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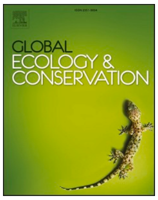

Specialist carabids in mixed montane forests are positively associated with biodiversity-oriented forestry and abundance of roe deer

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ABSTRACT

The ongoing transition within forest management towards more biodiversity-oriented practices, such as close-to-nature forestry and retention forestry, may benefit forest fauna such as forest-specialized ground beetles (Coleoptera: Carabidae). However, it remains unclear how forest carabids are jointly affected by these practices in Central European montane forests, which host particularly sensitive, range-restricted carabid species, and where biodiversity-oriented forestry is widely applied. Moreover, roe deer (*Capreolus capreolus*), the most common large herbivore in these forests, is intensively managed to reduce browsing pressure, but it is yet unknown how this may affect carabids, alongside the effect of silviculture. On 66 1-ha plots in the Black Forest region of Germany, we sampled carabids with pitfall traps, measured roe deer abundances using camera trapping, and measured several structural variables directly related to close-to-nature and retention practices, as well as variables describing microclimate and landscape-level forest cover. We found that the carabid assemblage was dominated by forest specialists, with little influence from fragmentation of the surrounding forest. Higher broadleaf share (and canopy cover for montane specialists) was correlated with higher carabid activity-density. Increasing stand maturity (and lying deadwood volume for montane specialists), was correlated with higher species richness. Plots with higher roe deer abundances showed higher carabid richness and activity-density. Assemblage composition changed along the altitudinal gradient, and both richness and activity-density increased with elevation. Thus, carabid communities, including montane specialists and several species of conservation interest, stand to benefit from close-to-nature and retention practices, if applied throughout the altitude range of montane forests. Forest carabids may additionally profit from maintaining higher roe deer abundances, but further research is needed to understand this causal link, as well as to weigh the costs and benefits of deer culling for forest biodiversity.

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1. Introduction

Timber extraction threatens forest-specialized organisms, through simplification and fragmentation of forest habitats (FAO and UNEP, 2020; Jung et al., 2022). To counter this, silviculture in Europe is gradually shifting from production-oriented to more biodiversity-oriented practices, incorporating biodiversity conservation as a management goal, such as close-to-nature forestry or retention forestry (Borrass et al., 2017; Spiecker, 2003). Carabid beetles (Coleoptera: Carabidae) are a hyperdiverse insect family, containing many forest-reliant species, often used as indicators for the structure and function of European forest ecosystems (Kotze et al., 2011). Carabids are responsive to changes in habitat structure (Koivula, 2011; Rainio and Niemelä, 2003), and forest carabids are primarily polyphagous predators (Riddick, 2008), with a key role in regulating their invertebrate prey (Lövei and Sunderland, 1996). They are also easily sampled and lend themselves to species-level identification (Koivula, 2011). Forest-specialized carabids, and especially brachypterous (flightless) and large-bodied species, which depend on stable environments (Blake et al., 1994), can persist even in small and isolated forest patches (Marrec et al., 2021), but are affected by stand-level management (Lange et al., 2014; Marrec et al., 2021). The few available long-term studies on forest carabids in temperate Europe indicate declining diversity (Homburg et al., 2019), even though overall abundance is stable or increasing (Brooks et al., 2012; Desender et al., 2010). Still, it remains unclear how biodiversity-oriented forestry may relate to these trends.

There are different ways of assessing the impact of forestry systems on biodiversity, with species richness being most commonly used (Paillet et al., 2010). However, species richness per se is an inappropriate indicator for forest conservation value for carabids (Lange et al., 2014; Niemelä, 1997). It is well-established that both forest fragmentation (e.g. Marrec et al., 2021; Niemelä et al., 2007; Rainio and Niemelä, 2003) and harvesting (e.g. de Warnaffe and Lebrun, 2004; Huber and Baumgarten, 2005; Lange et al., 2014) result in a spillover into forest habitats of a diverse set of macropterous (flight-able) and smaller species, with high dispersal abilities and tolerance to disturbance (Blake et al., 1994), which may even lead to overall richness increases, masking effects on forest specialists (Niemelä et al., 2007). However, in landscapes with high forest cover and rugged topography, as are Central European mountains, that spillover effect may be limited (Jelaska and Durbešic, 2009; Marrec et al., 2021), in which case overall richness and abundance would closely reflect effects on forest specialists. As most studies on forest carabids were carried out either in boreal forests (Paillet et al., 2010) or in lowland temperate forests, there remains a lack of research on mixed montane forests, which cover a significant area of Central Europe (Leuschner and Ellenberg, 2017). Montane forests also harbour characteristic carabid species, adapted to cold and humid conditions (de Groot and Vrezec, 2019; Trautner, 2017). These montane specialists are particularly at risk from climate change (Müller-Kroehling et al., 2014), but these impacts may be mitigated by management that fosters forest structural complexity (Braunisch et al., 2014). Undoubtedly, any evaluation of the effects of forestry on Central European carabids must focus not only on the full carabid assemblage, but also on sensitive functional groups, such as montane specialists.

Implemented since the early 1990s and now common in Central Europe, close-to-nature forestry (i.e. continuous-cover forestry) is based on single-tree selection and natural regeneration, creating uneven-aged stands (Bauhus et al., 2013), and promoting conversion of conifer monocultures to mixed stands (Bauhus et al., 2017; Seliger et al., 2023). In contrast with clearcutting, selection harvests succeed in maintaining forest-specialized carabids (Brouat et al., 2004; Elek et al., 2022; Huber and Baumgarten, 2005), but the resulting uneven age structure is not per se more beneficial for carabids than even-aged stands (de Warnaffe and Lebrun, 2004; Lange et al., 2014). Rather, changes in tree species composition are more impactful for carabid assemblage composition (Lange et al., 2014; Tinya et al., 2021; Werner and Raffa, 2000). Broadleaved forests tend to host higher carabid abundances (e.g. Fuller et al., 2008) and species richness (e.g. Magura et al., 2003) than coniferous forests, as leaf litter is more readily taken up by detritivores, with cascading effects for ground-active predators (Scheu et al., 2003; Vician et al., 2018). Moreover, close-to-nature systems maintain a high canopy cover, thereby providing a favourable microclimate for forest-specialized carabids (Fuller et al., 2008; Purchart et al., 2013), although shady conditions can also limit understorey cover and richness (Dormann et al., 2020), which in turn are linked with carabid richness and abundance (Jouveau et al., 2020; Tinya et al., 2021).

In the last decade, close-to-nature forestry has been complemented with retention forestry practices (Gustafsson et al., 2020), entailing the retention of late-successional structures - large living trees and deadwood - across harvesting cycles (Gustafsson et al., 2012). These practices originate in clearcutting systems, where retention of tree groups offers only limited and temporary benefits for carabids (Elek et al., 2022; Skłodowski, 2021; Sultaire et al., 2021). However, as with other taxa, it remains unclear how retention affects carabids in the context of continuous-cover systems. Positive effects of deadwood retention are well-reported for saproxylic invertebrates (Sandström et al., 2019), but recent studies reveal that deadwood can also positively impact non-saproxylic taxa (Rothacher et al., 2023; Tinya et al., 2021), including carabids (e.g. Fuller et al., 2008; Negro et al., 2014). Deadwood likely benefits carabids and other epigeal taxa by enhancing leaf litter accumulation, moisture retention (Kappes et al., 2009) and prey availability (Chen and Wise, 1999). Retention measures are also expected to increase stand maturity, which in turn is known to favour abundance (e.g. Isaia et al., 2015), biomass (e.g. Skłodowski, 2006), and richness (e.g. Marrec et al., 2021) of forest-reliant carabids. This is likely due to the accumulation of species with higher body sizes, lower dispersal abilities and longer developmental periods (Blake et al., 1994; Jelaska et al., 2011), along possibly higher resource availability in mature stands (Scheu et al., 2003).

In addition to forestry, large herbivores are also key drivers of forest biodiversity. High abundances of herbivores disrupt faunal communities through browsing-related habitat degradation (Chollet et al., 2016; Côté et al., 2004). Many studies assessing the relationship between forest-dwelling herbivores and other forest taxa focused on very high herbivore abundances (e.g. Brousseau et al., 2013; Crystal-Ornelas et al., 2021; Pendergast et al., 2016; Wheatall et al., 2013), creating the notion that large herbivores have a generally negative effect on forest biodiversity. However, large herbivores also fulfill a range of ecological functions, such as dung and carrion provisioning for the copro- and necrophagous fauna (Barton et al., 2013; Koike et al., 2014; Melis et al., 2004; Stiegler et al., 2020), or seed dispersal through endozoochory (Albert et al., 2015). Invertebrates are affected indirectly by herbivores through changes in vegetation structure (Bucher et al., 2021; Landsman and Bowman, 2017; Melis et al., 2006). Previous studies found that carabid beetles profited from microclimatic conditions in the understorey resulting from browsing, but high browsing intensity may negatively affect forest specialists (Iida et al., 2016a; Melis et al., 2007; Suominen et al., 2003). In areas of Central Europe where the larger red deer (*Cervus elaphus*) is extirpated (as in much of southern Germany, Balkenhol, 2023), roe deer (*Capreolus capreolus*) remains as the most ubiquitous herbivore, being intensively managed by hunting to limit browsing impacts (Hothorn and Müller, 2010). While several studies have focused on the effects of large cervids on carabids (Gobbi et al., 2018; Iida et al., 2016b; Suominen et al., 1999), the relationship between these insects and smaller species like roe deer has so far not been assessed.

With this study, we aim to understand how different facets of forest ecosystems, directly influenced by management practices (biodiversity-oriented silviculture and roe deer management), jointly influence carabids in a Central European montane forest region. Thus, we address a gap in knowledge and provide evidence that can inform further integration of biodiversity conservation into management practices. We hypothesized that *(1)* the carabid assemblage in this region is dominated by forest specialists, with little spillover of non-forest species caused by forest fragmentation. We expected that *(2)* overall carabid species richness and activity-density (a proxy for abundance), the richness and activity-density of sensitive functional groups (brachypterous carabids, large-bodied carabids, montane specialists), as well as assemblage-level body size and its diversity, respond positively to close-to-nature forestry, represented by the broadleaf tree share in a stand and the canopy cover. We similarly expected *(3)* positive responses to

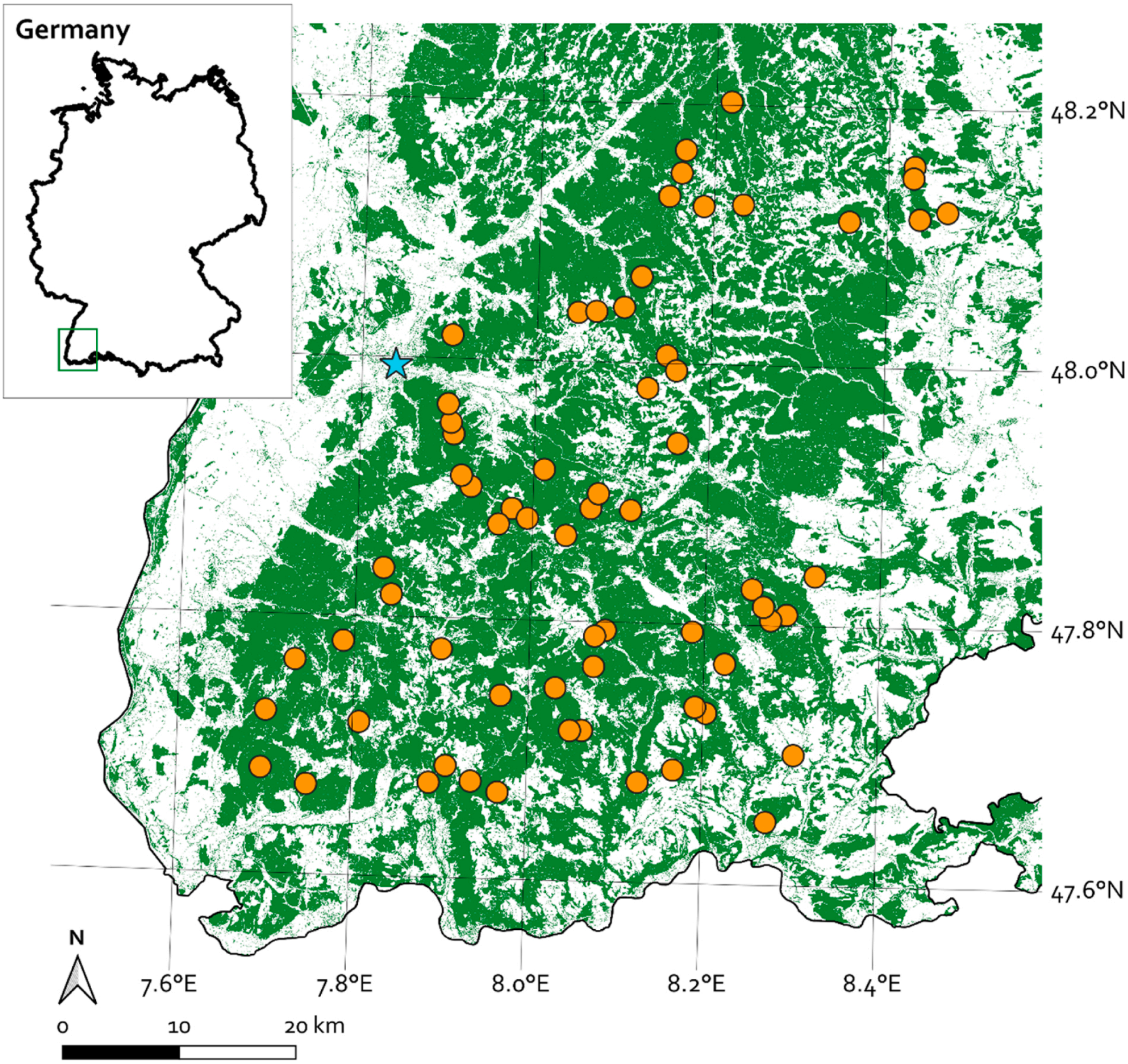

Fig. 1. Study area: Location of plots where carabids were sampled, marked as orange circles (tree cover in green). The insert shows the study area location within Germany. The blue star represents the largest city in the region, Freiburg im Breisgau. Coordinates are shown in decimal degrees.

retention practices, represented by stand maturity and the volume of lying deadwood. Moreover, we expected *(4)* roe deer to exert an additional, negative effect on richness and activity-density of carabids, particularly on sensitive functional groups. Finally, we investigate whether *(5)* carabid assemblage composition is structured primarily by management-driven forest structure, roe deer abundance, landscape composition or abiotic conditions.

2. Methods

2.1. Study area and plot selection

We conducted our study in 66 1-ha forest plots, in the Black Forest region of southwestern Germany (47.64–48.26° N, 7.65–8.50° E, Fig. 1). This is a low-elevation (up to 1493 m) mountain range, characterized by a temperate oceanic climate (subarctic at higher altitudes), with average annual temperatures of 4.3 to 10 °C and annual precipitation of 857 to 1893 mm (Source: Deutscher Wetterdienst). This region is extensively covered with mixed montane forests, dominated by Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*) and silver fir (*Abies alba*). Our plots were part of a wider set of 135 plots, spaced at least 750 m apart, established by the ConFoBi Research Training Group (https://confobi.uni-freiburg.de/en, Storch et al., 2020), all placed in state-owned forests, managed since the 1990s under a close-to-nature forestry paradigm. Since 2010, management practices have also gradually incorporated retention of deadwood and habitat trees ("Old and Deadwood Policy", ForstBW, 2016). ConFoBi plots were chosen to represent gradients in both forest structural complexity and landscape-level forest cover (Storch et al., 2020), and we selected for this study plots that are representative of the full range of variation in canopy cover, tree species composition and deadwood volumes found among ConFoBi plots.

2.2. Carabid beetle sampling

We sampled carabids through pitfall trapping, a well-established method for sampling active epigeal invertebrates (Kotze et al., 2011; Woodcock, 2005). Trap catches represent a compound measure of activity and abundance, i.e. activity-density, often used to reflect relative abundance and its changes across environmental gradients, under the assumption of similar activity levels (Kotze et al., 2011; Lövei and Sunderland, 1996). We placed three traps on each plot ($n = 198$), one at the plot center and two near the northwestern and southeastern corners (as in Knuff et al., 2020). To minimize depletion effects and prevent pseudo-replication, we ensured an inter-trap distance of more than 25 m (Digweed et al., 1995). We installed the traps between 20 April and 20 May 2020. To mitigate the effect of insect phenology and varying activity levels on trap catches, we placed traps sequentially in different plots along the altitudinal gradient. We collected trap contents after an average of 35.8 days (21 - 45 days, latest collection on 27 June 2020), thereby obtaining a representative sample of assemblage composition in the main carabid breeding season (Dülge, 1994; Niemelä et al., 1990; Skarbek et al., 2021). We opted for a single sampling interval, allocating survey effort to more spatial replicates rather than increased sampling duration, thus providing better coverage of the carabid assemblage (Lövei and Magura, 2011). Our trap design followed the suggestions by Brown and Matthews (2016). Each trap consisted of three nested 500 mL transparent polypropylene cups, with drainage holes on the lowest cup and a transparent acrylic glass rain cover (Fig. 2). Traps with large openings, such as ours, provide larger catches that are more responsive to habitat features (Jung et al., 2019). We filled the traps with 250 mL of 50% propylene glycol aqueous solution, preferred to ethylene glycol due to its non-toxicity (Brown and Matthews, 2016). After emptying traps and cleaning the catches, we placed specimens in a 99% ethanol solution. Subsequently, we counted and determined all Coleoptera specimens to family level and carabids to species level, using a regional identification key (Götz, 2021).

2.3. Relative roe deer abundance

We derived relative roe deer abundance from detection rates of camera traps (Bushnell Trophy Cam HD Aggressor Low Glow)

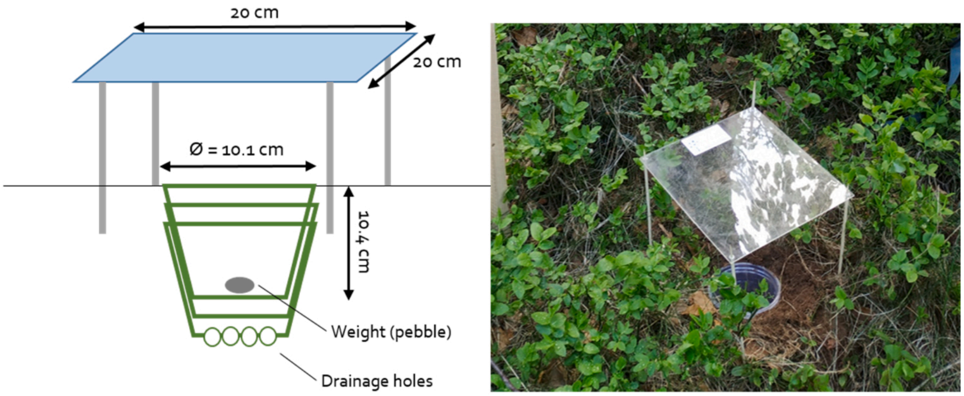

Fig. 2. Pitfall traps: Schematic of trap design and dimensions (left), and example of trap placed in the field (right).

positioned on the research plots during five sampling periods, between spring 2019 and spring 2021 (Carbone et al., 2001; Gilbert et al., 2021; Kämmerle et al., 2018). During each sampling period in spring (April to early July) or autumn (late August to November), we placed one camera per plot (a minimum of 750 m apart) at one of the three insect survey locations (a minimum of 25 m apart). The first position in spring 2019 was randomly assigned, and the camera trap position was then systematically shifted throughout the remaining sampling periods, ensuring it was never repeated in the same season (for a more detailed description, see Schwegmann et al., 2023a). We positioned camera traps aiming to detect roe deer, attaching them to trees 20–70 cm above ground (depending on the terrain and understorey cover) and facing parallel to the ground slope. We defined a detection event as one or more images with roe deer less than 5 min apart (Kämmerle et al., 2018). To obtain a plot-specific value of relative roe deer abundance, we first corrected the sum of all roe deer detection events per sampling period for trapping effort, afterwards averaging the resulting values over all five sampling periods. Overall, we detected 4,457 roe deer events over 24,687 trap nights (on average 374.04 trap nights per plot). Even though relative abundance may reflect not only density of individuals but also their activity (Gilbert et al., 2021), deer activity may affect carabids through similar mechanisms as deer density (e.g. increased browsing or trampling), and thus the use of relative abundance is well-suited to our goals.

2.4. *Environmental predictors*

We calculated three topographic variables for each plot - altitude above sea level, northness index and standard deviation of slope — from a Digital Terrain Model with 1 m resolution for the state of Baden-Württemberg (LGL, 2018), using QGIS (QGIS Development Team, 2023). We used the standard deviation of slope values within a plot to represent topographic heterogeneity (Heidrich et al., 2020). The northness index ranges from -1 (south-facing slope) to 1 (north-facing slope), reflecting differences in solar exposure and microclimate (Singh, 2018). We derived the northness index from the slope aspect of the plot as:

$$northness = \cos((aspect \times \pi)/180) \tag{1}$$

We calculated forest cover at two scales - a 1 km^2 and 25 km^2 circular buffer surrounding the plot. For this, we used a remotely-sensed Tree Cover Density dataset, with 10 m resolution (EU/CLMS/EEA, 2018), employing a 10% tree cover density threshold. Possible spillover effects from open areas on alpha-diversity of carabids in forests are most likely at the 1 km^2 scale (Marrec et al., 2021), whereas forest cover at the 25 km^2 was a selection criterion for ConFoBi plots (Storch et al., 2020) and may influence the regional species pool (Hendrickx et al., 2007).

To represent forest management in each research plot, we considered four variables: mean tree diameter at breast height (DBH), the share of basal area corresponding to broadleaf tree species (i.e. broadleaf share), the volume of lying deadwood, and the canopy cover. We calculated the first two variables from an inventory of all trees ($>$ 7 cm DBH) in ConFoBi plots, carried out between 2016 and 2018 (Storch et al., 2020). The volume of lying deadwood was the volume of coarse woody debris estimated from a V-transect carried out alongside the tree inventory (for details, see Storch et al., 2020; Van Wagner, 1982). No harvesting took place in the ConFoBi plots from their establishment in 2016 until collection of insect data for the present study. Canopy cover was calculated as the fraction of each plot containing vegetation above 5 m height, which in turn was derived from canopy height models, constructed with UAV-SfM (Unoccupied Aerial Vehicle - Structure from Motion) flights (Frey et al., 2018), carried out in 2019 and 2020. We present in Table 1 a summary of values for all predictors over our study plots.

2.5. *Statistical analyses*

We pooled specimen counts from all traps in each plot, to obtain activity-density for each species and for all carabids, as well as to derive species richness at the plot level. We expressed sampling effort in each plot as the product of the number of traps and the sampling duration, i.e. the number of trap-days (mean = 103.2, SD = 16.2). We excluded from these calculations eight traps that had been destroyed, damaged, collected too late ($>$ 50 days) or that were entirely filled with ants. We assessed sampling completeness for the full study area through an incidence-based species rarefaction-extrapolation curve (Chao et al., 2014), obtained by resampling species richness from a varying number of plots. We computed the curve with the R package *iNEXT* (Hsieh et al., 2016), and retrieved

Table 1

Predictor values: Predictors used to model richness, activity-density and assemblage composition of carabid beetles, and descriptive statistics for these variables across the 66 forest plots.

Predictor	Units	Mean (± SD)	Range
Altitude	m	862.9 ± 191.4	515 — 1334
Relative abundance of roe deer	-	0.192 ± 0.161	0.005 — 1.070
Canopy cover	%	70.2 ± 16.0	17.9 — 98.2
Broadleaf share	%	33.3 ± 26.0	0.3 — 92.4
Mean tree DBH	cm	30.4 ± 8.2	12.2 — 52.6
Lying deadwood volume	m^3	54.8 ± 56.2	6.7 — 282.9
Forest cover (100 ha)	%	82.6 ± 14.3	41.1 — 98.2
Forest cover (2500 ha)	%	70.0 ± 14.4	25.8 — 89.8
Northness	-	0.15 ± 0.62	-0.96 — 0.97
SD slope	%	4.5 ± 2.1	1.1 — 11.5

an estimate of asymptotic species richness (*Chao2*, Colwell and Coddington, 1994). We used R for this and all following analyses (R Core Team, 2022).

We then classified carabid species into functional groups: as forest specialists or non-forest (open-land or generalist) species, from a database of German species (Gesellschaft für Angewandte Carabidologie, 2009); as montane specialists or not, according to the same database; as brachypterous or macropterous (including dimorphic) species, according to their wing development (in Trautner, 2017), and as large-sized species ($>$ 22 mm body length, Jelaska and Durbešic, 2009) or not, according to their body length measurements reported by Müller-Motzfeld (2004). Additionally, we retrieved state-level (Trautner et al., 2005) and national (Schmidt et al., 2016) red list status for each species. Then, we recalculated activity-density and species richness for non-forest carabids, brachypterous carabids, large-bodied carabids and montane specialists. Based on the body length values and activity-density of each species, we determined the plot-level community-weighted mean (CWM) and community-weighted variance (CWV) of body size, reflecting the body size of dominant species and the body size diversity in the assemblage, respectively (Perez-Alvarez et al., 2021).

To address our first hypothesis, we modelled the proportion of specimens belonging to non-forest species as a function of canopy cover and forest cover at both 1 km^2 and 25 km^2 scales. For this we used a logistic Generalized Linear Mixed Model (GLMM), with the R package *lme4* (Bates et al., 2015), accounting for overdispersion by including the plot as an observer-level random effect (Harrison, 2015, 2014). We tested the fixed effects of predictors using likelihood-ratio tests, and calculated a marginal R^2 (as per Nakagawa and Schielzeth, 2013) with the R package *MuMIn* (Bartón, 2023). For this and all models described below, we only included non-collinear predictors ($R^2 < 0.5$, Dormann et al., 2020) and all predictors were scaled (mean $= 0$, SD $= 1$) to improve model fitting.

To model variation in activity-density and species richness of carabids and their functional groups (brachypterous species, large-bodied species and montane specialists), we built Generalized Linear Models (GLMs), taking as predictors all environmental variables representing biodiversity-oriented management (canopy cover, broadleaf share, mean tree DBH and lying deadwood volume), as well as altitude. Given the small proportion of non-forest carabids in our plots and the large overlap between forest specialists and brachypterous species, we did not analyze responses of forest specialists separately. Activity-density was analyzed with negative binomial GLMs, to account for overdispersion in count data, and including log-transformed trap-days as an offset to account for varying sampling effort (Kotze et al., 2012). In order to explore which species were driving significant effects on activity-density, we also ran single-species models for all commonly found species ($>$ 200 specimens), using the same set of predictors. Species richness was analyzed with quasipoisson GLMs, since richness data was underdispersed, and taking trap-days as an additional predictor in the model rather than an offset. Then, we evaluated whether adding the relative abundance of roe deer as predictor significantly improved the fit of models for total carabid richness and activity-density, through a F-test and a likelihood-ratio test, respectively. Based on the outcome of these comparisons, we reran these and all other models including roe deer abundance as a predictor. We used the same set of predictors to model CWM and CWV of body size, using linear regression. Given the outcome of our first hypothesis, we did not include landscape-level forest cover in any of these models. Besides, in models for montane specialists, we did not include broadleaf share as a predictor and instead added the northness index and the standard deviation of slope, since we believed those two microclimatic predictors to be more ecologically relevant. We log-transformed the relative abundance of roe deer and the volume of lying deadwood, to adjust for strong skew in their values. We checked assumptions of all models by inspecting their residuals with R package *DHARMa* (Hartig, 2022). We assessed the goodness-of-fit of GLMs with McFadden's R^2 (Faraway, 2016).

We employed a nonmetric multidimensional scaling (NMDS) ordination to represent the variation in carabid assemblage composition across our plots. We opted for this ordination technique since it makes no prior assumptions on which and how many predictors drive assemblage structure, and it is not too sensitive to species' absences (Minchin, 1987; Paliy and Shankar, 2016). We used 2 axes and Sørensen distances, in R package *vegan* (Oksanen et al., 2022). We used only presence-absence data, as these are less susceptible to sampling error (Hirst and Jackson, 2007) and may represent rules of community assembly better than abundance data (Wilson, 2012). As recommended by Dexter et al. (2018), we assessed reliability of our ordination by testing if its stress value differs significantly from the stress value of a randomly-organized assemblage. For that purpose, we used function *oecosimu()* to run 1000 simulations of a random assemblage using the quasiswap algorithm, which preserves total occurrences for each plot and species (Miklós and Podani, 2004), and computes the NMDS stress for each. Lastly, we tested whether each of seven environmental predictors - altitude, relative abundance of roe deer, forest cover in 1 km^2 and all forest structure variables - can explain the assemblage composition represented in the ordination, by means of permutation tests (10,000 permutations) with function *envfit()*, and using a Bonferroni-corrected significance threshold ($\alpha = .0071$).

3. Results

3.1. *Description of carabid assemblage*

Across 66 forest plots and 190 traps, we captured 5,574 carabid specimens of 41 species (Table A1). Among all specimens, 98.3% were forest specialists (31 species), 93.8% were brachypterous (24 species), 27.9% were montane specialists (9 species), and 22.6% were large-sized carabids ($>$ 22 mm body length, 9 species, all in genus *Carabus*). Four species - *Abax parallelepipedus*, *Abax ovalis*, *Pterostichus burmeisteri* and *Carabus auronitens* - were eudominant across our samples, each accounting for more than 10% of all captured specimens. We also detected 7 species that are red-listed (including 'Near Threatened') at the state level, and 5 at the national level, the most numerous being *Carabus intricatus* (20 specimens, 'Threatened' at both levels). For each red-listed species, in Table B1 we present the range of environmental conditions where we detected it, and whether it was found in plots located in protected areas. The mean body size of captured specimens was 17.7 mm, with a median of 20 mm. Sampling completeness was high in relation to sampling effort, since additional sampling plots would have a very low probability (0.02%) of yielding additional species (rarefaction-

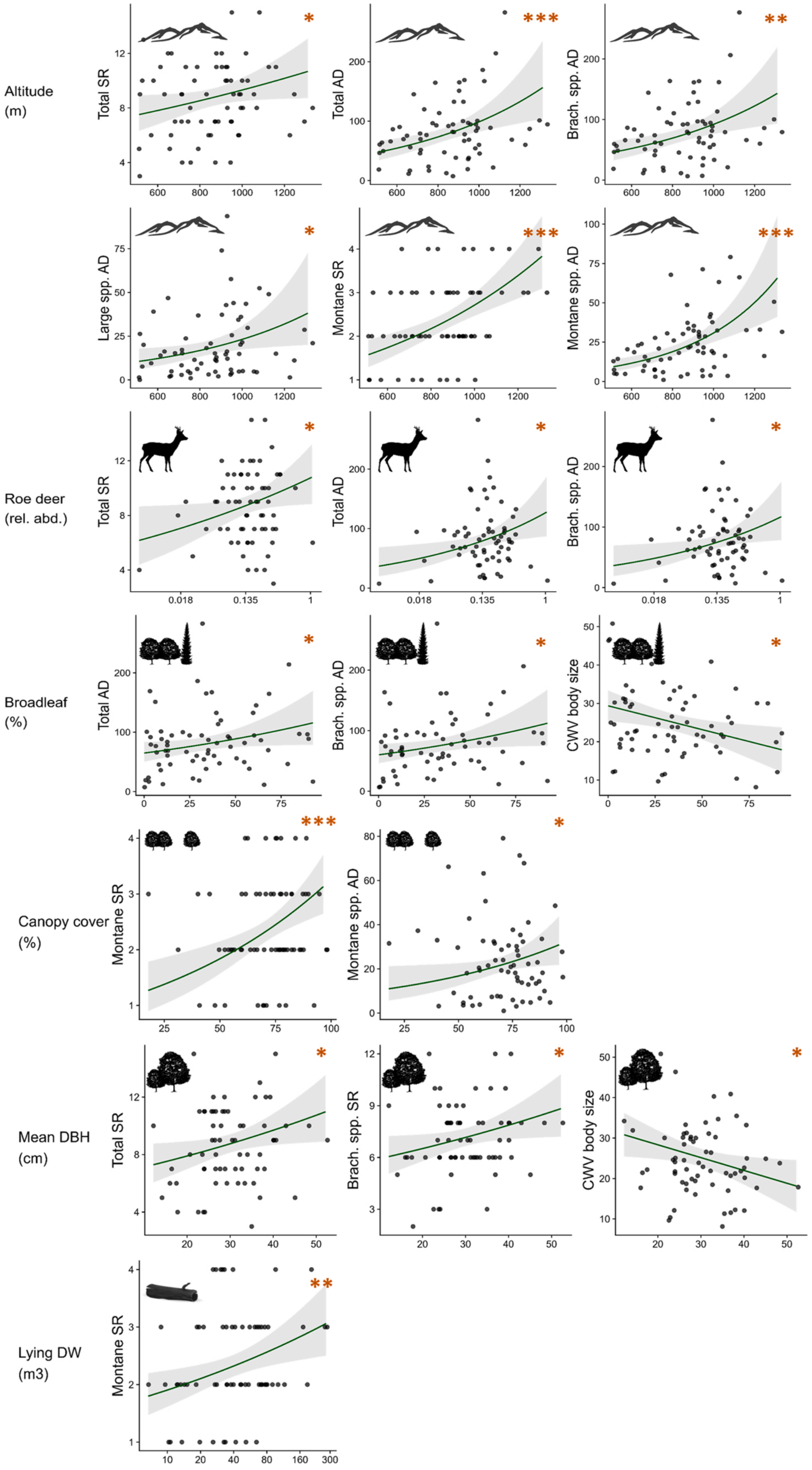

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Fig. 3. Significant modelled effects on carabid activity-density and richness: Significant modelled relationships between predictors, listed on the left side and each represented by an icon – altitude, relative abundance of roe deer, broadleaf share (Broadleaf), canopy cover, mean tree DBH and volume of lying deadwood (Lying DW) – and variables representing the carabid assemblage, on y axes of graphs – total species richness (Total SR), total activity-density (AD), activity-density of brachypterous species (Brach. spp. AD), activity-density of large-sized species (Large spp. AD), richness of montane species (Montane SR), activity-density of montane species (Montane spp. AD), and community-weighted variance of body size (CWV body size). Activity-density is standardized for the average trapping effort (103.2 trap-days). Points represent observations on the 66 sampling plots. Significance level is shown on the top right of each graph (* $p < .05$, ** $p < .01$, *** $p < .001$).

extrapolation curve in Figure C1). Still, asymptotic species richness (*Chao2*) was estimated at 53 species, with a high associated uncertainty (95% CI: 41 – 80 species).

3.2. Non-forest species

We captured 95 specimens of non-forest carabids, belonging to 10 species. After accounting for total captured specimens, higher canopy cover was associated with a significantly lower probability that a given captured specimen belongs to a non-forest species ($\chi^2 = 4.555$, d.f. $= 1$, $p = .0328$). After standardizing for 84 captured specimens (the average across plots), an increase in canopy cover from 50% to 90% was linked to a decrease in the mean predicted number of non-forest specimens from 0.96 to 0.23. On the other hand, the probability of capturing a non-forest species was not significantly associated with forest cover in the surrounding landscape, neither at 1 km^2 nor at 25 km^2 scale. The logistic GLMM model had a marginal R^2 of 10.5%.

3.3. Effects of close-to-nature forestry practices

Carabid activity-density, but not species richness, was positively associated with broadleaf share ($z = 1.997$, $p = .046$). Carabid activity-density also increased with altitude ($z = 3.402$, $p < .001$). Similar patterns were evident for the activity-density of brachypterous species (broadleaf share: $z = 2.062$, $p = .039$; altitude: $z = 3.108$, $p = .002$), but not for the activity-density of large-bodied carabids, which only increased with altitude ($z = 2.321$, $p = .020$). Based on single-species models (Table D1), the relationship of carabid activity-density with altitude is primarily driven by changes in activity-density of *P. burmeisteri* and *C. auronitens*, whereas the relationship with the share of broadleaf trees is mainly driven by *P. burmeisteri*. CWM of carabid body size was not significantly associated with any predictor, but CWV of body size was significantly lower in plots with higher broadleaf share ($t = -2.624$, d.f. $= 58$, $p = .011$). We show all significant relationships mentioned in this section (as well as Sections 3.4 and 3.5) in Fig. 3, and we summarize them in Table 2. Detailed model outputs, including percentages of variance explained by each model, are shown in Table E1.

As for canopy cover, neither richness nor activity-density of the full carabid assemblage, brachypterous species or large-bodied carabids were significantly associated with that predictor. Rather, both richness ($t = 3.781$, d.f. $= 57$, $p < .001$) and activity-density ($z = 2.134$, $p = .033$) of montane specialists were significantly higher in plots with higher canopy cover. Montane specialist carabids were also significantly affected by altitude (positive effect on richness: $t = 4.684$, d.f. $= 57$, $p < .001$; positive effect on activity-density: $z = 4.361$, $p < .001$), but not by the other two topographic variables considered (northness index and standard deviation of slope).

3.4. Effects of retention forestry practices

Carabid species richness was positively associated with mean tree DBH ($t = 2.243$, d.f. $= 58$, $p = .029$), altitude ($t = 2.034$, $p = .046$) and sampling effort (trap-days, $t = 2.892$, $p = .005$). Also richness of brachypterous species increased with mean tree DBH ($t = 2.131$, d.f. $= 58$, $p = .037$). CWV of carabid body size, but not CWM, was significantly lower in plots with higher mean tree DBH ($t = -2.327$, d.f. $= 58$, $p = .023$). Mean tree DBH showed no significant association with activity-density of the full assemblage or any evaluated functional group. As for the volume of lying deadwood, this predictor was positively associated with the species richness of montane specialists ($t = 892$, d.f. $= 57$, $p = .005$), but with no other response variable.

3.5. Effects of roe deer

For both richness and activity-density models, model fit was significantly improved with the inclusion of relative abundance of roe deer as a predictor (F-test for richness: $F(1,58) = 4.869$, $p = .031$; likelihood-ratio test for activity-density: $\chi^2 = 4.343$, d.f. $= 1$, $p = .037$). Carabid species richness ($t = 2.160$, d.f. $= 58$, $p = .035$) and activity-density ($z = 2.540$, $p = .011$), as well as the activity-density of brachypterous species ($z = 2.282$, $p = .022$), were positively associated with relative abundance of roe deer (Fig. 3, third

Table 2

Summary of effects: Simplified output of GLM and LM models, with predictors listed on the right (* indicates log-transformed predictors) and response variables on top, using the same abbreviations as in Fig. 3. Cells show estimated means of slope coefficients for each significant predictor or “ns” when non-significant. Blue, red and light grey colours indicate positive, negative and non-significant effects, respectively. Note that coefficients cannot be directly compared across response variables, since model link functions may differ. Dark grey cells represent either model offsets or predictors whose effect was not modelled for a given response variable.

Predictor	Total AD	Brach. spp. AD	Large spp. AD	Montane spp. AD	Total SR	Brach. spp. SR	Montane spp. SR	CWM body size	CWV body size
Altitude	+ 0.29	+ 0.27	+ 0.31	+ 0.47	+ 0.085	ns	+ 0.21	ns	ns
*Roe deer**	+ 0.20	+ 0.19	ns	ns	+ 0.089	ns	ns	ns	ns
Canopy cover	ns	ns	ns	+ 0.21	ns	ns	+ 0.18	ns	ns
Broadleaf	+ 0.16	+ 0.17	ns		ns	ns		ns	- 3.16
Mean DBH	ns	ns	ns	ns	+ 0.083	+ 0.077	ns	ns	- 2.59
*Lying DW**	ns	ns	ns	ns	ns	ns	+ 0.12	ns	ns
Northness				ns			ns		
SD slope				ns			ns		
Trap-days	Offset	Offset	Offset	Offset	+ 0.007	ns	ns	ns	ns

row). Single-species models show that the relationship of activity-density with roe deer is primarily driven by *A. parallelepipedus* and *Carabus nemoralis* (Table D1). Conversely, roe deer abundance had no significant relationship with richness of brachypterous species, activity-density of large bodied carabids, CWM or CWV of carabid body size, and richness or activity-density of montane specialists.

3.6. *Assemblage composition*

Our 2-axis NMDS ordination (stress: 0.231, Fig. 4) is a reliable representation of carabid assemblage structure, based on a null-model test against 1000 simulated randomly-structured assemblages ($p < .001$). Assemblage composition was structured by altitude, which was the only predictor significantly associated with NMDS axes (test based on 10,000 permutations, $R^2 = 0.18, p = .0017$). Plots at higher altitudes had more similar assemblage composition among them than plots at lower altitudes, which were more dispersed in the ordination space (Fig. 4). Still, higher-altitude and lower-altitude plots overlapped in the ordination space, indicating that multiple carabid species occur across both (e.g. *P. burmeisteri*, *C. nemoralis*, *A. ovalis*). Examining the position of species in the ordination space (Fig. 5), species such as *Pterostichus melanarius*, *Pterostichus pumilio*, *Carabus sylvestris* and *Harpalus laevipes* were characteristic of higher-altitude plots, whereas species such as *Abax parallelus*, *C. intricatus*, *Carabus problematicus* and *Cychrus attenuatus* were characteristic of lower-altitude plots. One plot (CFB052) was a clear outlier in the ordination space, since it yielded two species that were not detected in any other plot - *Pterostichus diligens* and *Pterostichus nigrita* (Fig. 5) - and shared few species with the remaining plots.

4. Discussion

In this study we show that, in a Central European montane forest region, biodiversity-oriented forestry practices, as well as increased roe deer abundances, have positive outcomes for carabid activity-density and species richness. We also reveal that montane specialists respond to a different set of management-related structural variables than the full carabid assemblage. We discuss below each of our hypotheses in further detail.

4.1. *Forest specialists vs. non-forest species*

In accordance with our first hypothesis, forest specialists and brachypterous species dominated the carabid assemblage, as in other forested mountainous landscapes (de Groot and Vrezec, 2019; Jelaska and Durbešic, 2009; Kacprzyk et al., 2021). In addition, the small number of non-forest carabids did not respond to the amount of open habitat in the surrounding landscape, but instead decreased with canopy cover. This contrasts with the commonly reported effect of spillover of open-land species into fragmented forests (e.g. Niemelä et al., 2007). That may be explained by such species being themselves habitat-limited in a forest-dominated landscape (Deppe and Fischer, 2023), and rugged topography presenting an additional obstacle to dispersal into forests (Marrec et al., 2021), namely

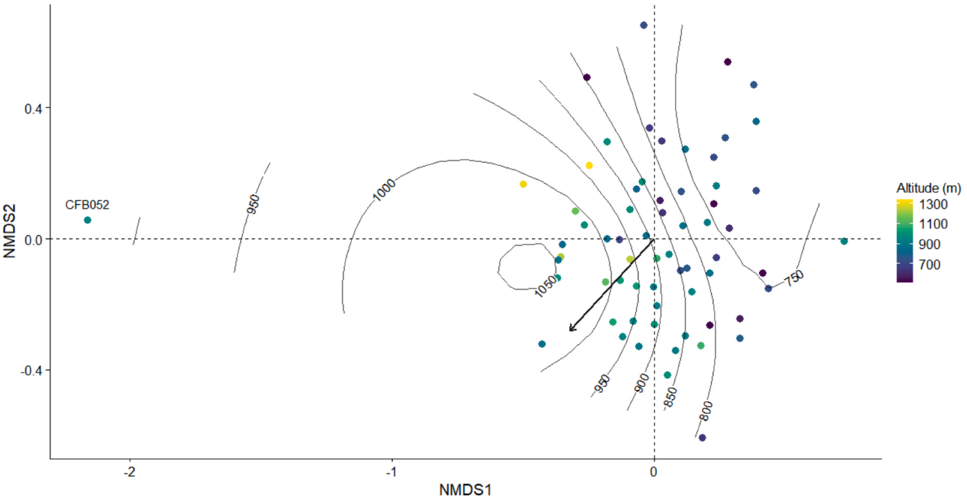

Fig. 4. NMDS ordination of sampling plots: Plots (n = 66) are coloured according to their altitude, and the black arrow represents the direction of strongest change in assemblage composition along the altitude gradient. Contour lines represent altitude (m) fitted to the ordination space with a generalized additive modelling approach, as implemented in function *ordisurf()* of package *vegan* (deviance explained = 37.2%). The labelled plot (CFB052) is an outlier in terms of assemblage composition.

from pastures and fields located in the valleys to forests located on slopes and ridges. Moreover, grasslands, which are the prevalent open habitat in the Black Forest, tend to host lower carabid abundances than crop fields (Batáry et al., 2012) and are also less conducive to spillover into wooded areas (Marrec et al., 2021). The effect of canopy cover aligns with the known effects of creating canopy gaps on non-forest carabids (e.g. Lange et al., 2014). In our area, it concerned primarily habitat generalists which easily disperse into and settle in more open forests - *Carabus violaceus* and *Pterostichus melanarius* (Thomas et al., 1998) -, but also species linked to specific open-forest habitats, which are absent in the open-land matrix - e.g. *C. micropterus*, or *P. diligens* and *P. nigrita* (Trautner, 2017), the latter two exclusively found in a plot characterized as a wooded raised bog.

4.2. Effects of close-to-nature forestry practices

As expected, the share of broadleaved trees (mostly beech) was linked to higher activity-density of both overall carabids and brachypterous carabids. However, this pattern appeared to be driven by a single mid-sized brachypterous species, *P. burmeisteri*. That explains why we did not find an effect on species richness, on the activity-density of large carabids or on the mean body size of the assemblage, whereas body size diversity was reduced. *Pterostichus burmeisteri* is known to be dominant in montane beech forests (Müller-Kroehling et al., 2014; Walentowski et al., 2014) and reproduces at higher rates in mixed beech-conifer forests than in conifer-dominated stands (Ziesche and Roth, 2007). It seemingly monopolized additional leaf litter resources in our mixed forest plots, as previously found with another species (*Pterostichus oblongopunctatus*) in leaf litter addition experiments (Koivula. et al., 1999; Magura et al., 2005). Despite that, we also found two red-listed species, *C. irregularis* and *N. rufipes*, in plots with higher-than-average broadleaf share, matching the preferences of these species for humid deciduous and thermophilous beech forests, respectively (Trautner, 2017).

Regarding canopy cover, this predictor was positively linked to richness and activity-density of the montane specialist group, a pattern that was not driven exclusively by the two dominant montane carabids (*P. burmeisteri* and *C. auronitens*). Previous studies noted that *P. burmeisteri* can withstand canopy openings (Borchard et al., 2014; Huber and Baumgarten, 2005), but conifer-associated species are less resistant to effects of harvesting (Wu et al., 2020). Moreover, canopy closure is a strong moderator of temperature extremes in montane forests (Thom et al., 2020; Vandewiele et al., 2023), which underscores its relevance for species with a narrow climatic niche, as most montane specialists. As canopy cover in our plots was generally high, the effects of slope aspect or plot topographic complexity are likely dampened, explaining why these predictors were only marginally significant for montane specialists. Although canopy openness in our plots was well-correlated with understorey cover, which could benefit carabids (Jouveau et al., 2020), we did not find a positive effect of canopy openness on the full assemblage. Possibly, this is due to increased competition with spiders, another important group of epigeal predators (Lövei and Sunderland, 1996), whose activity-density increases with canopy openness (Černecká et al., 2020, and unpublished data from our pitfall traps).

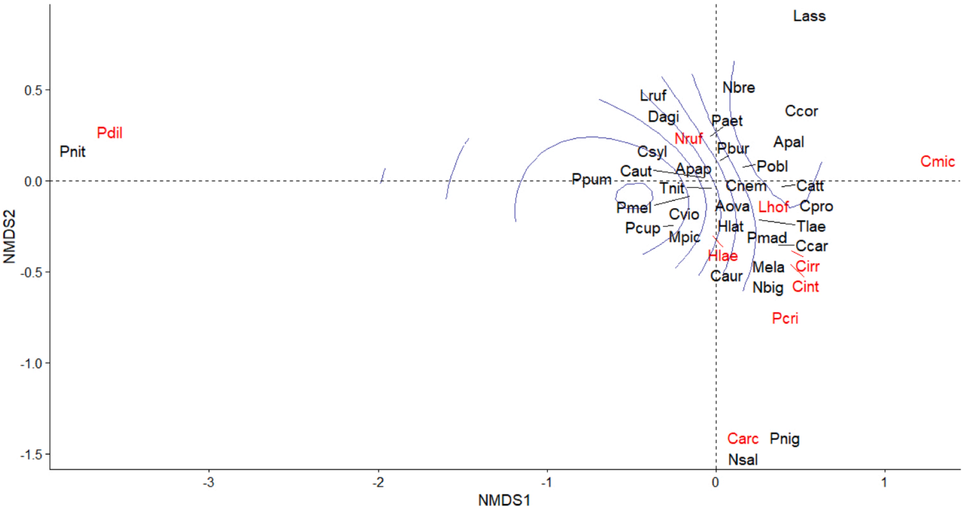

Fig. 5. NMDS ordination of carabid species: Positions of carabid species on NMDS ordination, labelled with abbreviated names, in red if red-listed regionally or nationally - **Aova:** *Abax ovalis*, **Apap:** *A. parallelepipedus*, **Apal:** *A. parallelus*, **Cmic:** *Calathus micropterus*, **Carc:** *Carabus arcensis*, **Caur:** *C. auratus*, **Caut:** *C. auronitens*, **Ccor:** *C. coriaceus*, **Cint:** *C. intricatus*, **Cirr:** *C. irregularis*, **Cnem:** *C. nemoralis*, **Cpro:** *C. problematicus*, **Csyl:** *C. sylvestris*, **Cvio:** *C. violaceus*, **Catt:** *Cychrus attenuatus*, **Ccar:** *C. caraboides*, **Dagi:** *Dromius agilis*, **Hlae:** *Harpalus laevipes*, **Hlat:** *H. latus*, **Lruf:** *Leistus rufomarginatus*, **Lhof:** *Licinus hoffmanseggii*, **Lass:** *Limodromus assimilis*, **Mela:** *Molops elatus*, **Mpic:** *M. piceus*, **Nbre:** *Nebria brevicollis*, **Nsal:** *N. salina*, **Nbig:** *Notiophilus biguttatus*, **Nruf:** *N. rufipes*, **Pcup:** *Poecilus cupreus*, **Paet:** *Pterostichus aethiops*, **Pbur:** *P. burmeisteri*, **Pcris:** *P. cristatus*, **Pdil:** *P. diligens*, **Pmad:** *P. madidus*, **Pmel:** *P. melanarius*, **Pnig:** *P. niger*, **Pnit:** *P. nigrita*, **Pobl:** *P. oblongopunctatus*, **Ppum:** *P. pumilio*, **Tlae:** *Trichotichnus laevicollis*, **Tnit:** *T. nitens*. Contour lines represent altitudes, as in Fig. 4.

4.3. Effects of retention forestry practices

Retention-related structures showed positive effects on carabid richness, but not activity-density. Central European beech forests, managed under close-to-nature practices, differ from their old-growth counterparts in their reduced availability of deadwood and senescent trees, but are otherwise structurally similar (Brunet et al., 2010). Thus, epigeal arthropods, which do not rely directly on deadwood resources, are probably not as strongly limited by resource availability in these managed forests as other groups (Kacprzyk et al., 2021), e.g. saproxylic insects (Rappa et al., 2022) or hole-nesting birds (Moning and Müller, 2009). Nevertheless, retention practices in our plots likely provide additional microhabitats and increase forest floor heterogeneity, thereby increasing species richness (Marrec et al., 2021; Niemelä et al., 1996; Seibold et al., 2016).

We found a positive effect of mean tree DBH on overall species richness and richness of brachypterous species, consistent with previous studies (e.g. Isaia et al., 2015; Marrec et al., 2021; Taboada et al., 2010). As stands age, the stable environment allows for gradual accumulation of slow-dispersing carabids in the assemblage (Marrec et al., 2021; Riley and Browne, 2011). The increase of richness with DBH was also accompanied by a decrease in body size diversity, but not mean assemblage body size, a pattern which is consistent with dispersal filtering, i.e. mid-sized species have the optimal mix of dispersal ability and size of source populations that allows them to colonize forest stands (Etienne and Olff, 2004). Additionally, we found a positive effect of lying deadwood volume on the richness of montane carabids. This supports the assertion that deadwood regulates soil moisture and temperature (Floriancic et al., 2023; Seibold et al., 2016), given the sensitivity of montane specialists to microclimatic conditions, particularly in their egg and larval stages (Müller-Kroehling et al., 2014; Sota, 1996). In fact, in the study by Seibold et al. (2016), the positive effect of deadwood addition on carabids was restricted to shady plots, which in our study were favourable to montane specialists. Deadwood may also provide a low-competition environment (Basile et al., 2023; Dittrich et al., 2014), favouring species coexistence at the plot scale. One of the montane specialists that we found exclusively in high-deadwood plots was *Licinus hoffmanseggii*, an old-growth obligate in beech forests (Walentowski et al., 2014), threatened in both Germany and in Baden-Württemberg.

4.4. Effects of roe deer abundance

Contrary to our expectations, we found positive effects of roe deer on a carabid assemblage dominated by forest specialists. Positive effects on carabids are well-reported for various ungulate species (e.g. Gobbi et al., 2018; Iida et al., 2016a; Melis et al., 2007), typically due to the response of non-forest carabids, able to take advantage of warmer and drier conditions created by understorey browsing (Iida et al., 2016a; Melis et al., 2006). However, non-forest species were rare in our plots, while activity-densities of the full assemblage and of brachypterous carabids, particularly *A. parallelepipedus* and *C. nemoralis*, increased with roe deer abundance. Whereas studies have shown contrasting effects of deer on the abundance of leaf litter invertebrates (e.g. Bressette et al., 2012; Chips et al., 2015), deer may still increase prey availability for carabids through mobilization of soil and leaf litter (Furusawa et al., 2003; Saitoh et al., 2008), through their dung, which attracts many coprophagous invertebrates (Koike et al., 2014; Persson et al., 2000), or by creating open understorey conditions that support a higher biomass of smaller invertebrates (Iida et al., 2018). *C. nemoralis*, although considered a forest specialist, was also frequently captured in meadows created for red deer in the northern Black Forest (Buse et al., 2018). Besides, it has been suggested that openings created by browsing in the understorey can improve hunting success for carabids (Gobbi et al., 2018; Melis et al., 2007). Given that roe deer abundance was linked with higher total species richness, but not richness of brachypterous carabids, a more open understorey may also be favouring colonization of stands by flight-able species, with better dispersal ability. Nevertheless, roe deer are a small cervid species and intensively managed in our study area, so that browsing impact is likely more limited than where deer reach very high densities (e.g. Iida et al., 2016b) or where larger ungulates are present. Ungulate herbivory also has less pronounced effects on carabids than on invertebrate groups that directly depend on a dense understorey (spiders and lepidopterans, in Bernes et al., 2018). This could explain why we found no relationship between roe deer abundances and montane specialists, large-bodied carabids, carabid body size or its variation, contrasting with studies that found negative effects of larger ungulates on large-bodied carabids (Iida et al., 2016b), or on beetles reliant on dark and humid conditions (Gobbi et al., 2018; Melis et al., 2007).

Large herbivores can generate trophic cascades with strong repercussions for invertebrate communities (Vandegehuchte et al., 2017), but we are unsure of the exact causal relationship between roe deer and carabids in our study. Thus, future studies should examine causal pathways by which roe deer benefit forest carabids, accounting for dung and carrion provisioning, browsing intensity and preferences, understorey composition, and availability of invertebrate prey. Nonetheless, our results suggest that, at the abundances found in an intensively-managed population, roe deer are not detrimental for sensitive carabid functional groups, and may even be beneficial for the wider forest carabid assemblage. As Central European forests undergo a conversion to mixed-species stands, deer culling is a widely used tool to promote the regeneration of silver fir (*Abies alba*) and various broadleaf species (Hothorn and Müller, 2010; Meier et al., 2017). Thus, a trade-off may be at play between intensification of deer culling to support close-to-nature forestry practices and negative effects of reduced deer abundances on carabids (among other forest taxa). This is worthy of further investigation, as beneficial effects of deer to forest ecosystems remain under-researched (Putman and Reimoser, 2011). A possible solution to minimize such trade-off lies in promoting forest structures that change deer browsing behaviour, rather than focusing on reducing deer abundances (Schwegmann et al., 2023b; Smit et al., 2012).

4.5. *Assemblage composition and the effect of altitude*

The clearest change in assemblage composition took place along the altitude gradient. This can be explained by the fact that higher-elevation plots had a richer carabid assemblage, due to both more montane specialists and addition of species such as *P. melanarius* or *H. laevipes*, while maintaining species present at lower altitudes. Still, we found species of conservation concern that were restricted to lower elevations, namely *C. intricatus*, *C. irregularis*, *C. arcensis* and *N. rufipes*, and low-elevation plots were more diverse in assemblage composition. Our findings support that carabids, as ectotherms, are strongly influenced by climatic conditions (Müller-Motzfeld, 2001). de Groot and Vrezec (2019) similarly observed a clear turnover in carabid assemblage composition with increasing altitude, stronger than for birds or hoverflies. Additionally, higher-altitude plots had higher overall activity-density, of brachypterous carabids, of large-bodied species and of montane specialists, an effect which could be attributed to two dominant species, *C. auronitens* and *P. burmeisteri*. Despite their large populations, these species have a narrow climatic niche, benefitting from colder and humid conditions at higher altitudes, and are restricted to montane areas of Central and Eastern Europe (Müller-Kroehling et al., 2014).

4.6. *Study limitations*

With this study, we investigate for the first time the joint effect of different biodiversity-oriented forestry practices on carabids in mixed montane forests. However, close-to-nature or retention forestry are likely too recent to have yet achieved the full range of structural features that they aim for (Großmann et al., 2023; Seliger et al., 2023). Since we employ an observational approach at one point in time, our results can only reflect short-term effects of these practices, along with the pre-existing structural variation in managed forests, which is in turn limited by a historical legacy of management (Munteanu et al., 2016). For example, we found no effect of retention practices on carabid activity-density, but high deadwood volumes have been associated with increased leaf litter retention (Kappes et al., 2009; Seibold et al., 2016), and Scheu et al. (2003) found that carabid biomass in 120-year old forests was more strongly related with leaf litter than in younger forests. Consequently, a complete evaluation of the outcomes of these management practices will only be achieved through long-term monitoring (e.g. Rosenvald et al., 2019). Such evaluation should also account for dark diversity (Pärtel et al., 2011), given that strict forest specialists may be locally extinct due to historical forest loss (Gossner et al., 2014; Richard et al., 2004), and since then unable to recolonize managed forests (Desender et al., 2005).

4.7. Conclusions and management recommendations

Still, we found compelling evidence for the benefits of biodiversity-oriented forestry practices for forest-dwelling carabids. In the last decades, Central European forests have become more structurally diverse, richer in deadwood and in tree species (Brändli et al., 2020; Großmann et al., 2023; Puletti et al., 2017). Considering the links we found between carabid activity-density and broadleaf share or canopy cover, close-to-nature forestry has likely contributed towards the stable or increasing forest carabid populations reported for Europe (e.g. Desender et al., 2005). Furthermore, our data support that retention practices contribute to increased carabid species richness, through increasing deadwood volumes and stand maturity. Even if current declines in forest carabid diversity are driven by factors acting at wider scales, such as climate change or pesticide use (Homburg et al., 2019; Müller-Kroehling et al., 2014), adoption of retention forestry may help counteract those effects. Besides, creating a denser network of set-aside patches (e.g. “Waldrefugien” in ForstBW, 2016) may ease settlement of dispersal-limited carabids into increasingly mature managed forests (as proposed for grasslands by Le Provost et al., 2020). The warming climate impacts disproportionately montane specialists, for which Central European countries have a high conservation responsibility (Müller-Kroehling et al., 2014; Schmidt and Trautner, 2016). Our results suggest that promoting high canopy cover, lying deadwood volumes and broadleaf share in higher-altitude forests will result in higher abundance and richness of montane specialists. Nevertheless, given the altitudinal turnover in assemblage composition, beneficial management practices must be implemented throughout the altitude gradient. Lastly, our study showed evidence of a positive effect of roe deer abundances on carabid richness and activity-density. Although this finding must be interpreted with caution, it discourages calls for intensification of deer culling for the sake of biodiversity conservation. In all, our study supports the implementation of close-to-nature and retention forestry practices in Central European forests, but points to the need of a stronger evidence base for roe deer management and how to integrate it with said practices, to work towards of a common goal of restoring biodiverse forest ecosystems.

CRediT authorship contribution statement

Storch Ilse: Supervision, Writing – review & editing. **Denter Martin:** Investigation, Writing – review & editing. **Mikusiński Grzegorz:** Supervision, Writing – review & editing. **Schwegmann Sebastian:** Conceptualization, Investigation, Writing – review & editing. **Massó-Estaje Clàudia:** Investigation, Writing – review & editing. **Cordeiro Pereira João Manuel:** Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data and R code are publicly accessible, available through Dryad.

Data for: Specialist carabids in mixed montane forests are positively associated with biodiversity-oriented forestry and abundance of roe deer (Original data) (Dryad)

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Appendix

Table A1

Species list: List of all captured carabid species, including number of specimens (No. inds.), frequency of occurrence in plots (No. plots), classifications of species into functional groups (forest specialist or not, montane specialist or not, and brachypterous or macropterous according to wing development), body length (large-bodied species in bold), and red list status for Germany (2016, Status DE) and the state of Baden-Württemberg (2005, Status BW). Displayed red list categories are: * Ungefährdet (Not Threatened), V Vorwarnliste (Near Threatened), 3 Gefährdet (Threatened). The taxonomy follows Trautner (2017).

Species	No. inds.	No. plots	Forest specialist	Montane specialist	Wing development	Body length (mm)	Status DE	Status BW
Abax ovalis	786	48	Yes	No	Brachypterous	13	*	*
Abax parallelepipedus	1659	65	Yes	No	Brachypterous	20	*	*
Abax parallelus	180	28	Yes	No	Brachypterous	15	*	*
Calathus micropterus	2	1	No (semi-open habitats)	No	Brachypterous	7.75	*	**3**
Carabus arcensis	1	1	Yes	No	Brachypterous	18	**3**	**V**
Carabus auratus	3	2	No (open habitats)	No	Brachypterous	**23.5**	*	*
Carabus auronitens	668	59	Yes	Yes	Brachypterous	**26**	*	*
Carabus coriaceus	3	2	Yes	No	Brachypterous	**37**	*	*
Carabus intricatus	20	5	Yes	No	Brachypterous	**30**	**3**	**3**
Carabus irregularis	3	3	Yes	Yes	Brachypterous	**24.5**	**3**	*
Carabus nemoralis	492	50	Yes	No	Brachypterous	**23**	*	*
Carabus problematicus	9	6	Yes	No	Brachypterous	**25**	*	*
Carabus sylvestris	24	9	Yes	Yes	Brachypterous	**24**	*	*
Carabus violaceus	39	19	No (generalist)	No	Brachypterous	**30**	*	*
Cychrus attenuatus	10	7	Yes	Yes	Brachypterous	14	*	*
Cychrus caraboides	6	5	Yes	No	Brachypterous	17	*	*
Dromius agilis	1	1	Yes	No	Macropterous	5.8	*	*
Harpalus laevipes	3	3	Yes	No	Macropterous	10.4	*	**V**
Harpalus latus	8	5	Yes	No	Macropterous	9.5	*	*
Leistus rufomarginatus	2	2	Yes	No	Macropterous	8.5	*	*
Licinus hoffmanseggii	1	1	Yes	Yes	Brachypterous	12	**3**	**3**
Limodromus assimilis	1	1	Yes	No	Macropterous	11	*	*
Molops elatus	69	22	Yes	No	Brachypterous	15	*	*
Molops piceus	223	38	Yes	No	Brachypterous	11.5	*	*
Nebria brevicollis	3	3	No (generalist)	No	Macropterous	12	*	*
Nebria salina	1	1	No (open habitats)	No	Macropterous	11	*	*
Notiophilus biguttatus	15	10	Yes	No	Macropterous	4.5	*	*
Notiophilus rufipes	3	2	Yes	No	Macropterous	4.75	*	**V**
Poecilus cupreus	1	1	No (open habitats)	No	Macropterous	11	*	*
Pterostichus aethiops	17	10	Yes	Yes	Brachypterous	13.25	*	*
Pterostichus burmeisteri	817	58	Yes	Yes	Brachypterous	13.25	*	*
Pterostichus cristatus	1	1	Yes	Yes	Brachypterous	14.5	**V**	*
Pterostichus diligens	1	1	No (moist habitats)	No	Macropterous	5.25	*	**V**
Pterostichus madidus	184	19	Yes	No	Macropterous	15.5	*	*
Pterostichus melanarius	33	6	No (generalist)	No	Macropterous	15	*	*
Pterostichus niger	1	1	No (generalist)	No	Macropterous	18	*	*
Pterostichus nigrita	11	1	No (moist habitats)	No	Macropterous	10.25	*	*
Pterostichus oblongopunctatus	216	33	Yes	No	Macropterous	10.5	*	*
Pterostichus pumilio	13	9	Yes	Yes	Brachypterous	5.3	*	*
Trichotichnus laevicollis	16	9	Yes	No	Macropterous	7.25	*	*
Trichotichnus nitens	28	18	Yes	No	Macropterous	8.25	*	*

Table B1

Red-listed species: Position of red-listed carabids along environmental gradients. For each species and each environmental variable, the value or range of values of the plots where the species was captured is indicated (where applicable, weighted mean in brackets). "No. inds." and "No. plots" indicate the number of specimens and the number of plots where specimens were captured, respectively. Superscript numbers on species names indicate the protected areas on which the species was found.

Species	No. inds.	No. plots	Altitude (m)	Northness	Slope s.d. (°)	Forest cover (100 ha, %)	Roe deer (Rel. abd.)	Broadleaf share (%)	Canopy cover (%)	Mean Tree DBH (cm)	Lying DW volume (m^3)
Calathus micropterus[1]	2	1	947	0.40	2.0	95.4	0.628	9.1	56.5	26.0	46.2
Carabus arcensis	1	1	649	0.49	3.2	89.5	0.210	47.3	67.1	39.3	26.0
Carabus intricatus[2]	22	6	516 — 903 (686.9)	0.10 — 0.89 (0.46)	3.2 — 7.8 (3.9)	81.5 — 98.2 (90.6)	0.021 — 0.210 (0.140)	6.2 — 47.3 (32.8)	67.1 — 97.9 (77.3)	22.6 — 52.6 (35.2)	6.7 — 68.0 (29.8)
Carabus irregularis	3	3	533 — 787 (644.3)	0.03 — 0.88 (0.39)	2.8 — 10.9 (6.4)	53.4 — 74.4 (62.1)	0.095 — 0.389 (0.263)	46.8 — 68.4 (56.7)	72.9 — 87.3 (79.2)	22.9 — 36.9 (28.5)	38.8 —55.9 (44.7)
Harpalus laevipes[3]	3	3	924 — 1334 (1113.3)	-0.86 — 0.97 (−0.12)	3.4 — 6.2 (4.8)	71.9 — 91.3 (83.8)	0.017 — 0.393 (0.190)	39.5 — 79.3 (59.7)	17.9 — 70.6 (52.8)	21.5 — 32.2 (27.5)	13.5 — 269.7 (126.5)
Licinus hoffmanseggi[4]	2	2	512 — 665 (588.5)	0.31 — 0.44 (0.37)	3.4 — 3.5 (3.5)	97.4 — 99.8 (98.6)	0.065 — 0.125 (0.095)	30.2 — 50.6 (40.4)	82.3 — 84.0 (83.1)	35.9 — 36.9 (36.4)	90.0 — 203.5 (146.7)
Notiophilus rufipes	3	2	632 — 682 (648.7)	-0.86 — 0.11 (−0.53)	3.8 — 5.4 (4.9)	82.6 — 92.7 (86.0)	0.112 — 0.248 (0.157)	61.3 — 67.9 (65.7)	85.9 — 86.5 (86.3)	23.9 — 31.1 (28.7)	68.0 — 72.6 (71.1)
Pterostichus cristatus[2]	1	1	787	0.88	10.9	58.5	0.095	68.4	77.4	22.9	39.4
Pterostichus diligens[5]	1	1	945	-0.49	3.0	78.5	0.243	0.8	55.6	17.8	9.6

[1] Bannwald Faulbach; FFH-Gebiet Hochschwarzwald um den Feldberg und Bernauer Hochtal (1 plot, CFB010)

[2] FFH-Gebiet Wutachschlucht (1 plot, CFB186)

[3] Naturschutzgebiet Feldberg; Bannwald Napf; FFH-Gebiet Hochschwarzwald um den Feldberg und Bernauer Hochtal (1 plot, CFB007)

[4] Bannwald Schwarzahalden; FFH-Gebiet Täler von Schwarza, Mettma, Schlücht, Steina (1 plot, CFB007)

[5] Naturschutzbiet Elzhof; Schonwald Elzhof; FFH-Gebiet Schönwalder Hochflächen (1 plot, CFB052)

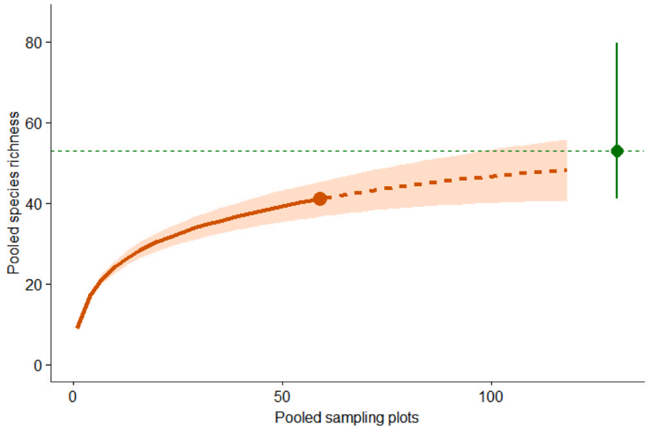

Fig. C1. Species accumulation curve: In orange, incidence-based rarefaction-extrapolation curve for species richness, with shaded 95% confidence interval. The curve is based on 59 plots for which three traps were retrieved. The green point and line represent the Chao2 estimate for asymptotic species richness and its 95% confidence interval.

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Table D1

Single-species models: Simplified output of negative binomial (log-link) single-species models for carabid activity-density, indicating the number of specimens captured (No. inds.) and explained deviance of the model. Cells show the estimated means of slope coefficients for each significant predictor (with green fill), alongside the corresponding significance level (*** α = .001, ** α = .01, * α = .05), or "ns" when non-significant. Sampling effort (trap-days) was an offset in all models. Grey cells represent predictors that were not included in a model.

Species	*Abax parallelepidus*	*Pterostichus burmeisteri*	*Abax ovalis*	*Carabus auronitens*	*Carabus nemoralis*	*Molops piceus*	*Pterostichus burmeisteri*	*Carabus auronitens*
No. inds.	1659	817	786	668	492	223	817	668
Explained deviance	6.5%	19.3%	14.2%	14.0%	18.7%	2.2%	16.2%	12.8%
Altitude	NS	**+ 0.57*** **	NS	**+ 0.40** **	NS	NS	**+ 0.56*** **	**+ 0.39** **
Log(Roe deer)	**+ 0.25* **	NS	NS	NS	**+ 0.70*** **	NS	NS	NS
Canopy cover	NS	NS	NS	NS	NS	NS	NS	NS
Broadleaf share	NS	**+ 0.28* **	NS	NS	NS	NS		
Mean tree DBH	NS	NS	NS	NS	NS	NS	NS	NS
Log(Lying deadwood volume)	NS	NS	**+ 0.46* **	NS	NS	NS	NS	NS
SD Slope							NS	NS
Northness							NS	NS

Table E1

Model outputs: Model outputs for carabid species richness (SR), activity-density (AD), community-weighted mean (CWM) and community-weighted variance (CWV) of body size, for all carabids (Total), brachypterous carabids (Brach. spp.), large-bodied carabids (Large spp.) or montane specialists (Montane spp.). The type of model, its link function and the explained variation are indicated on top. Significant effects are marked in bold.

Response variable	Total SR			Total AD			Brach. spp. SR			Brach. spp. AD		
Model (link function)	Quasipoisson GLM (log-link)			Negative Binomial GLM (log-link)			Quasipoisson GLM (log-link)			Negative Binomial GLM (log-link)		
Explained variation	25.6%			18.5%			22.1%			16.5%		
	Estimate (± SE)	$t_{d.f. = 58}$	P	Estimate (± SE)	Wald-z	P	Estimate (± SE)	$t_{d.f. = 58}$	P	Estimate (± SE)	Wald-z	P
(Intercept)	1.3942 (± 0.2627)	5.306	< .0001	-0.2499 (± 0.0705)	-3.546	.0004	1.4998 (± 0.2441)	6.144	< .0001	-0.3108 (± 0.0739)	-4.206	< .0001
Altitude	**0.0852** **(± 0.0419)**	**2.034**	**.0465**	**0.2874** **(± 0.0845)**	**3.402**	**.0007**	0.0601 (± 0.0406)	1.479	.1446	**0.2754** **(± 0.0886)**	**3.108**	**.0019**
log (Roe deer)	**0.0889** **(± 0.0411)**	**2.160**	**.0349**	**0.1974** **(± 0.0777)**	**2.540**	**.0111**	0.0753 (± 0.0401)	1.879	.0653	**0.1859** **(± 0.0814)**	**2.282**	**.0225**
Canopy cover	0.0428 (± 0.0458)	0.934	.3542	0.0188 (± 0.0898)	0.210	.8337	0.0437 (± 0.0445)	0.982	.3300	0.0276 (± 0.0941)	0.293	.7692
Broadleaf share	0.0345 (± 0.0403)	0.856	.3956	**0.1593** **(± 0.0798)**	**1.997**	**.0458**	0.0682 (± 0.0389)	1.752	.0851	**0.1725** **(± 0.0837)**	**2.062**	**.0392**
Mean tree DBH	**0.0833** **(± 0.0371)**	**2.243**	**.0287**	0.0684 (± 0.0747)	0.916	.3598	**0.0771** **(± 0.0362)**	**2.131**	**.0374**	0.0512 (± 0.0783)	0.653	.5136
log (Lying deadwood volume)	0.0517 (± 0.0392)	1.317	.1929	0.0304 (± 0.0776)	0.392	.6949	0.0567 (± 0.0380)	1.492	.1410	0.0386 (± 0.0813)	0.474	.6353
SD slope	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Northness	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Trap-days	**0.0072** **(± 0.0025)**	**2.892**	**.0054**	**Offset**			0.0043 (± 0.0023)	1.875	.0658	**Offset**		

Response variable	Large spp. AD			CWM body size			CWV body size			Montane spp. SR		
Model (link function)	Negative Binomial GLM (log-link)			Linear model			Linear model			Quasipoisson GLM (log-link)		
Explained variance	7.7%			6.3%			19.6%			42.3%		
	Estimate (± SE)	Wald-z	P	Estimate (± SE)	$t_{d.f. = 58}$	P	Estimate (± SE)	$t_{d.f. = 58}$	P	Estimate (± SE)	$t_{d.f. = 58}$	P
(Intercept)	-1.7157 (± 0.1116)	-15.377	< .0001	19.9410 (± 1.7335)	11.503	< .0001	15.6991 (± 6.9888)	2.246	.0285	0.6791 (± 0.2562)	2.650	.0104
Altitude	**0.3106** **(± 0.1339)**	**2.321**	**.0203**	-0.3113 (± 0.3119)	-0.998	.322	0.8001 (± 1.2573)	0.637	.5267	**0.2154** **(± 0.0460)**	**4.684**	**< .0001**
log (Roe deer)	0.2171 (± 0.1236)	1.757	.0789	-0.2934 (± 0.2844)	-1.032	.306	-1.7620 (± 1.1464)	-1.537	.1297	0.0403 (± 0.0449)	0.897	.3734
Canopy cover	0.03412 (± 0.1422)	0.240	.8103	-0.1294 (± 0.3360)	-0.385	.702	1.6167 (± 1.3547)	1.193	.2376	**0.1817** **(± 0.0480)**	**3.781**	**.0004**

(*continued on next page*)

Table E1 (*continued*)

Broadleaf share	0.0207 (± 0.1265)	0.163	.8703	-0.1058 (± 0.2987)	-0.354	.725	**-3.1594 (± 1.2043)**	**-2.624**	**.0111**	NA	NA	NA
Mean tree DBH	0.0909 (± 0.1183)	0.768	.4422	0.0441 (± 0.2755)	0.160	.874	**-2.5850 (± 1.1108)**	**-2.327**	**.0235**	0.036145 (± 0.0401)	0.901	.3712
log (Lying deadwood volume)	0.1041 (± 0.1229)	0.847	.3972	-0.1125 (± 0.2896)	-0.388	.699	0.7637 (± 1.1676)	0.654	.5157	**0.1194 (± 0.0413)**	**2.892**	**.0054**
SD slope	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0740 (± 0.038721)	1.913	.0608
Northness	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.0721 (± 0.0404)	1.782	.0801
Trap-days	**Offset**			-0.0218 (± 0.0166)	-1.314	.194	0.0873 (0.0670)	1.303	.1976	0.0015 (± 0.0024)	0.625	.5346

Response variable	Montane spp. AD		
Model (link function)	Negative Binomial GLM (log-link)		
Explained variance	26.4%		
	Estimate (± SE)	Wald-z	P
(Intercept)	-1.5476 (± 0.0808)	-19.153	< .0001
Altitude	**0.4728 (± 0.0988)**	**4.787**	**< .0001**
log (Roe deer)	0.0098 (± 0.0909)	0.108	.9141
Canopy cover	**0.2082 (± 0.0976)**	**2.134**	**.0329**
Broadleaf share	NA	NA	NA
Mean tree DBH	0.0978 (± 0.0850)	-0.698	.4851
log (Lying deadwood volume)	-0.0821 (± 0.0870)	1.124	.2611
Northness	0.0286 (± 0.0862)	-0.952	.3409
SD slope	0.0978 (± 0.0841)	0.341	.7334
Trap-days	**Offset**		

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