation	-0.120	0.045	0.008	**	-0.171	0.049	<0.001	***	-0.163	0.047	<0.001	***
Edge density x Landscape shape index					-0.197	0.078	0.012	*	-0.305	0.077	<0.001	***
Landscape shape index x Precipitation	0.083	0.050	0.095	(*)	0.223	0.058	<0.001	***	0.144	0.060	0.016	*
%broadleaves x Slope					-0.207	0.050	<0.001	***	-0.166	0.049	<0.001	***
%broadleaves x Precipitation					-0.178	0.050	<0.001	***				
%mixed forests x precipitation					-0.105	0.024	<0.001	***				
Shannon landscape diversity x Slope					-0.121	0.054	0.024	*				

Table 3. Standardized estimates of the best models predicting the occurrence of Black woodpecker cavities at three study scales (10ha, 100ha and 250ha). Grey cells correspond to variables not included in the models. SE: Standard Error. *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$, (*) $p < 0.1$.

<u>Model validation</u>

We fitted the selected model for each scale on the 10 different thinned validation datasets. Globally the standardized estimates were consistent for the different datasets with standard deviations of the values below – or the same order of magnitude than – the standard errors of the best models (Table 4).

Variable	10ha scale	100ha scale	250ha scale
Intercept	0.0731	0.0776	0.0725
Slope	0.0210	0.0279	0.0272
Mean annual precipitations	0.0269	0.0348	0.0242
%broadleaves		0.0161	0.0257
%conifers	0.0217		
%mixed forests	0.0107	0.0231	0.0214
Edge density		0.0188	0.0359
% forest cover	0.0420		0.0218
Landscape shape index	0.0251	0.0193	0.0208
Shannon landscape diversity		0.0143	0.0193
Slope x Precipitation	0.0198	0.0191	0.0141
Edge density x Landscape shape index		0.0269	0.0260
Landscape shape index x Precipitation	0.0219	0.0270	0.0313
%broadleaves x Slope		0.0233	0.0207
%broadleaves x Precipitation		0.0188	
%mixed forests x precipitation		0.0136	
Shannon landscape diversity x Slope		0.0280	

Tableau 4. Mean standard errors of estimates for the ten validation datasets.

Discussion

Heterogeneous and diversified forest types favour cavity digging by the Black woodpecker

We partially validated the hypothesis that mixed and diversified forests favoured the digging of cavity by the Black woodpecker. Indeed, landscapes composed of broadleaves and conifers positively influenced the presence of cavities: the probability of cavity occurrence increased from 14 to 47% when the proportion of mixed forests in the landscape increased from 50 to 75% at the 100ha scale, and from 25 to 68% at the 250ha scale (Figure 2). Mixed broadleaf and coniferous forests favour the presence of the Black woodpecker since broadleaves are preferentially selected for cavity digging (Karimi *et al.* 2018) while conifers provide food resources, in particular wood ants and saproxylic larvae (Rolstad *et al.* 2000, Brambilla and Saporetti 2014). Indeed, in central and western Europe, the Black woodpecker seems to dig cavities preferentially in beech (Fagus sylvatica L.), while in Scandinavia, the bird digs more on conifers like Scots pine (*Pinus sylvestris* L., Pirovano and Zecca 2014). Tree species with smooth bark, like beech, would be preferred to prevent predation by the pine Marten since climbing on such trees species seems more difficult (Kosiński and Kempa 2007, Olano 2015, Puverel *et al.* 2019). In the Alps, beech stands would also be favoured because they present larger mean diameter due to a less intensive harvesting and lower densities compared to other forests (De Rosa *et al.* 2016). The Black woodpecker also avoids coniferous stands with low branches, that favour predation (Bocca *et al.* 2007). This is confirmed by our results on forest composition at different scales. At the 10ha scale, although the variable proportion of broadleaves has not been selected, the proportion of conifers had a negative effect on the presence of cavities. At the 100ha scale, that corresponds to the core zone of the home range of the species (nesting, breeding, and active defence of the territory), the effect of broadleaves proportion became positive. Conversely, at the larger 250ha scale, this effect was negative. Therefore, the Black woodpecker selects broadleaves at the local scale and in the core zone of its home range, while the presence of conifers at the larger scale may be positive as a feeding site. However, we did not observe significant effects of forest diversity indices on the cavity presence at the two larger scales, so the presence of cavities is more linked to the abundance of broadleaves.

Black woodpecker cavities occur more in unfragmented and connected forest landscapes

The quantity of edges (between forest and non-forest areas) negatively affected the presence of Black woodpecker cavities, which validated our second hypothesis. Indeed, the occurrence of cavities decreased significantly with increasing edge abundance, and was almost null when the proportion of edge reached 100m per hectare (Table 3). We observed the larger impact of edges at the 100ha scale, which shows that the Black woodpecker needs large continuous forest areas to dig cavities in its core home range. This was confirmed by the positive effect of the contagion index at the three scales: the occurrence probability doubled when the index increased from 80 to 100 (Table 3). While the Black woodpecker may cover large distances for foraging, it seems that large unfragmented forest areas are necessary for cavity digging. However, this result does not seem to be generalizable over the whole distribution of the species. Indeed, in Sweden, Tjernberg *et al.* (1993) showed that the Black woodpecker also occurs in fragmented forest landscapes, as long as it can fly from one feeding ground to another. Thus, it can live in landscapes with as little as 26% of forested areas (Dorresteijn *et al.* 2013) which confirms the contextualised response of the species to fragmentation.

We did not validate our third hypothesis on landscape heterogeneity. Indeed, we showed that increasing heterogeneity favoured the occurrence of the Black woodpecker cavities, although the magnitude of this effect was low. The positive effect of heterogeneity may be linked to the fact that the species may also need some open, non-forested habitats, eventually with patches of conifer, to feed, and that these zones may be located in the home range (translated in our study by an increasing effect at the 250ha scale).

The probability of cavity digging is context dependant

Slope and mean annual precipitation were often selected as variables characterizing the general context as well as in the interactions of the model. While occurrence of cavities generally increased with slope and precipitations across all scales, these variables also had a negative effect on the interactions with other variables, notably composition (Table 3). Although elevation was not selected in our models, it is clear that higher slopes and precipitations are characteristics of mountainous landscapes, where the effects of forest composition are less pronounced than in lowlands, but where cavities are also less abundant. These effects probably traduce other factors not included in these analyses like tree diameter, a minimum of which is necessary for the Black woodpecker to dig a suitable cavity (e.g. Basile *et al.*

2020). In addition, high precipitations increase the risk of cavity flooding (Cuisin 1967) and are therefore detrimental to the survival of the species.

Limitations and research perspectives

The dataset we analysed was, by essence, heterogeneous since it originated from management and naturalist prospections without a real systematic approach. Ideally, it would have been worth verifying at least a sample of the data in the field, for example using a pole camera since, from the ground, full cavities may be confounded with cavity initiations (Cuisin 1967). In terms of model, this generates false positives that may bias the results and that could be taken into account by adding a detection probability term (aka. N-mixture models). However, given the total number of observations, verifying all the cavities would have been impossible, and we also assume that the bias remains marginal and not systematic, since the birds very probably initiate cavities in conditions similar as for full cavities digging. Some observers may have also indirectly controlled the effective presence of cavities by observations of nesting animals or insects, but such validation was not systematically reported. In addition, model validation did not show strong variations when changing the dataset, we are thus confident that our results are robust, but would be more precise with full cavities. Such modelling approach would also be more informative with nesting cavities only, but at such a scale, would require huge fieldwork to have a dataset allowing the analysis. We think our approach is a good compromise regarding the value of the compiled dataset.

We could not analyse the effects of forest structure and precise composition at different scales around cavities observations, notably the degree of stand maturity and the quantity of deadwood at the large scale. Such data would have been interesting to specify the needs of the species, notably in terms of food resources linked to deadwood. These variables could be derived from airborne LIDAR interpretation (e.g. Zellweger *et al.* 2013), but such data was not available across all the sites we studied, and would have required additional field data to calibrate LIDAR models. In a near future, the ongoing French nation-wide LIDAR acquisition program could help completing the present study, using the same processes of data selection, as well as specifying the requirements of the Black Woodpecker in terms of forest structure. Also, composition could be assessed using multispectral data such as Sentinel 2 (see https://sentinel.esa.int/web/sentinel/missions/sentinel-2). More precise mapping of forest and

landscape attributes could also be of use in the study of cavity digging by the Black Woodpecker. For example, mapping issued of the BD Forêts v2 has a resolution of 0.5ha, which may cause noise for the results at the 10ha scale. However, it was the most precise data systematically available for the whole dataset, and our results are reproducible since they gather field data and public data sources.

Finally, generalisation of our approach in other locations of the distribution range of the species would be interesting, since it seems that its ecological preferences may vary with the biogeographical context. In turn, all this would help the preservation of this keystone species for the forest ecosystem, and the cavities it digs that support numerous secondary species from other taxa.

Conclusions and implications for forest management.

We studied the forest and non-forest landscapes variables that influenced cavity digging by the Black Woodpecker. From a strict forest management point of view, landscape variables are rarely under the control of forest management. However, some results may be transferred to management planning at the forest or a larger scale. At the 10ha (management unit) scale, we showed that forest composition (mixed forests) was the most influential variable, while at larger 100ha (core vital range) and 250ha (vital range) scales, fragmentation and connectivity had stronger effects. Therefore, maintaining and favouring mixed stands locally would be beneficial to the Black Woodpecker and all the species that depend on its cavities for living. Mixed forests have proved to be beneficial both for biodiversity conservation and a large panel of other services (e.g. Liang *et al.* 2016). Black Woodpecker cavities seem to benefit from either a mix at the stand scale or the juxtaposition of broadleaved and coniferous stands, providing that broadleaved stands are large enough. Such action should then be integrated at the management planning level. At a larger scale, large continuous forested areas reveal the forest character of the Black Woodpecker, but also the need to maintain connectivity at the landscape scale to favour forest species. Cavity digging by the Black Woodpecker is also sensitive to edges, as are many other forest bird species, the conservation of which is then conditioned by the conservation of large unfragmented areas (Robinson *et al.* 1995, Villard *et al.* 1999). These recommendation may ultimately be applied at the larger scale, e.g. for a regional or national parks, that have an objective of biodiversity conservation.

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