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What kind of tree should be preserved from logging for biodiversity conservation is a matter of debate. Large and old trees are potential candidates due to the structures they can bear, like cavities and other tree-related microhabitats (TreMs). One of the most studied TreM is woodpecker-made cavities, which, in addition to be breeding sites for primary cavity-nesters, are often the main breeding sites for secondary cavity-nesters, especially in managed forests. Therefore, understanding which trees woodpeckers select for cavities is relevant to forest management, especially in management regimes where individual trees are logged or spared, as in retention forestry. We used data from a forest inventory, TreM inventory and woodpecker counts in one-hectare plots in the Black Forest (southwest Germany) to investigate which features make a retention tree suitable for woodpeckers. By employing a resource selection probability function, we tested several variables for their influence on the probability of tree choice by woodpeckers including altitude, tree species, TreM richness and abundance, diameter at breast height (DBH) and deviation from the mean DBH per plot. The results show that the probability of selection by woodpeckers does not correlate with individual tree diameter. Instead, the probability is driven mainly by the deviation from the mean DBH per plot. We were able to identify a relative size for the selection of trees indicating that woodpeckers prefer trees that are about 15–20 cm larger than the mean DBH per plot. Thereby, we argue, that using absolute diameter thresholds to select retention might not be the best management solution in the short-term, as in managed forests woodpeckers might select sub-optimal trees. Apparently, more knowledge concerning relative thresholds, as detected in our study, is required to improve our understanding of the potential ecological value of retention trees.

Keywords: hole nesters, large trees, nest site selection, retention forestry, tree-related microhabitats

Large trees are natural features potentially acting as keystone structures in many terrestrial ecosystems (Lindenmayer 2017). In late successional stages of forest ecosystems, large and old trees may play key functions, due to the diverse structures they can bear, like cavities and other tree-related microhabitats (TreMs) (Winter and Möller 2008, Bauhus et al. 2009). The resources provided by large trees to forest-dwelling species have been recognised by forestry practices, such as retention forestry (Gustafsson et al. 2012), which benefits for the conservation of biodiversity are well documented (Lindenmayer et al. 2012, Fedrowitz et al. 2014). The practice of setting aside these trees addresses the still open question of how to select retention trees. This mostly depends on the conservation targets set by practitioners (Bauhus et al. 2013). One possible way to select trees is to look at features bear by trees like TreMs, important for forest-dwelling organisms. TreMs are distinct, well delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or communities during at least a part of their life cycle to develop, feed, shelter or breed' (Larrieu et al. 2018). For this reason, TreMs have been incorporated in European management schemes as a tool to select trees in harvest operations, due to their link with biodiversity (Larrieu et al. 2018, Paillet et al. 2018).

In commercially-managed forests, the formation of TreMs can be precluded due to early harvests or by the suppression of commercially-worthless trees (Newton 1994, Samuelsson et al. 1994, De Zan et al. 2014). Several studies have shown that larger trees have a higher abundance of TreMs compared with smaller ones, suggesting that size can guide the selection of retention trees (Paillet et al. 2017, 2018, Asbeck et al. 2019). Nonetheless, this system may not work in commercial forests, where the variability in size is reduced

by thinning operations retaining the healthiest trees, which bear less TreMs, as those features are often viewed as defects by foresters (Niedermann-Meier et al. 2010).

One of the TreMs most commonly considered in inventory schemes is the group of woodpecker cavities (Bütler et al. 2013). Woodpeckers are considered environmental architects, being able to excavate their own cavities, often located in old, large trees and snags (Angelstam 1990, Bütler et al. 2004, Wesołowski 2011, Kajtoch et al. 2012, Walczak et al. 2013). Due to these characteristics, their abundance and diversity is considered as a potential indicator of forest naturalness (Mikusiński et al. 2001, Roberge et al. 2008). They also provide cavities to secondary cavity-nesters, i.e. species that cannot excavate their own cavities (Newton 1994). Secondary cavity-nesting birds compete for cavities as nesting and roosting sites, and in several forest ecosystems woodpeckers drive these interactions, influencing forest bird assemblage composition (Martin and Eadie 1999, Cockle et al. 2011). Evidences show that forestry often leads to the decrease of potential excavation substrates such as snags and large living trees (Rietbergen 2001, Larsson et al. 2001, Franklin et al. 2002) and that, as a consequence, cavities are rare in managed forests (Conner et al. 1975, Scott 1979). In contrast, in protected forests the importance of woodpecker-made cavities for secondary cavity-nesters may be quite low, due to the abundance of natural cavities from different origins as demonstrated in Białowieża Forest in Poland (Wesołowski and Martin 2018). Therefore, in managed forests, where natural cavities are rare, woodpecker-made cavities are of major importance for birds (Remm and Lõhmus 2011, Andersson et al. 2018).

The suitability of a tree as a substrate for excavating cavities by woodpeckers depends on several factors, but tree species, tree age (health), tree dimensions as well as the presence of chemical agents produced by e.g. fungi that can soften the wood, are apparently of key significance (Newton 1994, Wesołowski 2011, Wesołowski and Martin 2018). Nest-tree selection is then fundamental for reproductive success. The selected tree should give the opportunity to excavate the cavity that provides enough security from predators and thermal comfort. However, in managed forests, woodpeckers may be 'forced' to adjust their selection of cavity trees to their relative availability and quality i.e. selecting for best available trees (Rudolph and Conner 1991, Zwicker and Walters 1999). The outcome of such selection process affects the quality of the cavities for nesting of both woodpeckers and secondary cavity users in terms of e.g. predation risk but also the future 'life-span' of this important microhabitat (Wesołowski 2011). Therefore, information on the features a potential cavity-tree might display can be relevant to forest management, especially in management regimes where single trees are selected, as in retention forestry. Hence, we investigated cavity tree selection by woodpeckers in a managed forest system. Given that management can decrease the variability in tree size, we tested whether tree size can explain woodpecker cavity tree selection in managed forests, or relatively small trees are equally selected compared to larger ones, due to the other characteristics, proxied by TreMs. Such information can potentially increase the efficiency of the tree selection process in retention forestry for preserving cavity-dependent communities. In our study, we adopted the 'forester's approach' to investigate single trees. We considered two groups of trees, defined by the current forest management criteria of our study area: the first group includes the largest trees in the study plots; the second group includes trees selected for the TreMs they bear. We hypothesised that woodpeckers would select randomly cavity trees within the group of large ones, as we do not expect significant differences among these trees that could lead to a non-random selection. Conversely, we hypothesised a selection driven by tree features in the second group of trees, as those trees were selected by the presence of TreMs, which may indicate a particular health status, such as occurrence of fungi, which favours cavity establishment by woodpeckers. Our aim here is to understand what would make a large tree or a tree characterised by the presence of TreMs special for woodpeckers, given that forest managers can potentially focus on these two aspects (size and/or microhabitats) for selecting retention trees. Finally, by extending our results to the entire forest system studied, we hypothesized that more woodpeckers are found in forests with higher occurrence of potential cavity trees. We therefore investigated the occurrence of woodpeckers, woodpecker cavities, and their relationships with trees. Since living trees are the primary target of management (i.e. green tree retention), we focused on living trees only.

Methods

Study area

The study area is located in the southern part of the Black Forest (south-western Germany), in which 135 1-ha plots were established within the framework of the ConFoBi project (Storch et al. 2020), at a minimum distance of 1 km from each other (Fig. 1). ConFoBi plots are distributed across two environmental gradients that follow an increase in forest cover in 25 km² surrounding the plots and an increase in the number of snags identified by aerial photo stereo viewer technique. The forest predominantly consists of Norway spruce *Picea abies*, European silver fir *Abies alba* and European beech *Fagus sylvatica* (Ludemann 2010). The plots were all placed on publicly owned forest land, at an altitude ranging from 500 to 1400 m a.s.l. A full inventory of trees and snags with diameter at breast height (DBH) at least 7 cm was performed in each plot, and tree species was determined whenever possible. The inventory also comprised lying deadwood, collected with the line intersect method (Van Wagner 1982), by walking a V shaped transect touching the north-western, southern and north-eastern corners of the plot, totalling ~ 224 m per plot. Additional variables were derived from a digital terrain model (Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, LGL. Digitale Geländemodelle (DGM)), and included the terrain ruggedness index, computed using GDALDEM 2015, in addition to the altitude and the slope.

Sampling methods

Woodpecker-made tree cavities were identified during the inventory of TreMs in two groups of living trees. The tree groups were defined by current forest management schemes employed by forest managers in the study area to set aside
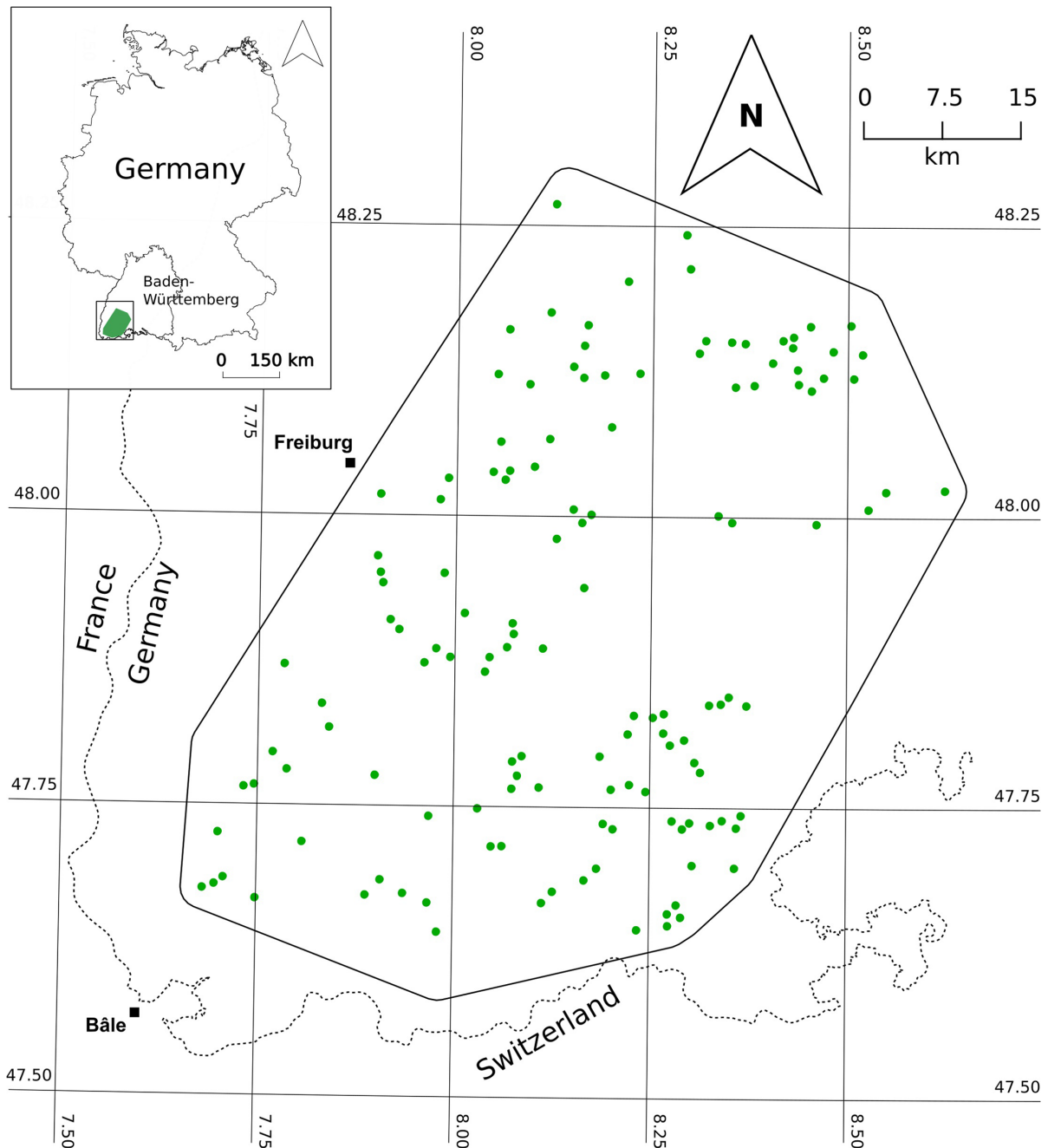
Figure 1. Study area with 1-ha study plots.

trees from harvesting: 1) selection of up to 15 living large trees ha^{-1} meant to serve, at present or in the future, as habitat trees (sensu Whitford and Williams 2001); 2) selection of living trees that bear relevant structure for biodiversity (e.g. TreMs). Hence, we selected the 15 living trees with the largest crown radius in each study plot, for a total of 1770 so called 'standard' trees. The selection was based on the canopy size using aerial images (Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, LGL, Geobasisdaten <www.lgl-bw.de> Az.: 2851.9–1/19. 2015.) and by employing the TreeVis software (Weinacker et al. 2004). An ancillary set of living trees (referred to as 'ancillary' trees) was, instead, identified in the field based on the rarest TreMs found in the study area, without

any constraints on diameter and mostly driven by expertise, number of plots, trees or structures, and consisted in the end of 118 TreM-bearing trees across 70 plots. TreMs are 'distinct, well delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or communities during at least a part of their life cycle to develop, feed, shelter or breed' (Larrieu et al. 2018). For the inventory of TreMs (including tree cavities), we employed the Integrate+ Catalogue of microhabitats and a recent classification as reference (Kraus et al. 2016, Larrieu et al. 2018). An overview of the TreMs found on the trees included in the two datasets is available in the Supplementary material Appendix 1 Table A1.

Woodpecker data was collected on 49 plots during spring 2017, with playback-assisted point counts (Blondel et al. 1970). The point counts consisted of a 5-min settle down period, 1 min of playback and 3 min of listening for each species. The playback was set to be not audible for human ears at more than 500 m. The sampling design targeted all woodpecker species recorded in the area, though the vast majority of records included only the two most common species: the great spotted woodpecker *Dendrocopos major* and the black woodpecker *Dryocopus martius*, considered as forest generalist and forest specialist, respectively (Mikusiński et al. 2018). These two species, being strong excavators, were assumed to produce the majority of woodpecker cavities.

Statistical analyses

Prior to analysing cavity tree selection by woodpecker, we aimed to verify the assumption that our two groups of trees, standard and ancillary, are statistically different. Therefore, we assessed whether the tree diameters differ significantly between the two groups by employing a one-tail Mann–Whitney test with continuity correction. We carried the test out only for the cavity trees included in each group since the remaining standard trees were already selected for their larger size and we only needed to confirm our assumption for the cavity trees. In addition, we tested for DBH differences of cavity and non-cavity trees independently for the two groups of trees, as a preliminary assessment of the characteristics of the tree selected by woodpeckers. However, we restricted the test for the standard trees to plots in which at least one cavity was found.

A resource selection analysis estimated the probability of choice by woodpeckers (Lele et al. 2013) by applying a weighted logistic regression to the inventoried trees (1 = with cavity/selected; 0 = without cavity/not selected). We assessed which of the following predictors best explained woodpecker choice: altitude, TreM richness, TreM abundance, DBH and diameter deviation (Table 1). The latter predictor is the deviation (cm) of a tree diameter from the plot mean diameter, i.e. the mean of all trees (DBH > 7 cm) present in the plot. Moreover, tree species was tested by employing a standard logistic regression only for the four main species of the dataset, Norway spruce, silver fir, European beech and Scots pine *Pinus sylvestris*, to avoid overparameterization in the model estimates. In addition, we did not consider woodpecker cavities in the variables TreM richness and TreM abundance. Thereafter, we built resource selection probability functions with logit-link function (Lele 2009) and selected

the best model as the model with significant predictors only. If more than one model resulted significant, we used the BIC (Schwarz 1978) to select the best one. Since in the model that includes tree species, the number of tree species was reduced to only the four main ones, we did not compared it with other models. We performed this analysis separately for each of the two datasets, including the standard and the ancillary trees. In addition, since we did not find cavity trees in every plot and in order to avoid overestimating the resource selection probability by including non-selected trees from plots where any cavity tree was found, we repeated the analysis by including only the standard trees from plots where at least one cavity tree was found, using plot as grouping factor. We used the best model to predict the probability of choice for every tree in the plots and estimated the mean probability of choice at plot level. Models and tests were computed using the R package 'ResourceSelection' (Lele et al. 2017).

Woodpecker abundance was modelled by employing single-visit N-mixture models, assuming a negative-binomial error distribution (Sólymos et al. 2012). These models are built hierarchically and allow to model the detectability as a function of the abundance. Both abundance and detectability can be modelled in response to environmental and detection predictors. We built three global models, i.e. models including all the environmental and detection predictors, to estimate the abundance of the woodpecker assemblage and the abundance of both great spotted and black woodpeckers. To avoid multi-collinearity in the environmental predictors, we excluded the predictors that scored a variance inflation factor > 2 from the analysis. The detectability in the global model was considered as a function of the altitude, the slope and the time of the day, assuming 1 = sunrise. The models and analysis were computed using the R package 'detect' (Sólymos et al. 2016). Finally, we assessed the relationship between woodpecker abundance and the occurrence of potential cavity trees, by employing a linear regression between the fitted woodpecker abundance per plot and the plot mean probability of choice. A summary of the analysis performed is available in the Supplementary material Appendix 1 Table A2.

Results

The TreM inventory returned 16 cavity trees among the standard trees and 12 cavity trees among the ancillary trees. The respective woodpecker selection ratio in the two tree groups was 0.009 and 0.102, showing a ratio one order of

Table 1. Tree variables included in the model for woodpecker tree selection with mean values (SD). 'Used plots' refers to plots where at least one woodpecker cavity was found. The models with the variable 'tree species' included only the four most common tree species: Norway spruce, European silver fir, Scots pine and European beech. DBH = diameter at breast height; TreMs = tree-related microhabitats (see Supplementary material Appendix 1 Table A1 for further details).

| | | Dataset | | |
		Standard trees (n = 1770)	Standard trees in used plots (n = 165)	Ancillary trees (n = 118)
Variable	Description			
Altitude	meters	867.2 (185.9)	739 (148.7)	899.0 (199.5)
DBH	cm	55.16 (15.92)	60.07 (14.13)	49.84 (17.17)
Diameter deviation	cm difference from plot mean DBH	25.32 (16.39)	28.02 (13.78)	17.30 (19.72)
TreMs	number of TreMs/tree	2.74 (2.76)	3.75 (3.32)	5.93 (5.44)
TreM richness	types of TreMs/tree	1.85 (1.52)	2.57 (2.06)	3.85 (1.92)
Tree species	categorical variable	4 species	4 species	4 species

magnitude greater for the ancillary trees. The mean number of TreMs found among the standard trees was 2.74 (±2.77 SD) and the mean TreM type richness was 1.85 (±1.52 SD). The ancillary trees, instead, showed a mean number of TreMs of 5.93 (±5.244 SD) and a mean TreM type richness of 3.85 (±1.92 SD). Woodpeckers were found in 26 plots, in which we recorded 31 great spotted woodpeckers and 13 black woodpeckers.

The DBH for cavity trees in the standard and ancillary tree groups was significantly different (Fig. 2), with the standard cavity trees having a mean DBH of 63.13 cm (±8.83 cm SD) and thereby being significantly larger ($W = 143.5$, $p = 0.015$) than the ancillary cavity trees with a mean DBH of 53.38 cm (±11.56 cm SD). The difference in DBH between cavity and non-cavity trees for standard and ancillary trees, instead, was not significant ($W = 1428$, $p = 0.1$ and $W = 780$, $p = 0.1$, respectively).

According to the resource selection model, the DBH was not a significant predictor of tree choice by woodpeckers (Table 2). Neither number nor richness of TreMs (Table 2) affected their selection. This lack of relationships also holds true if considering only the trees in plots with cavities or the ancillary trees. Conversely, the diameter deviation was significant for the standard tree groups. In particular, we found that for diameter deviation > 16.43 cm probability of choice by woodpeckers is > 0.95 (Fig. 3). The group of ancillary trees did not show significant results (Fig. 3). In addition, the model including tree species provided indication that woodpeckers negatively select for Norway spruce and positively select for Scots pine and European beech (Table 2).

The abundance models for all woodpeckers showed that the best predictor, albeit not significant, is the share of conifer in the plot ($\beta = 1.11$, $p = 0.08$). The same predictor was positively and significantly correlated with the abundance of the great spotted woodpecker ($\beta = 1.86$, $p = 0.02$) as well. For the black woodpecker, instead, the best model included only the number of snags but it was not significant ($\beta = -0.47$, $p = 0.64$). The expected abundance of woodpeckers (Fig. 4) was negatively and weakly correlated with the mean plot probability of tree choice ($R^2 = 0.09$, $p = 0.03$). Yet, analyzing the woodpecker species separately revealed that such negative correlation holds true solely for the forest generalist great spotted woodpecker ($R^2 = 0.15$, $p = 0.006$), while for the forest specialist black woodpecker this correlation was positive, though R^2 was still very low and not significant ($R^2 = 0.0$, $p = 0.92$).

Discussion

Not all trees are equally suitable for the excavation of cavities by woodpeckers (Angelstam and Mikusiński 1994, Stenberg 1996, Martin et al. 2004). While they often select large trees, the absolute size might not be an unequivocal criterion for assessing the suitability of a tree for woodpeckers. The required minimum tree size depends on the body size of the woodpecker (Conner et al. 1975), and larger trees are used more often than smaller ones (Kosiński 2006). Larger trees are likely to be older and therefore potentially more decayed and softer for excavation (Newton 1994). The presence of fungal heart rot disease or other TreMs were found to be decisive in selection of trees for excavation in many woodpecker species (Hooper et al. 1991, Ojeda et al. 2007, Pasinelli 2007, Cockle et al. 2012, Zahner et al. 2012). Furthermore, large trees provide thicker walls, which are useful for thermal insulation around the nest cavity (Vierling et al. 2018) and deliver better protection from predators (Deeming and Mainwaring 2015). In several studies, woodpecker abundance was associated with the presence of old and large trees (Fernández and Azkona 1996, Hartwig et al. 2004, Pasinelli 2007). A recent meta-analysis showed that trees 13.3 cm larger than the available trees were selected as nesting trees by cavity nesters (both woodpecker-made and natural cavities considered) and on average, authors suggest trees with DBH > 20 cm as suitable cavity trees (Gutzat and Dormann 2018). However, in commercial forests, TreMs and other important structures for woodpecker and biodiversity in general tend to be eliminated and the tree size homogenised within each stand (Larrieu et al. 2012). In such forests, cavity substrate availability is different than in old-growth forests or forests where management is close-to-nature (Cockle et al. 2011). Woodpeckers, for instance, are the main source of cavities for secondary cavity-nesters (sensu Newton 1994) in intensively managed boreal and temperate forests (Pakkala et al. 2018), while in primeval temperate forests secondary cavity nesters rely mostly on natural cavities created by decay processes (Wesołowski 2007). In primeval forests, natural disturbance leads the forest succession and unhampered tree

Figure 2. Diameter differences between cavity and non-cavity trees in the two datasets (standard and ancillary trees) and between cavity trees of the two datasets. Bars indicate standard deviations. Letters indicate significant differences based on the results of the Mann–Whitney test.

Table 2. Model estimates of the cavity tree selection probability function for woodpeckers. Unstandardized estimates are returned from a (weighted) logistic regression and are on logit scale. 'Used plots' refers to plots where at least one woodpecker cavity was found. S = Norway spruce; F = European silver fir; P = Scots pine; B = European beech; DBH = diameter at breast height; TreMs = tree-related microhabitats; SE = standard error.

	Dataset								
	Standard trees (n = 1770)			Standard trees in used plots (n = 165)			Ancillary trees (n = 118)		
Variable	β	SE	p	β	SE	p	β	SE	p
Altitude	−0.004	2.68	0.99	0.005	5.60	0.99	−0.0003	5.76	1
DBH	0.03	0.15	0.85	0.09	0.94	0.92	0.01	2.32	0.99
Diameter deviation	2.25	0.71	**< 0.01**	1.54	0.70	**0.03**	6.74	10.69	0.53
TreMs	2.23	3.27	0.50	1.33	4.48	0.77	0.37	5.73	0.95
TreM richness	1.03	2.15	0.63	1.45	3.28	0.66	0.07	7.001	0.99
Tree species[1]									
S	−6.60	1.001	**< 0.01**	−3.14	1.02	**< 0.01**	−2.12	0.61	**< 0.01**
F	−13.96	980.5	0.99	−16.43	1744	0.99	−16.45	1882.9	0.99
P	3.10	1.16	**< 0.01**	1.67	1.20	0.17	−16.45	6522.6	1
B	2.96	1.05	**< 0.01**	1.43	1.08	0.18	0.49	0.72	0.50

[1] Datasets restricted as follows: standard trees = 1559; standard trees in used plots = 143; ancillary trees = 90.

ageing processes and TreM development is not suppressed by management (Kozák et al. 2018). Therefore, sustainable and multi-purpose forest management can learn from primeval forest dynamics that tree size does not need to be the ultimate feature for tree selection, as it is not the ultimate tree feature involved in woodpecker tree selection. In our study, woodpeckers seem to choose trees among the largest in the plots (DBH_{max} = 81 cm) but not necessarily the overall largest tree (DBH_{max} = 137 cm; 0.9 quantile = 76 cm). The difference between size in the standard and the ancillary trees suggests that smaller trees are chosen as well, and, considering that they bear on average more TreMs, we can hypothesise that other features play important role for woodpecker tree selection.

If we consider the largest trees in our study area, woodpeckers prefer trees ~ 15–20 cm bigger than the average available trees. Given this evidence, we would expect that in plots where there is high variability in tree size, we would expect more woodpeckers, as the key resource for nesting is not limiting. At the same time, in plots with very low variability in tree size (e.g. mature even-aged stands) we would expect higher randomness in selection of cavity trees by woodpeckers. The two main excavators of cavities in this study,

in addition to having different levels of specialisation in foraging (insectivorous versus omnivorous species), differ greatly in terms of home range, with great spotted woodpeckers occupying only a few hectares of forest (Bachmann and Pasinelli 2002), whereas black woodpeckers using hundreds of hectares (Bocca et al. 2007). That is possibly the reason why for the former species, some abundance predictors were significant at the plot level but were not for the latter.

Management implications

This study confirms the importance of large trees for the conservation of woodpeckers and thereby for the whole array of secondary users of these structures including birds, mammals and invertebrates (Johnsson 1995, Kotaka and Matsuoka 2002). In particular, we were able to identify a relative threshold for the selection of trees indicating that woodpeckers significantly prefer trees that are ~ 15–20 cm larger than the mean diameter measured in the target forest stands. We can thus hypothesise that in managed forest, woodpecker tree selection may switch to sub-optimal trees. Retaining trees with an absolute diameter threshold, for this reason, might not be the best solution on the short-term. This is a
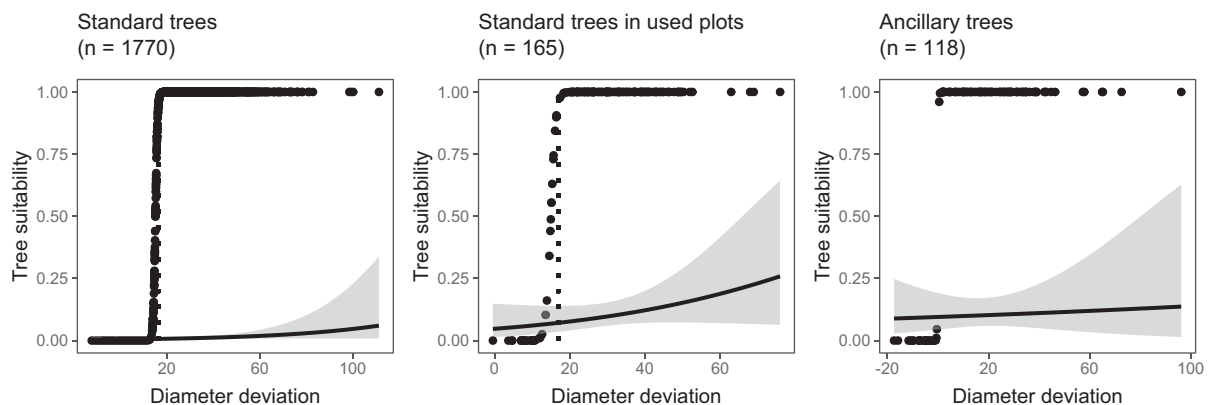

Figure 3. Estimated probability of choice for cavity trees (black dots) with increasing value of diameter deviation. Diameter deviation is measured as the diameter difference between a cavity tree and the mean plot diameter. Tree suitability equals the selection probability, according to a weighted logistic regression. The black line shows the probability of finding a cavity tree (estimated by standard logistic regression) for increasing diameter deviation (the shaded area is the 95% confidence interval). The dotted line indicates the diameter deviation when probability of choice > 0.95.
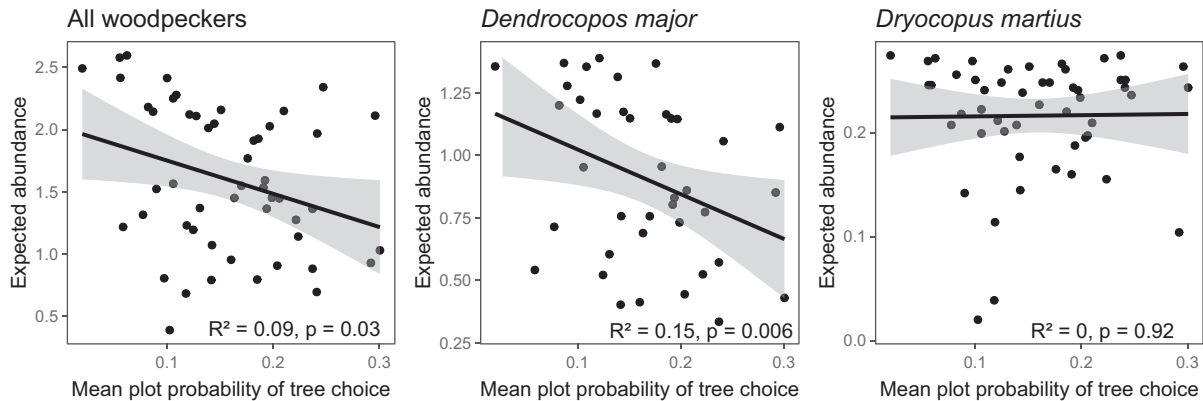
Figure 4. Relationship between woodpecker abundance and mean plot probability of tree choice. Mean probability of tree choice is estimated by predicting the probability of tree choice for each tree in the plot (based on the best resource selection model) and averaging it over the plot.

relevant finding especially for retention recommendations, as frequently absolute diameter thresholds for habitat trees are sought. This is reflected in existing forest management recommendations with retention elements, as large standing dead trees with a DBH above 40 cm have to be retained in our research area (ForstBW 2015). Moreover it has been suggested that all living trees above 100 cm DBH should be retained as legacies (Larrieu et al. 2014a, b), but in managed forests these large individuals are frequently absent. Other studies have already stressed that size alone cannot be the only criterion for setting trees aside (Cooke and Hannon 2012). We were not able to identify other drivers of tree choice by woodpeckers, beside tree species. TreMs did not prove significant, although many studies emphasised the importance of particular structures in favouring cavity excavation, such as fungi (Cockle et al. 2011). Thus, we stress that, if TreMs are adopted as selection criterion for retention trees, woodpecker-made cavities should bear particular relevance among the other TreMs. We emphasize that it is essential that individuals significantly larger than the average remain in the managed forest areas, even if those are not particularly large. However, given that absolute diameter thresholds are easier for managers to apply, an alternative might be to select trees with absolute larger diameter and allow them to grow until they reach a diameter greater than the surrounding trees. This might be particularly relevant in case of Scots pine and European beech, as these species are preferred by woodpeckers and beech, in particular, is also more prone to develop decay-formed cavities. Therefore, these two species should have priority in the process of retention tree selection. In temperate forests, this can be potentially achieved by retention forestry in continuous-cover forests (Gustafsson et al. 2019). Moreover, since the number of trees with cavities in the studied forests as well as in other managed forests has been proven very low in comparison to primeval conditions (e.g. in Białowieża Forest mentioned above), retention levels of such trees should be generous. Especially that black and great spotted woodpeckers, being the main producers of tree cavities in European managed and boreal forests, needs both nesting cavities (usually newly excavated every year) and also roosting cavities. For the black woodpecker, so called 'hole-centres' have been described as places where a necessary

minimum density of cavities was found (Lang and Rost 1990) indicating need of high densities of potential cavity-trees for this key-stone species as prerequisite for its favourable habitat quality. Our study did not address the quantity of those habitat trees or their spatial distribution, but it offers insight into the characteristics of trees used by woodpeckers producing nesting sites for secondary users. This kind of knowledge broadened by spatial patterning and life-span of cavities is required to improve our understanding of the potential ecological value of retention trees.

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Supplementary material (available online as Appendix wlb-00564 at <www.wildlifebiology.org/appendix/wlb-00564>). Appendix 1.