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Short Communication

Lying deadwood retention affects microhabitat use of martens (*Martes* spp.) in European mountain forests

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Biodiversity loss due to intensive timber production is a ubiquitous conservation issue across temperate and boreal forest ecosystems. Retention forestry, the retention of deadwood and old-growth features within production forest, is one management strategy that has been implemented in various countries around the world to conserve a wide range of taxa within managed forests. The success and ecological implications of retention forestry are currently subject to intensive investigation and while some taxa like birds and insects have already been studied frequently, larger mammals have received less attention. Pine martens are one of the few larger mammals in central Europe preferring older forest and potentially profiting directly from deadwood retention as a consequence of implemented retention forestry. The goal of our study was to assess the response of European marten species to deadwood retention in montane mixed forests. Using marten detection rates from camera traps on 135 research plots we assessed the response of martens to deadwood at three different spatial scales using generalized linear mixed models. We found no effect of lying deadwood on marten detections at the plot scale (1 ha) or in a 10 m radius around the camera traps. However, we found a significant increase of marten detections if logs (> 10 cm in diameter) were directly in front and in view of the camera trap. Our results show that deadwood retention as a measure of retention forestry does affect microhabitat use of martens, but not stand selection during the growing season. Logs directly in view of the camera trap increase marten detection rates as martens choose to move and forage along fallen trees when they are available. When using camera trapping to collect data on martens, trap positioning in front of logs can heavily bias trapping results when unaccounted for.

Keywords: beech marten, camera trapping, deadwood, logs, pine marten, retention forestry

Introduction

Intensive economic use of forests in central Europe is threatening its faunistic biodiversity (Bengtsson et al. 2000). The lack of old-growth features in timber production forests such as microhabitats or deadwood deprives a wide range of taxa (e.g.

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saproxylic insects) of suitable habitat (Lindenmayer 2002, Bauhus et al. 2009, Stokland et al. 2012, Basile et al. 2020). Recent approaches such as retention forestry aim to integrate timber production and conservation of biodiversity through retaining valuable old growth features like habitat trees and deadwood (Lindenmayer et al. 2012, Gustafsson et al. 2020). Evaluating the response of different faunistic groups to retention practices is a current topic in forest ecological research (Basile et al. 2019, Franklin et al. 2019, Storch et al. 2020, Hendel et al. 2023, Rappa et al. 2023).

The communities of large and medium-sized terrestrial mammals in central Europe consist largely of generalists, that are not critically dependent on specific forest features (e.g. roe deer *Capreolus capreolus* or red fox *Vulpes vulpes*) (Abbas et al. 2011, Lovari et al. 2016, Kämmerle et al. 2020, Hoffmann and Sillero-Zubiri 2021). Pine martens (*Martes martes*) are one of the few exceptions, as they are generally considered to prefer old and well-connected forests (Storch et al. 1990, Brainerd and Rolstad 2002, Vergara et al. 2016, Twining et al. 2020, Angoh et al. 2023). There is, however, ample evidence that pine martens also inhabit landscapes where forests are highly fragmented and subject to intensive human use (Pereboom et al. 2008, Balestrieri et al. 2011, Balestrieri et al. 2015, Weber et al. 2018). In much of Europe pine martens co-occur with beech martens (*Martes foina*, synonym stone marten), and both species overlap widely in their habitat use (Vergara et al. 2016). However, compared to pine martens, beech martens cope better with human proximity and are frequently found in residential areas (Sacchi and Meriggi 1995, Wereszczuk and Zalewski 2015, Fonda et al. 2021). Also, the food niches of both marten species overlap greatly (Petrov et al. 2016, Fonda et al. 2021). While both species are generalist feeders that consume insects, fungi, plants, as well as carrion (Jędrzejewski et al. 1993, Petrov et al. 2016), small mammals, especially rodents are the staple food (Storch et al. 1990, Russell and Storch 2004, Baltrūnaitė 2006). Forest habitat quality for small mammals is improved by deadwood (Suter and Schielly 1998, Hagge et al. 2019), and martens have been observed to frequently forage around logs (Jędrzejewski et al. 1993). Thus, it is possible that martens profit from higher volumes of lying deadwood in forests.

The relation of European marten species with deadwood has rarely been investigated (but see Twining et al. 2020), however, for closely related American marten (*Martes americana*) the dependency on deadwood (in the American literature often referred to as coarse woody debris) as a key habitat feature is well documented (Farnell et al. 2020). Especially in winter American martens depend on lying deadwood (logs) as they facilitate subnivean access to prey (Hargis and McCullough 1984). Additionally, dens of American marten are frequently found to be related to deadwood (Martin and Barrett 1983). Also, outside winter, hunting success of American martens has been found to be higher in forest sites with high amounts of deadwood, although prey availability did not differ significantly between sites (Andruskiw et al. 2008).

The goal of this study was to investigate the relation of two co-occurring marten species with lying deadwood in the context of retention forestry in central European montane mixed forest. We predicted that higher amounts of lying deadwood increase habitat use of martens as denning and foraging opportunities are increased. We tested this relationship with camera traps. To better understand the potential relationship of martens and deadwood we used deadwood variables at three spatial scales (one-hectare plot, 10 m radius around camera trap, view of the camera trap).

Material and methods

We conducted our study in the southern Black Forest, Germany (Latitude: 47.6–48.3°N, Longitude: 7.7–8.6°E, WGS 84), a temperate low mountain range reaching 1494 m a.s.l. The annual average precipitation was 1484 mm, and the average yearly temperature is 7.1°C (AM Online Projects, 2018). The montane-mixed forest stands were dominated by Norway spruce (*Picea abies*), followed by European beech (*Fagus sylvatica*) and silver fir (*Abies alba*), and frequently intersected by small villages and grasslands (MLR 2023). Retention forestry has been implemented in state forests as a strategy to retain forest biodiversity within production forests (ForstBW 2015). Among the measures of this strategy are the retention of deadwood as well as habitat tree groups. Next to other mustelids, pine marten and beech marten co-occur in our study area, and while both species are allowed to be hunted in autumn and winter this is practiced only at a very low level (MLR 2019).

We applied camera trapping on 135 one-hectare research plots (443–1334 m a.s.l.) that were designated previously for the Research Training Group ConFoBi (Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe) assessing the effects of retention forestry and forest fragmentation on forest biodiversity (Storch et al. 2020). All plots were positioned in state forest in at least 60-year-old stands and had a minimal distance of 760 m between each other. The plots were selected along gradients of forest fragmentation and number of snags (standing dead trees) as a proxy for forest structure. We used camera traps (Bushnell Trophy Cam HD Aggressor Low Glow) over five sampling rounds in spring (April–early July) and autumn (late August–November) from 2019 to 2021. The exact positions of the camera traps in the first sampling round were assigned randomly to one of three fixed points within the plot. Afterwards cameras were shifted systematically among those positions. One camera trap per plot was installed during each sampling round. In some cases (n = 22), two cameras per plot were used if the camera trap in the previous season had to be excluded due to malfunction or theft. The camera data from this study came from camera traps primarily targeting roe deer (Schwegmann et al. 2023a). Site conditions varied in slope, overall ruggedness and understory cover meaning that the height at which camera traps were attached to trees was not standardized. Depending on site conditions camera traps were attached between 20 and 70 cm above ground level, higher cameras were attached with a slight downward

Table 1. Table of variables used in the GLMMs. Marten_abundance is the dependent variable, while all other variables are predictors.

Variable	Description	Unit	Data range
Marten_abundance	Events based detection rate of martens (Pine marten and beech marten) derived from camera traps.	Count	Mean: 1.51 (0–79)
DW_View	Binomal variable describing whether a log >10 cm diameter was in the view of the camera trap.	Category	Yes: n = 177; No: n = 489
DW_Position	Count of logs >10 cm diameter within 10 m around the camera trap position.	Count	Mean = 2.8 (0–15)
DW_Plot	Volume of deadwood on one-hectare research plot, assessed during forest inventory in 2018.	m^3 ha^{-1}	Mean = 44.76 (2.68–282.9)
Vegetation	Binomial variable describing whether vegetation in view of the camera trap might have blocked detections of animals smaller than roe deer. 'High' vegetation indicates potential obstruction.	Category	High: n = 237; Low: n = 429
Season	Confounder variable. Season of camera trapping	Category	Autumn: n = 267; Spring: n = 399
Year	Confounder variable. Year of camera trapping: 2019, 2020, or 2021	Category	2019: n = 246; 2020: n = 279; 2021: n = 141

angle. For further details in the camera trapping set-up see Schwegmann et al. (2023a).

We aggregated marten detections in events, which included a sequence of detection of the same species with less than five minutes between pictures. For analysis we used the software FFM2 (Rahm 2021). We used the sum of marten events (per camera trap and sampling round) as index of relative abundance, at each of the respective camera trap position (Carbone et al. 2001). Due to the low quality of camera trap pictures, it was only possible to distinguish between pine and beech marten for seven percent of the detection events. In 92.8% of the cases where the marten species could be assigned (determined by throat patch and other characteristics like underfur and shape of the head), we detected pine martens. Thus, we assume that pine martens were the more abundant species in the study area, with the caveat that only 7.2% of marten events were assigned to species.

We used data on lying deadwood at three different spatial scales (Table 1). 1) Camera view (*DW_View*): Binary variable describing whether a log estimated above 10 cm in diameter was visible in the camera trap pictures; 2) Camera position (*DW_Position*): number of logs above 10 cm in diameter in or intersecting with the area in a ten-meter radius around the camera trap location; 3) Plot level (*DW_Plot*): volume (m^3 ha^{-1}) of lying deadwood on the entire one-hectare research plots assessed during a forest inventory in 2018 (Storch et al. 2020). To account for potential bias due to possible reduced detection of medium-sized mammals we created a variable for potentially blocking vegetation (*Vegetation*) in front of the camera trap. We derived this binary variable subjectively post-hoc from camera trap pictures as the original focus of camera trap placement was roe deer.

We fitted three generalized linear mixed models (GLMMs), one for each deadwood variable, using the detection rates of martens (*Marten_abundance*) as the dependent variable assuming a negative-binomial distribution. In every model we included the variable on vegetation as well as an interaction term between vegetation and deadwood to account for the possibility that deadwood increases marten detection in the case that understory vegetation reduces detection probability. Additionally, we added year and season as confounder variables as well as an offset term for trapping effort (log-transformed number of trapnights) and a random intercept

Table 2. Candidate models. We included all models with deltaAICc < 2 in averaged models. We also report first model with deltaAICc > 2 and the null model.

Candidate models	AICc	deltaAICc	Weight
Camera_View			
Intercept+DW+Vegetation+DW×Vegetation+Season	2011.99	0	0.72
Intercept+DW+Vegetation+DW×Vegetation	2015.71	3.72	0.12
Intercept	2070.04	58.05	0
Camera_Position			
Intercept+DW+Vegetation+Season	2035.99	0	0.33
Intercept+DW+Vegetation+DW×Vegetation+Season	2036.30	0.31	0.28
Intercept+Vegetation+ Season	2037.69	1.70	0.14
Intercept+DW+Vegetation+ Year+Season	2039.63	3.64	0.01
Intercept	2070.04	34.05	0
Plot			
Intercept+DW+Vegetation+Season	2037.52	0	0.34
Intercept+Vegetation+Season	2037.69	0.17	0.31
Intercept+DW+Vegetation+DW×Vegetation+Season	2039.51	1.99	0.13
Intercept+DW+Vegetation+Year+Season	2041.31	3.79	0.51
Intercept	2070.04	32.53	0

for research plots. Results were deemed to be significant when alpha was 0.05 or smaller. For the categorical variables *DW_View* and *Season* the baseline was the absence of deadwood in view of the camera and autumn respectively. We conducted all analysis in R 4.1.2 (www.r-project.org). We ran GLMMs using the '*glmmTMB*' function (Brooks et al. 2017). We selected and averaged the best fitting models ($\Delta AICc < 2$), using the MuMln package (Barton 2020). All included candidate models can be found in Table 2.

Results

We included a total of 666 camera trap positions with 1004 marten events over 49 455 trapnights into our analysis. While on 358 camera trap positions no martens were detected, at plot level, all but 12 plots had at least one marten detection.

Deadwood only affected marten detections at the smallest spatial scale (Table 3, Fig. 1). Specifically, the presence of a fallen log in direct view of the camera increased the average detection rate of martens by 0.44 detections per camera trap ($p = 0.012$), while the number of logs around the camera trap and lying deadwood volume on the one-hectare research plots had no significant effect ($p = 0.129$ and $p = 0.169$) although having positive coefficients (0.050 and 0.003). Vegetation in front of the camera trap significantly reduced marten detections in all models ($p < 0.001$). Depending on the model the presence of high vegetation in front of the camera trap led to 0.94–1.17 fewer average marten detections per camera trap. The interaction term of logs in view of the camera trap and vegetation was positive and significant ($p = 0.003$, Fig. 2), while the interactions of vegetation with deadwood variables at broader scales were not significant. For transparency and good practice we tested for the influence of two outliers (camera traps with very high marten counts), which resulted in a non-significant result for the interaction term in the 'Camera_View' model ($p = 0.093$), however we retained these values as these were true outliers and there was no reason for exclusion. The confounder *Season* had a significant effect on marten detection rate, more martens were detected during camera trapping in spring ($p < 0.05$). The confounding variable *Year* was not retained in any of the selected models.

Discussion

Overall, we found no consistent effect of lying deadwood on marten detections by camera traps and thus marten habitat use. Contrary to our prediction, deadwood amounts did not affect martens at the one-hectare scale or in the immediate surroundings of the camera trap locations. Only logs directly in view of the camera traps increased marten detection rates. It appears that availability of lying deadwood does affect marten microhabitat use, but not habitat use of larger spatial scales during the growing season. When on site, martens prefer to move along logs, possibly as movement is facilitated

Table 3. Conditional averaged Negative Binomial regressions results for marten detections. Significant relationships ($\alpha = 0.05$) are shown using bold text. For the variable Deadwood at the 'Camera_View' scale the absence of a log in view of the camera was used as a baseline.

	Camera_View				Camera_Position				Plot			
Variable	Estimate	SD	z-value	p-value	Estimate	SD	z-value	p-value	Estimate	SD	z-value	p-value
Intercept	**−4.270**	**0.150**	**−28.909**	**< 0.001**	**−4.274**	**0.173**	**24.358**	**< 0.001**	**−4.2126**	**0.173**	**24.436**	**< 0.001**
Deadwood	**0.440**	**0.175**	**2.514**	**0.012**	0.050	0.033	1.518	0.129	0.003	0.002	1.377	0.169
Vegetation_High	**−1.174**	**0.197**	**−5.977**	**< 0.001**	**−1.017**	**0.246**	**4.119**	**< 0.001**	**−0.942**	**0.0186**	**5.060**	**< 0.001**
*Deadwood*Vegetation*	**1.089**	**0.362**	**3.007**	**0.003**	0.098	0.074	1.313	0.189	0.001	0.003	0.227	0.820
Season_Spring	**0.339**	**0.141**	**2.412**	**0.016**	**0.371**	**0.143**	**2.593**	**0.014**	**0.377**	**0.143**	**2.629**	**0.009**

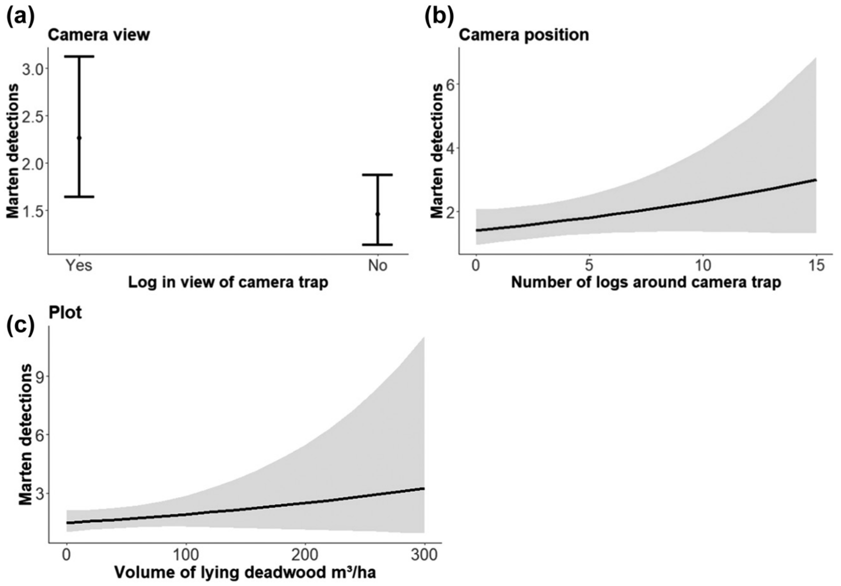

Figure 1. Effect plots displaying the effect of deadwood on marten detections at three different scales. (a) effect of deadwood in view of the camera trap, (b) number of fallen logs around camera trap position, (c) volume of deadwood on research plot.

and potential prey like small mammals are frequently found around deadwood (Suter and Schielly 1998, Hagge et al. 2019). However, high levels of deadwood in forest stands are not leading to a significantly increased habitat use by martens. It is possible that deadwood is more important in winter, especially for pine martens, when logs might facilitate access to subnivean prey (Hargis and McCullough 1984, Andruskiw et al. 2008). It is also possible that the overall volume of deadwood found on our research sites is still too low to have a significant impact on marten habitat selection. Deadwood retention as one measure of retention forestry has only been implemented recently (ForstBW 2015) and the volumes of deadwood found are still well below of what is found in natural mountainous forests (Bujoczek et al. 2018). While we focused on the effects of deadwood retention on martens during the growing season, future studies should investigate how deadwood retention affects marten habitat use in winter, when snow cover is making movement and foraging more difficult. Additionally, it would be valuable to assess the effect of standing deadwood retention on martens at the one-hectare scale, as pine marten den sites are often related to snags (Birks et al. 2005).

We were unable to consistently differentiate between pine and beech marten in this study, due to the low quality of the camera trap pictures. The species ratio of the events, where species could be assigned, suggests that more than 90% of the martens on our study sites are pine martens. This is supported by the pine marten's preference for mature forests (Brainerd and Rolstad 2002, Vergara et al. 2016, Twining et al. 2020) and the fact that all our study sites are positioned in forest stands of more than 60 years of age. While we are not clearly separating between marten species in this study, we assume that our results are mostly indicative of pine marten habitat selection, although it is possible that also beech martens hunt along fallen logs for small mammals.

In our study, we only assess the direct effects of deadwood retention on martens and while we found only small-scale effects, it is possible that further aspects of retention practices affect martens indirectly. It is for example well established that martens, especially pine martens, avoid open areas (Pullianinen 1981, Storch et al. 1990, Goszczyński et al. 2007). In boreal clear-cut harvesting systems, green tree retention can maintain some forest cover potentially allowing martens to use these sites as habitat (Goszczyński et al. 2007). Furthermore, tree species composition and stand age are forest management related aspects that might affect marten habitat selection (Storch et al. 1990, Baltrūnaitė 2010, Petrov et al. 2016, Fonda et al. 2021). Among terrestrial mammals, small mammals have been most intensively studied in their response to retention measures. While there is no overall pattern in relation to retention levels in general (Fedrowitz et al. 2014) some studies find positive responses of small mammal activity

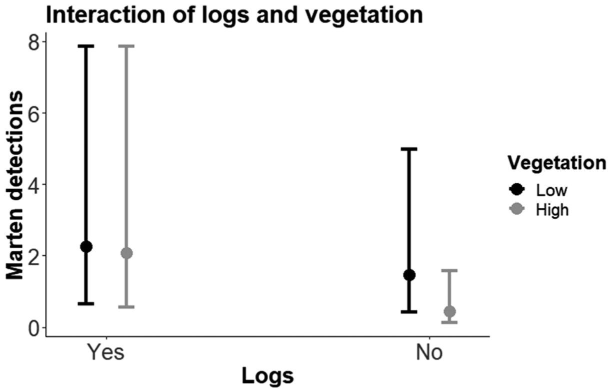

Figure 2. Effect plot displaying the interaction of logs in view of the camera trap and vegetation affecting the detection probability of martens.

Figure 3. Example of a pine marten moving on top of a log, detected by a camera trap.

to deadwood retention (Suter and Schielly 1998, Hagge et al. 2019), which could in turn improve prey-accessibility for martens. Despite possible indirect effects of retention measures on habitat use of martens, the only other study investigating this found no response of *Martes americana* to higher retention levels (Franklin et al. 2019).

While marten habitat use was not affected by plot-scale lying deadwood volume, martens chose to move along fallen logs, as shown by the significant increase of marten detections with logs > 10 cm in view of the camera trap. Microhabitat selection of martens for logs appears to increase the detection probability of martens (Fig. 2). In forest sites with high cover of understory vegetation, movement of martens might be facilitated by logs, as indicated by the significant positive interaction of *DW_view* and *Vegetation*. Specifically, this result shows, that in the presence of logs, vegetation only marginally affects the detection rates of martens (Fig. 3). This result is in line with previous studies that showed that pine martens use logs for hunting and scat deposition (Jędrzejewski et al. 1993, Baltrūnaitė 2006).

A recent study showed that boulders in front of camera traps can increase the detection probability of pine martens due to facilitated hunting and movement (Angoh et al. 2023). Our study now shows a similar effect in that positioning of camera traps in front of fallen trees might bias trapping yields due to differences in detection rates. While it is already frequently considered in camera trapping research on martens, this is to our knowledge the first time this aspect is systematically assessed. Similarly, the consistent negative effect of the *Vegetation* variable in all three models shows that camera trap positioning can lead to species-specific detection biases that have to be accounted for, which is consistent with previous studies (Rich et al. 2016, Hofmeester et al. 2019). Our study shows that large camera trapping datasets can often be used beyond their original focus, however species-specific biases need proper consideration.

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Author contributions

Sebastian Schwegmann: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ilse Storch**: Conceptualization (supporting); Funding acquisition (lead); Investigation (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xpnvx0knf (Schwegmann et al. 2023b).

References

Abbas, F., Morellet, N., Hewison, A. J. M., Merlet, J., Cargnelutti, B., Lourtet, B., Angibault, J. M., Daufresne, T., Aulagnier, S. and Verheyden, H. 2011. Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. – Oecologia 167: 401–411.

AM online projects 2018. Climate-Data.org. AM online projects – Alexander Merkel, https://de.climate-data.org/.

Andruskiw, M., Fryxell, J. M., Thompson, I. D. and Baker, J. A. 2008. Habitat-mediated variation in predation risk by the American marten. – Ecology 89: 2273–2280.

Angoh, S. Y. J., Thorsen, N. H., Hofmeester, T. R., Odden, J., Linnell, J. D. C. and Brainerd, S. M. 2023. Forestry and environmental conditions as determinants of pine marten *Martes martes* occurrence in Norway. – Wildl. Biol. 2023: e01113.

Balestrieri, A., Remonti, L., Ruiz-González, A., Vergara, M., Capelli, E., Gómez-Moliner, B. J. and Prigioni, C. 2011. Food habits of genetically identified pine marten (*Martes martes*) expanding in agricultural lowlands (NW Italy). – Acta Theriol. 56: 199–207.

Balestrieri, A., Remonti, L., Ruiz-González, A., Zenato, M., Gazzola, A., Vergara, M., Dettori, E. E., Saino, N., Capelli, E., Gómez-Moliner, B. J., Guidali, F. and Prigioni, C. 2015. Distribution and habitat use by pine marten *Martes martes* in a riparian corridor crossing intensively cultivated lowlands. – Ecol. Res. 30: 153–162.

Baltrūnaitė, L. 2006. Diet and winter habitat use of the red fox, pine marten and raccoon dog in Dzūkija national park, Lithuania. – Acta Zool. Lituanica 16: 46–53.

Baltrūnaitė, L. 2010. Winter habitat use, niche breadth and overlap between the red fox, pine marten and raccoon dog in different landscapes of Lithuania. – Folia Zool. 59: 278–284.

Barton, K. 2020. Package MuMIn: Multi-model inference. – https://cran.r-project.org/web/packages/MuMIn/index.html.

Basile, M., Mikusiński, G. and Storch, I. 2019. Bird guilds show different responses to tree retention levels: a meta-analysis. – Glob. Ecol. Conserv. 18: e00615.

Basile, M., Asbeck, T., Jonker, M., Knuff, A. K., Bauhus, J., Braunisch, V., Mikusiński, G. and Storch, I. 2020. What do tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds, and insects? – J. Environ. Manage. 264: 110401.

Bauhus, J., Puettmann, K. and Messier, C. 2009. Silviculture for old-growth attributes. – Forest Ecol. Manage. 258: 525–537.

Bengtsson, J., Nilsson, S. G., Franc, A. and Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. – Forest Ecol. Manage. 132: 39–50.

Birks, J. D. S., Messenger, J. E. and Halliwell, E. C. 2005. Diversity of den sites used by pine martens *Martes martes*: a response to the scarcity of arboreal cavities? – Mamm. Rev. 35: 313–320.

Brainerd, S. M. and Rolstad, J. 2002. Habitat selection by Eurasian pine martens *Martes martes* in managed forests of southern boreal Scandinavia. – Wildl. Biol. 8: 289–297.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 2017: 378–400.

Bujoczek, L., Szewczyk, J. and Bujoczek, M. 2018. Deadwood volume in strictly protected, natural, and primeval forests in Poland. – Eur. J. Forest Res. 137: 401–418.

Carbone, C. et al. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. – Anim. Conserv. 4: 75–79.

Farnell, I., Elkin, C., Lilles, E., Roberts, A.-M. and Venter, M. 2020. The effects of variable retention forestry on coarse woody debris dynamics and concomitant impacts on American marten habitat after 27 years. – Can. J. Forest Res. 50: 925–935.

Fedrowitz, K., Koricheva, J., Baker, S. C., Lindenmayer, D. B., Palik, B., Rosenvald, R., Beese, W., Franklin, J. F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. and Gustafsson, L. 2014. Can retention forestry help conserve biodiversity? A meta-analysis. – J. Appl. Ecol. 51: 1669–1679.

Fonda, F., Chiatante, G., Meriggi, A., Mustoni, A., Armanini, M., Mosini, A., Spada, A., Lombardini, M., Righetti, D., Granata, M., Capelli, E., Pontarini, R., Roux Poignant, G. and Balestrieri, A. 2021. Spatial distribution of the pine marten (*Martes martes*) and stone marten (*Martes foina*) in the Italian Alps. – Mamm. Biol. 101: 345–356.

ForstBW 2015. Alt und Totholzkonzept Baden-Württemberg, Stuttgart. – https://www.forstbw.de/fileadmin/forstbw_pdf/waldnaturschutz/Alt-_und_Totholzkonzept_2017.pdf.

Franklin, C. M. A., Macdonald, S. E. and Nielsen, S. E. 2019. Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forest. – Ecosphere 10: e02632.

Goszczyński, J., Posłuszny, M., Pilot, M. and Gralak, B. 2007. Patterns of winter locomotion and foraging in two sympatric marten species: *Martes martes* and *Martes foina*. – Can. J. Zool. 85: 239–249.

Gustafsson, L. et al. 2020. Retention as an integrated biodiversity conservation approach for continuous-cover forestry in Europe. – Ambio 49: 85–97.

Hagge, J., Müller, J., Bässler, C., Biebl, S. S., Brandl, R., Drexler, M., Gruppe, A., Hotes, S., Hothorn, T., Langhammer, P., Stark, H., Wirtz, R., Zimmerer, V. and Mysterud, A. 2019. Deadwood retention in forests lowers short-term browsing pressure on silver fir saplings by overabundant deer. – Forest Ecol. Manage. 451: 117531.

Hargis, C. D. and McCullough, D. R. 1984. Winter diet and habitat selection of marten in Yosemite national park. – J. Wildl. Manage. 48: 140.

Hendel, A.-L., Winiger, N., Jonker, M., Zielewska-Büttner, K., Ganz, S., Adler, P. and Braunisch, V. 2023. Bat habitat selection reveals positive effects of retention forestry. – Forest Ecol. Manage. 531: 120783.

Hoffmann, M. and Sillero-Zubiri, C. 2021. *Vulpes vulpes*. – IUCN red list of threatened species.

Hofmeester, T. R., Cromsigt, J. P. G. M., Odden, J., Andrén, H., Kindberg, J. and Linnell, J. D. C. 2019. Framing pictures: a conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. – Ecol. Evol. 9: 2320–2336.

Jędrzejewski, W., Zalewski, A. and Jędrzejewska, B. 1993. Foraging by pine marten *Martes martes* in relation to food resources in Białowieża National Park, Poland. – Acta Theriol. 38: 405–426.

Kämmerle, J.-L., Rondeaux, S. and Storch, I. 2020. Circadian activity patterns of red foxes (*Vulpes vulpes*) in montane forests under different culling regimes. – Mamm. Res. 65: 615–619.

Lindenmayer, D. B. 2002. Conserving forest biodiversity. A comprehensive multiscaled approach. – Island Press.

Lindenmayer, D. B., Franklin, J. F., Lõhmus, A., Baker, S. C., Bauhus, J., Beese, W., Brodie, A., Kiehl, B., Kouki, J., Pastur, G. M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A. and Gustafsson, L. 2012. A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. – Conserv. Lett. 5: 421–431.

Lovari, S., Herrero, J., Masseti, M., Ambarli, H., Lorenzini, R. and Giannatos, G. 2016, *Capreolus capreolus*. – IUCN red list of threatened species.

Martin, S. K. and Barrett, R. H. 1983. The importance of snags for pine marten habitat in the northern Sierra Nevada. In: Davis, J. W., Goodwin, G. A. and Ockenfels, R. A. (eds), Proceedings of the symposium on snag habitat management, pp. 114–116.

MLR 2019, Wildtierbericht für Baden-Württemberg 2018. – Ministerium für Ländlichen Raum und Verbraucherschutz (Hrsg.).

MLR 2023. Naturräume Baden-Württembergs: – Schwarzwald.

Pereboom, V., Mergey, M., Villerette, N., Helder, R., Gerard, J.-F. and Lodé, T. 2008. Movement patterns, habitat selection, and corridor use of a typical woodland-dweller species, the European pine marten (*Martes martes*), in fragmented landscape. – Can. J. Zool. 86: 983–991.

Petrov, P. R., Popova, E. D. and Zlatanova, D. P. 2016. Niche partitioning among the red fox *Vulpes vulpes* (L.), stone marten *Martes foina* (Erxleben) and pine marten *Martes martes* (L.) in two mountains in Bulgaria. – Acta Zool. Bulg. 68: 375–390.

Pullianinen, E. 1981. Winter habitat selection, home-range, and movements of the pine marten (*Martes martes*). – In: Chapman, J. A. and Pursley, D. (eds), Proceedings of the Worldwide Furbearer Conference, Frostburg, Md., 3–11 August 1980. R. R. Donelly and Sons Forstburg, Md., pp. 1068–1087.

Rahm, L. 2021. FFM – software für Fotofallemonitoring.

Rappa, N. J., Staab, M., Ruppert, L.-S., Frey, J., Bauhus, J. and Klein, A.-M. 2023. Structural elements enhanced by retention forestry promote forest and non-forest specialist bees and wasps. – Forest Ecol. Manage. 529: 120709.

Rich, L. N., Miller, D. A., Robinson, H. S., McNutt, J. W. and Kelly, M. J. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. – J. Appl. Ecol. 53: 1225–1235.

Russell, A. and Storch, I. 2004. Summer food of sympatric red fox and pine marten in the German Alps. – Eur. J. Wildl. Res. 50: 53–53.

Sacchi, O. and Meriggi, A. 1995. Habitat requirements of the stone marten (*Martes foina*) on the Tyrrhenian slopes of the northern Apennines. – Hystrix Ital. J. Mammal. 7: 99–104.

Schwegmann, S., Hendel, A.-L., Frey, J., Bhardwaj, M. and Storch, I. 2023a. Forage, forest structure or landscape: what drives roe deer habitat use in a fragmented multiple-use forest ecosystem? – Forest Ecol. Manage. 532: 120830.

Schwegmann, S. and Storch, I. 2023b. Data from: Lying deadwood retention affects microhabitat use of martens (*Martes* spp.) in European mountain forests. – Dryad Digital Repository, https://doi.org/10.5061/dryad.xpnvx0knf.

Stokland, J. N., Sitonen, J. and Jonsson, B. G. 2012. Biodiversity in deadwood. – For. Chron. 88: 660.

Storch, I., Lindström, E. and de Jounge, J. 1990. Diet and habitat selection of the pine marten in relation to competition with the red fox. – Acta Theriol. 35: 311–320.

Storch, I. et al. 2020. Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of central Europe using an interdisciplinary, multi-scale approach. – Ecol. Evol. 10: 1489–1509.

Suter, W. and Schielly, B. 1998. Liegendes Totholz: Ein wichtiges Strukturmerkmal für die Habitatqualität von Kleinsäugern und kleinen Carnivoren im Wald. – Schweiz. Z. Forstwesen: 795–807.

Twining, J. P., Montgomery, W. I., Reid, N., Marks, N., Tosh, D. G. and Scantlebury, D. M. 2020. All forests are not equal: population demographics and denning behaviour of a recovering small carnivore in human modified landscapes. – Wildl. Biol. 2020: 1–10.

Vergara, M., Cushman, S. A., Urra, F. and Ruiz-González, A. 2016. Shaken but not stirred: multiscale habitat suitability modeling of sympatric marten species (*Martes martes* and *Martes foina*) in the northern Iberian Peninsula. – Landsc. Ecol. 31: 1241–1260.

Weber, D., Roth, T., Tesini, C. and Thiel, D. 2018. Widespread distribution of pine martens (*Martes martes*) in a fragmented suburban landscape. – Mamm. Res. 63: 349–356.

Wereszczuk, A. and Zalewski, A. 2015. Spatial niche segregation of sympatric stone marten and pine marten – avoidance of competition or selection of optimal habitat? – PLoS One 10: e0139852.