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Exploring the multi-scale drivers of predation on artificial caterpillars by insectivorous birds in a Central European montane forest region

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Abstract

Background Insectivorous birds provide a key ecosystem service as predators of folivorous insects. Changes in forest structural complexity and composition, currently underway in temperate forests, may affect the predation pressure exerted by birds on folivores, by altering the abundance of avian predators. However, studies examining this are few, as well as on how predation rates vary within forest stands. We aimed to address these gaps, by focusing on beech (*Fagus sylvatica*) trees in managed montane forests of the Black Forest region, in Central Europe. We measured abundance and diversity of birds using point counts on 135 1-ha plots in 2017–2022. To assess bird predation pressure on caterpillars, we placed 3153 artificial caterpillars on selected 24 plots for a week, in the spring of 2021, and inspected them for bird bite marks. We placed caterpillars on up to four focal tree locations in each plot, in both the canopy and the understorey of each tree. We also measured forest structure and composition both at the scale of plots and the vicinity of focal trees.

Results We found that higher shrub-layer cover and share of broadleaf trees at the plot scale were associated with higher overall abundance of foliage-gleaning insectivorous birds. However, predation rates on artificial prey appeared to be more closely related with the abundance of single species (particularly the Eurasian chaffinch, *Fringilla coelebs*), which in turn responded to other facets of forest structural complexity. Within plots, predation pressure was overall higher in the canopy than in the understorey, but this may reflect observer effects rather than true differences between vegetation layers. Predation rates also showed strong variation across trees, being higher in beech crowns with a monospecific neighbourhood, and in saplings surrounded by a mixed-species shrub layer.

Conclusions Our results suggest that specific bird species and particular facets of forest structural complexity contribute disproportionately to the predation pressure exerted by birds on caterpillars, and that fine-scale management decisions may also affect the role of birds as predators. However, further research is needed to confirm these patterns and overcome the limitations we identified.

Keywords Natural enemy, Natural control, Insect herbivory, Defoliator, Sentinel prey, Dummy caterpillar, Trophic interaction, Close-to-nature forestry, Forest management

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Background

Lepidoptera larvae (caterpillars) make up an important portion of the invertebrate biomass in temperate forests (Moran and Southwood 1982; Wagner and Hoyt 2022). Caterpillar herbivory can affect the photosynthesis, growth and vitality of trees, and thus forest structure, especially at outbreak densities (Myers 1993; Jacquet et al. 2012; Gottardini et al. 2020). These impacts can have extended consequences for ecosystem functioning (e.g. Metcalfe et al. 2014; De Grandpré et al. 2022), and affect timber yields in production forests (MacLean 2016). Caterpillars are also a relevant food source for a variety of forest organisms, and in particular for bird nestlings due to their high nutritional value (Tremblay et al. 2004; Eeva et al. 2010; Nyffeler et al. 2018). Insectivorous birds in temperate forests consume up to 137 kg ha⁻¹ year⁻¹ of invertebrates, with caterpillars making up 20–90% of nestling diets of many songbird species (Nyffeler et al. 2018, and references therein). Caterpillar densities on trees are highly variable over space and time, with free-living species typically reaching the highest densities in broadleaf trees following spring bud burst (Kamata and Igarashi 1996; Wesołowski and Rowiński 2006; Turčáni et al. 2009; Nadolski et al. 2021; Molleman et al. 2022). Although caterpillar availability is not always a limiting factor for the reproductive success and population size of forest birds (Hogstad 2004; Wesołowski and Rowiński 2014; Schöll et al. 2016), birds often exhibit functional responses to high caterpillar densities, e.g. by switching prey types to take advantage of this resource (Crawford and Jennings 1989; Connor et al. 1999; Hogstad 2004), or adapting their breeding phenology to peaks in caterpillar biomass (Perrins 1991; Van Noordwijk et al. 1995; Hegyi et al. 2013). Consequently, birds, alongside other predators (e.g. insects or small mammals), have the potential to regulate caterpillar populations (Tanhuanpää et al. 2001; Venier and Holmes 2010; Böhm et al. 2011), with cascading effects in reducing leaf damage and increasing tree vitality (Mäntylä et al. 2011; Böhm et al. 2011; Dekeukeleire et al. 2019).

European forests are increasingly managed according to a multi-functional forestry paradigm (Kraus and Krumm 2013; European Commission 2021). Conserving biodiversity within managed ecosystems may result not only in trade-offs with resource yields, but also in synergies (Grass et al. 2019; Ambarlı et al. 2021). An example of the latter is the strengthening of biological control of herbivory and crop pests by natural predators, which constitutes a regulatory ecosystem service (Begg et al. 2017). The natural enemies hypothesis (Root 1973) postulates that higher plant diversity favours the natural predators of insect herbivores, such as birds and parasitoids, thereby reducing herbivory levels.

This has been amply demonstrated within agricultural and agroforestry systems, especially in the tropics (e.g. Poch and Simonetti 2013; Maas et al. 2013, 2016). Plant diversity in grasslands (Barnes et al. 2020) and tree diversity in tropical forests (Grossman et al. 2018; Nell et al. 2018; Vázquez-González et al. 2024a) have also been shown to decrease herbivory by enhancing predation on arthropod herbivores. However, fewer tests of the natural enemies hypothesis have been carried out in temperate forests (Staab and Schuldt 2020), where, in contrast to the tropics, predation of insect herbivores by birds is more important than predation by other arthropods (Roslin et al. 2017; Zvereva et al. 2019). Existing studies in temperate forests indicate that tree species diversity per se is not an important driver of herbivory control by natural predators (Koricheva et al. 2006; Staab and Schuldt 2020; Jactel et al. 2021; Stemmelen et al. 2022; but see Vázquez-González et al. 2024a), and suggest that tree species identity, as well as forest structural complexity, play a more prominent role (Riihimäki et al. 2005; Penone et al. 2019; Staab and Schuldt 2020), but these factors have only seldom been the focus of studies.

Birds do not forage over all areas of a forest stand equally (Korňan and Adamík 2017), and predation on caterpillars likely varies at finer scales. Studies in tropical forests have shown that predation pressure on invertebrates is higher in the canopy than in the understorey (Loiselle and Farji-Brener 2002; Van Bael et al. 2003). However, Aikens et al. (2013) found the opposite pattern in a Canadian temperate forest, and Šigut et al. (2018) proposed that vertical stratification of leaf-chewing insects was consistent with higher predation in both the understorey and upper canopy. Thus, Staab and Schuldt (2020) called for more studies examining herbivory control at the canopy level. Previous research has also revealed that tree-level features can be more important than stand-level structure in top-down regulation of caterpillars by birds (Muiruri et al. 2016). Specifically, bird foraging effort can be influenced by canopy volume, canopy gaps and the identity of neighbouring trees, due to variations in availability and visibility of prey, as well as perceived predation risk (Suhonen et al. 1992, 1993; Muiruri et al. 2016). Moreover, current forest management practices in temperate Europe involve designating and retaining so-called veteran or habitat trees (Gustafsson et al. 2020; Mölder et al. 2020), but it remains unclear whether these retained trees may affect ecosystem processes such as regulation of herbivory. For instance, Wetherbee et al. (2020) found that that arthropod predation on caterpillars was higher in veteran oak trees or in their vicinity, in comparison to younger trees, and that this was accompanied by higher diversity of predatory beetles.

Close-to-nature forestry and single-tree selection systems (Bauhus et al. 2013; Bürgi 2015), alongside retention forestry more recently (Gustafsson et al. 2020), are management approaches that aim to structurally enrich production forests. By promoting features such as diversity of age classes and vegetation layers, large-diameter trees and deadwood, these practices are expected to increase forest bird diversity and abundance (Basile et al. 2021), e.g. through increased provision of nest sites for cavity-nesting birds (Wesołowski and Martin 2018) or general diversification of available habitat (Felton et al. 2021; Lindbladh et al. 2022; Komlós et al. 2024). Higher densities of foliage-gleaning birds can then result in increased predation pressure on caterpillars (e.g. Sanz 2001; Roels et al. 2018). Indeed, Bereczki et al. (2014) and Pereira et al. (2014) showed that structurally complex oak (*Quercus* spp.) forests exhibited higher density of foliage-gleaning birds, reduced leaf damage and, in the former study, higher predation on caterpillars. Still, Stemmelen et al. (2022) called for more studies that simultaneously assess the abundance of natural enemies and the biological control they exert on herbivores. No such studies have been carried out in mixed montane forests, which comprise a significant proportion of the forested area in Central Europe (Leuschner and Ellenberg 2017). In this region, monocultures of Norway spruce (*Picea abies*) are undergoing conversion towards a more natural, mixed tree species composition, with European beech (*Fagus sylvatica*) as the dominant broadleaf tree (Hilmers et al. 2020; Seliger et al. 2023). This raises the question of whether increasing structural complexity, alongside an increasing share of broadleaf trees, affects foliage-gleaning birds and the predation they exert on folivorous caterpillars.

To examine the multi-scale effects of forest structure and composition on the predation pressure exerted by birds on caterpillars, we measured the abundance of foliage-gleaning birds in a Central European montane forest region, and paired this with the well-established method of using artificial prey (Howe et al. 2009; Low et al. 2014), to compare overall predation pressure by foliage-gleaning birds on caterpillars across stands, forest strata and trees. Specifically, we investigated whether: (Q1) stands with a higher share of broadleaf trees and higher structural complexity, as promoted by close-to-nature and retention forestry practices, host higher abundances of bird species that are important predators of caterpillars; (Q2) stand-level predation rates on artificial caterpillars increase with the abundance of their avian predators; (Q3) predation rates differ between the understorey and canopy layers, and are also higher in plots with a higher broadleaf share and higher structural complexity; and (Q4) predation rates at the single-tree

level change with tree size, the presence of adjacent canopy gaps and the species composition of the tree and shrub layers in the vicinity.

Methods

Study area and plot selection

The study took place in the Black Forest, a mountainous region in southwestern Germany (Fig. 1), in the framework of the ConFoBi Research Training Group (<https://confobi.uni-freiburg.de/en>). This region is largely covered by mixed montane forests, with Norway spruce, European beech and silver fir (*Abies alba*) as dominant tree species, managed under a close-to-nature forestry paradigm (Bauhus et al. 2013), and since 2010 with retention of single trees and patches (ForstBW 2016). ConFoBi set out to evaluate the effects of retention practices on multi-taxon forest biodiversity, using the Black Forest as a model system for multi-functional forests in Central Europe (Storch et al. 2020). To achieve this, 135 quadratic 1-ha research plots (>60 years old stand age, >750 m apart) were selected in state-owned forests, representing gradients in stand structural complexity and landscape-level forest cover (Fig. 1; further details in Storch et al. 2020).

Bird surveys and plot-level predictors

To address Q1, we used data from bird surveys on all plots, alongside measures of forest composition and structural complexity. We surveyed birds using point counts, carried out yearly from 2017 to 2022 during the spring breeding season (late February–early July). We carried out all counts in the morning period (half an hour after sunrise to 12:00 CET) and replicated counts in each plot up to three times a year. A survey consisted of identifying audio-visually and counting all individuals detected within a 50 m radius from the plot centre, over four consecutive 5-min periods. For our analyses, we focused exclusively on foliage-gleaning bird species that are known to forage significantly on caterpillars in woody deciduous vegetation during the breeding season (hereafter, simply “foliage-gleaners”), based on Glutz von Blotzheim and Bauer (1985).

To represent different facets of forest structural complexity that may affect bird abundances, we measured four variables in all 135 plots (see Appendix S1 for descriptive statistics of all predictors). We extracted the standard deviation of tree diameter at breast height (DBH) and the number of large living trees (>40 cm DBH, Bereczki et al. 2014) from an inventory of all living and dead trees >7 cm DBH, carried out in 2016–2018. We calculated the canopy openness, i.e. proportion of plot area with vegetation <5 m, from a canopy height model. This model was constructed from the height differences

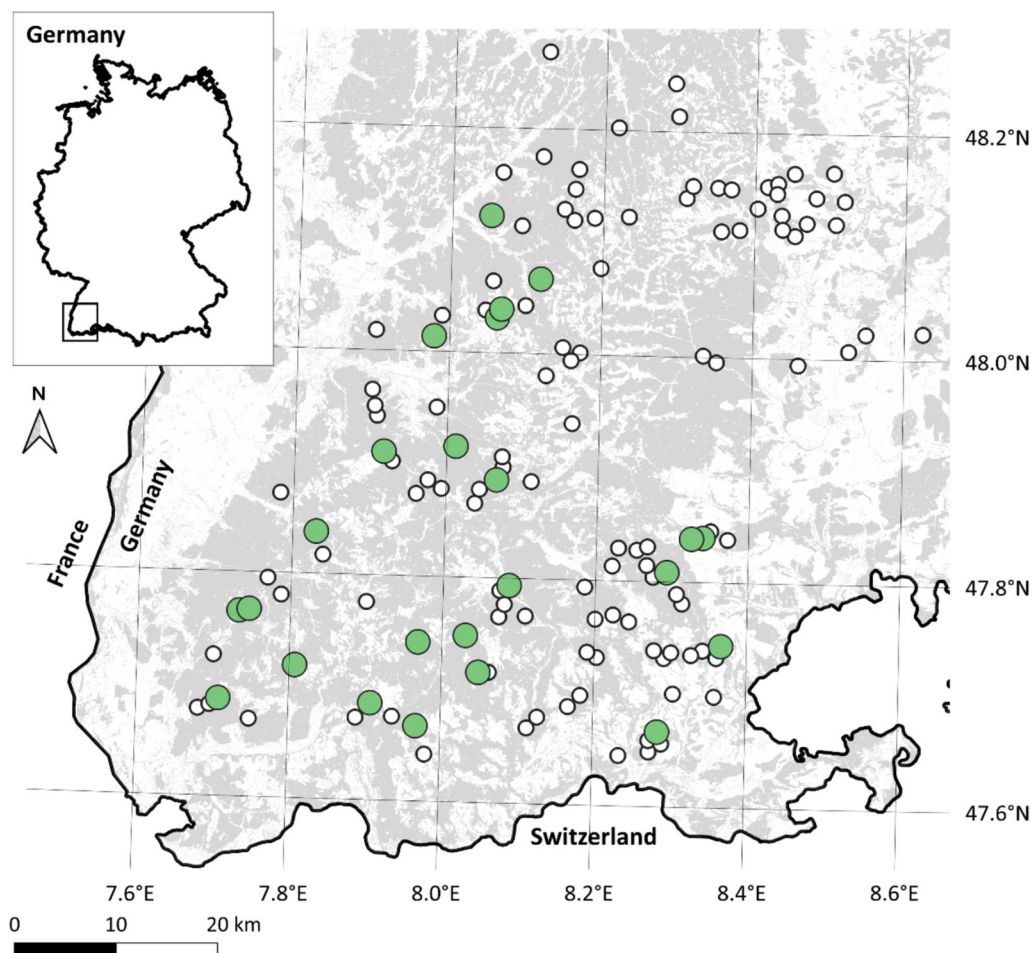


Fig. 1 Study area, with circles showing the location of all ConFoBi sampling plots, in which bird surveys took place ($n = 135$). Plots where we obtained reliable data from the artificial prey experiment ($n = 24$) are highlighted as larger, green-coloured circles. The inset shows the location of the study area within Germany

between a Digital Terrain Model with 1-m resolution (LGL 2018), and canopy surface points obtained from drone flights over all plots in the growing seasons of 2019 and 2020, using the Structure from Motion (SfM) technique (details in Frey et al. 2018). We also calculated the shrub-layer cover (1–5 m height, including tree saplings) from vegetation surveys conducted in the growing seasons of 2016–2018, averaged across a grid of 5×5 m subplots in each plot (details in Helbach et al. 2022). Among these four variables, three (standard deviation of DBH, number of large trees and shrub-layer cover) were also identified by Bereczki et al. (2014) as best distinguishing structurally heterogeneous from homogeneous stands. No silvicultural treatments were applied in any of the 135 plots since their establishment in 2016.

We described stand composition by calculating the broadleaf share in each plot, i.e. the proportion of plot basal area occupied by broadleaf trees, from

forest inventory data. Given that bird abundance may also be influenced by the proportion of mixed and broadleaf forests in the landscape surrounding each plot (Basile et al. 2021), we extracted the total cover of these two land cover types in a circular 1000 ha buffer (BM cover) around the centre of each plot, from pre-classified satellite imagery (Landsat TM5 2010, with 30-m resolution, source: Landesanstalt für Umwelt Baden-Württemberg (LUBW); for details see Mahr and Reifenstein 2013), using R package *terra* (Hijmans 2024).

Artificial prey experiment

To address our remaining questions, we exposed artificial caterpillars to predation on 40 plots in the spring of 2021. The number of bite marks on artificial prey is well-established as an indicator of how natural predation rates vary across space and time, although it cannot be used to derive absolute predation rates on natural prey (Howe et al. 2009; Low et al. 2016; Lövei and Ferrante 2017;

Zvereva et al. 2024). Besides, the identity of bite marks can be assigned with reasonable confidence to broad categories of predators, such as birds, insects or mammals (Low et al. 2014). The 40 plots were selected among all ConFoBi plots, to cover a representative gradient in structural complexity and basal area of beech (minimum of 5%). We focused this experiment on beech trees as this is the most widespread broadleaf species in our study area. Our artificial prey mimicked a variety of common, cryptically-coloured folivorous caterpillars, which are perceived as palatable by birds (as in Bereczki et al. 2014; Ambarlı et al. 2021). We built them with light-green water-repelling polymer clay (CERNIT Number One), shaped as a caterpillar with approximately 2 cm length and 0.5 cm width, through which we threaded a thin wire for attachment to branches (Fig. 2). We initially made the artificial prey using a different material (Giotto Patplume modelling clay), but this was not resistant to the rainy conditions at the start of our experiment, so that we only retrieved reliable data from 24 of our 40 plots (Fig. 1).

In each plot, we selected in situ 2–4 (average: 3.3) focal beech trees (out of an average of 60.2 trees/ha > 20 cm DBH, range 6–296 trees), ensuring that they could be safely climbed, were spaced > 30 m from each other, and varied in DBH and diversity of neighbouring trees. The number of focal trees selected in each plot also depended on the availability of mature beech trees, time necessary for tree climbers to access the canopy, and conditions such as rain or difficult access. At each focal tree location, we placed 20 caterpillars on the tree canopy (> 5 m height) and 20 on the deciduous understorey below (1–2 m height, < 15 m from focal tree), whenever possible on beech saplings. We ensured that caterpillars were separated by a minimum of 50 cm. Two teams of field workers, each with two tree climbers and one person

on the ground, conducted the experiment from 26 April to 18 June 2021, operating in parallel to ensure that all plots are visited in the narrow time window following the leafing-out of beech, when the demand of birds for nestling food can be expected to be highest. We exposed caterpillars for 6–7 days in each plot, and visited plots sequentially, with the experiment taking place at earlier dates in plots with lower elevations and southern slope aspects, where birds lay eggs earlier (e.g. Sanz 1997). After retrieving the caterpillars, we counted how many showed bird bite marks (e.g. Figure 2), identified as per Low et al. (2014), and calculated, for each canopy or understorey location, each focal tree and each plot a daily attack rate (DAR), i.e. the proportion of retrieved caterpillars with bird bite marks, divided by number of exposure days. It was not always possible to find all 20 caterpillars. For example, a bird could have bitten the artificial caterpillar such that it fell off its wire. We also cannot exclude that caterpillars may have been missing due to fallen branches, heavy rain, or the inability of the field workers to relocate them. Thus, we excluded missing caterpillars from the calculation of attack rates, as they could not be assumed to have been predated (as in Ambarlı et al. 2021).

For each focal tree, we identified the five nearest neighbouring trees (> 5 m height). Out to a 15-m radius from the focal tree, we visually estimated the vegetation cover at 1–2 m height (shrub-layer cover), assessed the shrub layer composition—whether it consisted only of beech saplings or not, as a binary categorical variable—and we estimated the percentage of open canopy surrounding the focal tree crown (see Appendix S1 for descriptive statistics of all predictors). Furthermore, we measured the focal tree DBH with a diameter tape, and used a laser range-finder (TruPulse 360° R, Laser



Fig. 2 On the left, an artificial caterpillar placed in the understorey layer, on a beech sapling; on the right, an example of a caterpillar with a visible bird bite mark

Technology Inc.) to measure the height of the focal tree, the height of the crown base, and the horizontal distance between each of six crown driplines (in four cardinal directions, minimum and maximum crown driplines) and the nearest point on the tree trunk. With these measurements, we calculated tree crown volume based on an ellipsoidal approximation (Korhonen et al. 2013; Zhu et al. 2021):

$$\begin{aligned} \text{Crown volume} &= \frac{1}{6} \times \pi \times CD^2 \times CL \\ CD(\text{Crown Diameter}) &= (\text{sum of all dripline distances}) \div 3 + DBH \\ CL(\text{Crown Length}) &= \text{tree height} - \text{crown base height} \end{aligned}$$

Statistical analyses

To assess the effects of forest structure and composition on avian natural enemies (Q1), we modelled the abundance of foliage-gleaners in each plot and year as a function of altitude, broadleaf share, BM cover and the four variables reflecting structural complexity. For this we employed a Bayesian multi-species *N*-mixture model (Yamaura et al. 2012), including only sufficiently frequent foliage-gleaner species, i.e. that occurred in > 10 plots between 2017 and 2022. This modelling approach consists of two hierarchical components—a negative binomial sub-model for abundance at each plot-year combination, including plot-level predictors, and a binomial sub-model for observed counts on each survey, conditional on the former, that accounts for imperfect detection (Royle 2004). In the latter sub-model, we modelled detection probability as a function of the time of day (minutes since sunrise), the ordinal date and the observer (as a random effect). As this is a multi-species model, the effect coefficients for a given predictor on the abundance or detectability of each bird species are drawn from a normal distribution governed by community-level mean and variance hyperparameters (Yamaura et al. 2012). We also allowed the expected abundance in each plot-year combination to vary with random intercepts of plot and year, to control for non-independence in abundance values (a “stacked” approach to multiannual data, as in Rhinehart et al. 2024).

We conducted this and all following analyses in R (R Core Team 2022). We fitted the *N*-mixture model with R package *spAbundance* (Doser et al. 2024), using weakly informative priors (detailed in Appendix S2). We scaled all predictors (mean = 0, SD = 1) to facilitate convergence, and verified that no strong correlations were present among them ($|\rho| < 0.7$). We approximated the posterior distributions of parameters using 5 chains with 25,000 iterations each, from which we discarded the first 15,000 and thinned by 25, resulting in a total of 2000 posterior

samples. We assessed convergence by checking if Gelman-Rubin statistics (\hat{R}) of all fixed effect parameters were < 1.1, and assessed goodness-of-fit by carrying out posterior predictive checks with function *ppcAbund()*. We considered the effect of a predictor on bird abundance or detectability as significant if its 90% Bayesian credible interval (BCI) did not overlap zero, i.e. > 95% of the probability distribution for the parameter

is either above or below zero (as in Frishkoff and Karp 2019; Basile et al. 2021; Roy and Gilliland 2022).

To test the effect of bird abundance on plot-level predation rates (Q2), we first extracted the median of posterior draws for each species in each plot and year as an estimate of abundance. We then selected abundance estimates from 2021, to ensure a temporal match with our artificial prey experiment. We employed a negative binomial Generalized Linear Model (GLM) to model the DAR in each plot as a function of the total abundance of foliage-gleaners. Following this, we ran a set of similar models, where total abundance was replaced by each bird species' abundance, and compared the fit of these models using a pseudo- R^2 and the Akaike Information Criterion corrected for small sample sizes (AICc). For these and all following models, we diagnosed their fit based on simulated residuals, using R package *DHARMA* (Hartig 2024), and assessed significance of effects at the $\alpha = 0.05$ threshold. For Q2 we used a negative binomial rather than Poisson model since the latter showed overdispersed residuals.

To assess whether predation rates varied between vegetation layers (Q3), we ran a Poisson Generalized Linear Mixed Model (GLMM), with R package *lme4* (Bates et al. 2015). We took as a response the DAR in each vegetation layer of each plot, and as predictors the vegetation layer (canopy or understorey), the field work teams (team A or team B, to account for observer effects), the interaction between layer and team, and all plot-level variables that were found in Q1 to have a significant effect on overall abundance of foliage-gleaners, i.e. altitude, broadleaf share and shrub-layer cover. We used a random effect of plot identity, to account for the use of plot-level predictor values and other unmeasured sources of variation in DAR across plots. We determined the significance of each fixed effect by using likelihood-ratio tests.

Lastly, to investigate the drivers of predation rates at the focal tree level (Q_4), we modelled the DAR at the canopy of each focal tree as a function of its DBH, its crown volume, the percentage of canopy openings surrounding it, the species richness of its five neighbouring trees, the number of broadleaf trees among them, and the field work team (A or B). We fitted this model as a Poisson GLMM, with plot identity as a random effect. We log-transformed crown volume, to reduce skew in its values. We then fitted a similar model for the attack rates in the understorey of each focal tree, but replacing tree DBH and crown volume with shrub-layer cover and composition as predictors. Additionally, we checked these models for focal trees that strongly affected model estimates (Cook's distance > 1, Cook and Weisberg 1982) with R package *influence.ME* (Nieuwenhuis et al. 2012). We reported the output of models refitted without these influential points, alongside the original models.

Results

Effects of forest structure and composition on avian natural enemies

We carried out 1394 bird surveys on our plots between 2017 and 2022, detecting 17 species of foliage-gleaners (Appendix S2) that potentially predate on folivorous caterpillars. Among these, we excluded 6 species due to very low frequency of occurrence. Among the remaining 11 species, the most frequently detected were the Eurasian chaffinch (*Fringilla coelebs*), Eurasian blackcap (*Sylvia atricapilla*) and common chiffchaff (*Phylloscopus collybita*). The total abundance of foliage-gleaners per plot, as estimated by the *N*-mixture model and averaged across years, ranged from 20.33 to 61.75 individuals (mean = 35.10, SD = 16.13).

The total abundance of foliage-gleaners was significantly linked with forest composition and structural complexity. In aggregate, foliage-gleaners were significantly more abundant in plots with higher broadleaf share (mean effect: 0.162; 90% BCI: 0.004–0.318; Fig. 3A) and higher shrub-layer cover (mean effect: 0.109, 90% BCI: 0.003–0.223; Fig. 3B). Additionally, higher-altitude plots had lower overall abundance of foliage-gleaners (mean effect: −0.179, 90% BCI: −0.317 to −0.045; Fig. 3C). When examining the responses of single bird species, significant effects emerged for other facets of structural complexity (for details, see Appendix S3), but these effects often varied in direction across and within species. For example, plots with higher numbers of large trees had significantly higher abundances of *F. coelebs* (mean effect: 0.089; 90% BCI: 0.030–0.148; Fig. 3D) and lower abundances of *P. collybita* (mean effect: −0.116; 90% BCI: −0.201 to −0.034), but the abundance of the

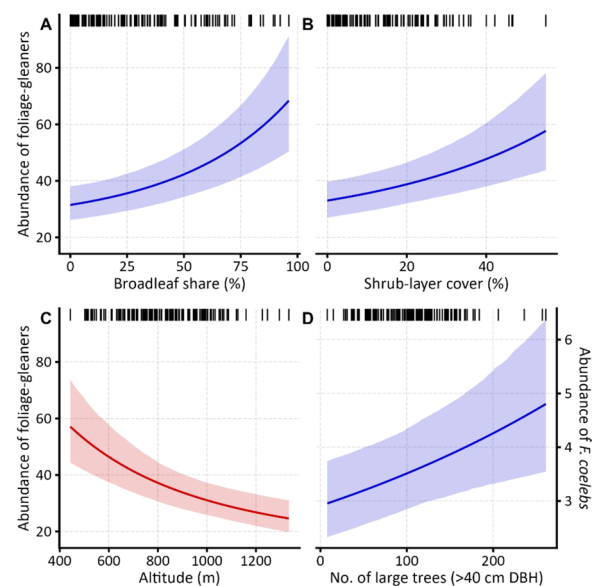


Fig. 3 Effects (predicted values and 90% BCI) of broadleaf share (A), shrub-layer cover (B) and altitude (C) on the total expected abundance (λ) of foliage-gleaners, and effect of the number of large trees on the expected abundance (λ) of Eurasian chaffinch (*Fringilla coelebs*) (D). Observed values for predictor variables are displayed on top of each plot. Blue and red colours denote positive and negative relationships, respectively

latter species increased significantly with canopy openness (mean effect: 0.142; 90% BCI: 0.071–0.209).

Effects of bird abundance on plot-level predation rates

In the 24 plots with reliable data from our artificial prey experiment, we placed 3153 caterpillars (on average 131.4 per plot) and retrieved 3002 (95.2%) after a week of exposure, of which 207 (6.9%) showed bird bite marks. Attack rates at each location in the understorey or canopy of a focal tree ranged from 0 to 6.43% per exposure day (mean = 1.03, SD = 1.28).

Plot-level DAR showed no significant relationship with overall abundance of foliage-gleaners ($z = 0.638$, $n = 24$, $p = 0.523$). When ranking the fit of this model alongside models containing the abundance of single species, the top-ranked model (both in terms of AICc and Pseudo- R^2) was that where abundance of *F. coelebs* had a positive effect on plot-level DAR (Table 1, Fig. 4). However, that effect remained non-significant ($z = 1.529$, $p = 0.126$) and that model did not clearly outperform five other models ($\Delta\text{AICc} < 2$, Table 1).

Predation rates in canopy versus understorey

Despite a significant effect of the vegetation layer on DAR (likelihood-ratio $\chi^2 = 35.5$, $d.f. = 2$, $p < 0.001$, Fig. 5), which was on average higher in the canopy (1.28%) than in the understorey layer (0.83%), predation rates also

differed between the field work teams (likelihood-ratio $\chi^2=24.3$, $d.f.=2$, $p<0.001$) and this effect interacted with that of the vegetation layer (likelihood-ratio $\chi^2=23.9$, $d.f.=2$, $p<0.001$). That is, the difference between canopy and understorey predation rates was pronounced for one team (A) but nearly absent for the other (B), as shown in Fig. 5. Plot altitude, broadleaf share and shrub-layer cover showed no significant effects on predation rates. Differences in DAR between field work teams could not be clearly explained by differences in forest structure and composition variables between the sets of plots where each team worked, or in the caterpillar retrieval rates (see boxplots and t-tests on Appendix S4).

Drivers of predation rate at the focal tree level

When modelling canopy DAR at the focal tree level, we identified a single focal tree as a highly influential point (Cook's distance > 1). When removing it, we found a negative significant effect of neighbouring tree species richness ($z=-2.645$, $n=78$, $p=0.008$, Fig. 6). In contrast, when including that point, we found an only suggestive negative effect of neighbouring tree species richness ($z=-1.815$, $n=79$, $p=0.069$). As for DAR at the understorey level, we also found one highly influential data point, and after removing it we detected a significant negative effect of a pure beech shrub layer (vs. mixed-species shrub layer, $z=-2.395$, $n=79$, $p=0.017$, Fig. 6). When including the influential focal tree, that negative effect became only suggestive ($z=-1.665$, $n=80$, $p=0.096$).

Discussion

With this study we provide an insight into the drivers of predation of folivorous caterpillars by birds, at both the stand and tree scales, in the context of a typical Central

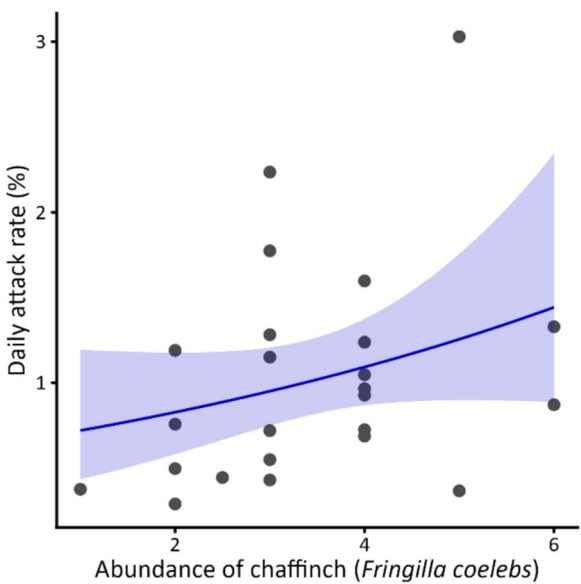


Fig. 4 Effect (predicted values and 95% confidence interval) of estimated abundance of *F. coelebs* in 2021 on plot-level bird attack rates on artificial caterpillars. Points denote observed values

European montane forest. In particular, we found that increasing the share of broadleaf trees and enhancing the structural complexity of stands through a denser shrub layer is linked with higher abundance of birds that potentially predate on folivorous caterpillars (Q1). However, predation rates on caterpillars may be more strongly driven by individual bird species, which respond to other aspects of structural complexity (e.g. higher numbers of large trees), rather than by total abundance of foliage-gleaners (Q2). Moreover, we found that predation pressure varied within plots. While it was not clear whether a higher predation rate in the canopy layer than in the

Table 1 Model comparison, ranking models for plot-level daily attack rate (DAR, $n=24$) based on AICc

Models	AICc	Δ AICc	Coefficient estimate	Pseudo- R^2 (%)
Plot-level DAR~abundance of <i>F. coelebs</i>	141.6	0.00	0.1390	8.41
Plot-level DAR~abundance of <i>P. palustris</i>	142.2	0.54	0.0388	6.29
Plot-level DAR~abundance of <i>S. atricapilla</i>	142.4	0.76	0.1402	5.43
Plot-level DAR~abundance of <i>D. major</i>	143.2	1.60	-0.0511	2.09
Plot-level DAR~total abundance of foliage-gleaners	143.4	1.75	0.0055	1.49
Plot-level DAR~abundance of <i>C. coccothraustes</i>	143.5	1.86	0.0302	1.07
Plot-level DAR~abundance of <i>P. collybita</i>	143.7	2.10	0.0101	0.07
Plot-level DAR~abundance of <i>P. major</i>	143.7	2.11	0.0071	0.03
Plot-level DAR~abundance of <i>A. caudatus</i>	143.8	2.11	0.0025	0.02
Plot-level DAR~abundance of <i>G. glandarius</i>	143.8	2.12	-0.0049	0.02
Plot-level DAR~abundance of <i>S. europaea</i>	143.8	2.12	-0.0047	0.01
Plot-level DAR~abundance of <i>C. caeruleus</i>	143.8	2.12	-0.0005	0.00

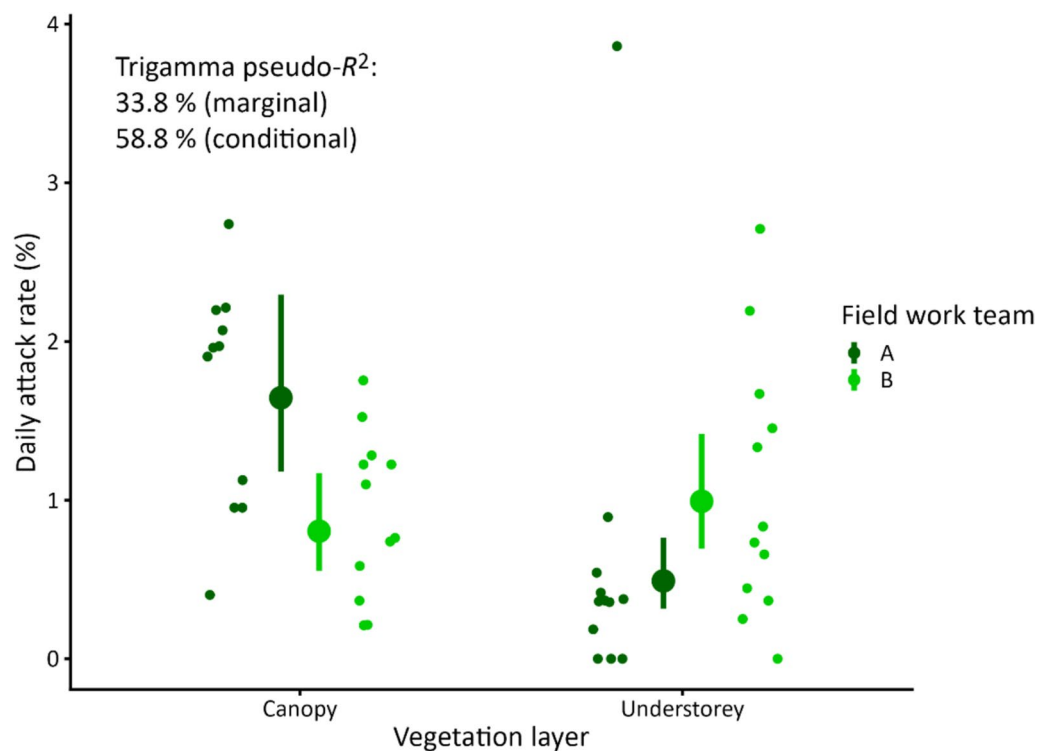


Fig. 5 Effect of vegetation layer on daily attack rates (mean and 95% confidence interval), considering differences between field work teams (A and B, represented as two shades of green). Marginal and conditional pseudo- R^2 values (as per Nakagawa et al. 2017) are displayed on top. Observed attack rates are depicted as points next to the modelled means and confidence intervals

understorey actually resulted from an observer effect (Q3), predation rates also varied across focal trees, partly as a function of the species composition of the tree and shrub layers in the vicinity (Q4). Below we discuss these results, limitations of our findings and their implications in further detail.

Bird predation on caterpillars at the plot scale

One of the facets of forest structural complexity, namely shrub-layer cover, correlated positively with the overall abundance of foliage-gleaning birds, in line with other studies in temperate forests (Pereira et al. 2014; Bereczki et al. 2014). However, contrary to Bereczki et al. (2014) in a lowland oak forest, we did not find a general response of foliage-gleaners to the number of large trees in our plots. In our study region, although the average number of large living trees (> 40 cm DBH) is similar to that of old-growth forests (100–150 trees/ha, Nilsson et al. 2002), a majority among them are Norway spruce. Moreover, the number of very large trees (> 70 cm DBH) is markedly lower than in old-growth forests (4.9 vs. 30 trees/ha, Nilsson et al. 2002), due to a long management history. Microhabitats associated with old and decaying living trees, such as rot-holes and crown deadwood, are especially rare in spruce (Courbaud et al. 2022; Spinu et al. 2022).

Cavity-nesters, which use such microhabitats for nesting, made up half of the foliage-gleaner species analysed. Since these microhabitats are overall scarce in our study area, their availability likely remains below thresholds at which cavity-nesting birds start exhibiting a positive response (Moning and Müller 2009; Kebrle et al. 2021, 2023). Instead, foliage-gleaners responded positively to a developed shrub layer, which may provide safer nesting habitats for bird species nesting at the ground or in low vegetation (Pereira et al. 2014; Lewandowski et al. 2021). Moreover, the species we targeted, which all forage on broadleaf vegetation, responded numerically to the availability of this foraging substrate, expressed as the broadleaf share of stands. Therefore, our results indicate that, even in relatively young, even-aged managed forests with few large trees, increasing structural complexity by promoting a denser shrub layer, paired with admixing broadleaf trees, can promote higher densities of predators of caterpillars.

Against our expectations, predation pressure on caterpillars did not correlate with total abundance of foliage-gleaners. Although our small sample size for Q2 ($n = 24$), and thus statistical power, was low, it appeared that the abundance of individual bird species, such as *F. coelebs*, was more closely related with predation

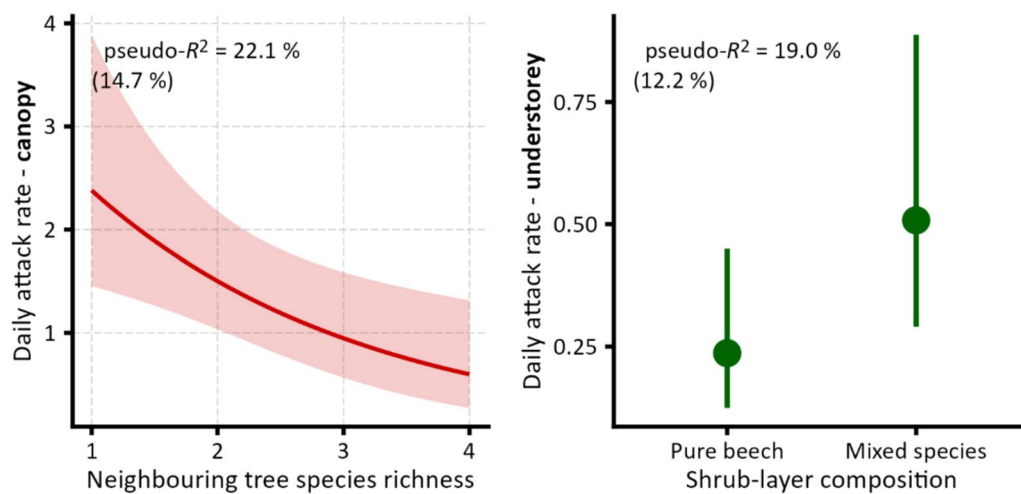


Fig. 6 Effects (means and 95% confidence intervals) of tree-level variables on attack rates on artificial caterpillars in the canopy (left) and understorey (right), after removing highly influential focal trees (a single data point in each case). Trigamma marginal pseudo- R^2 values (as per Nakagawa et al. 2017) for each model are displayed on the top left corner of each plot (values in brackets are those of the alternative model including highly influential data points)

pressure. *F. coelebs* is one of the most ubiquitous species in our plots, as in most Central European forest types (Mikusiński et al. 2018; Payevsky 2020), and is known to prefer beech trees for foraging (Adamík et al. 2003). It has been often reported that the abundance of common and generalist species plays a larger role in the provision of specific ecosystem services than species richness or diversity (Winfree et al. 2015; Houadria and Menzel 2017; Gaston et al. 2018; Rehling et al. 2023). In tropical agroforests, Philpott et al. (2009) and Maas et al. (2015) noted that a single bird species and functional group had an outsized influence in driving arthropod removal. Vázquez-González et al. (2024b) have also shown, in a tropical forest experiment, that overall abundance of birds and their functional groups were decoupled from variations in attack rates on caterpillars. An alternative explanation for a stronger relationship of individual species with predation rates may lie on the species' breeding phenology. It is possible that the period during which we exposed our artificial caterpillars overlapped more closely with the nestling stage of certain species that year, when the need for caterpillar prey is highest, than for other, earlier-breeding foliage-gleaners, such as the great tit (*Parus major*) or the Eurasian nuthatch (*Sitta europaea*) (Glutz von Blotzheim and Bauer 1985). Hence, future studies would profit from monitoring the breeding phenology of species alongside artificial prey experiments. Individual species also deviated from the whole of foliage-gleaners in how they responded to structural complexity, as seen with the response of *F. coelebs* to the number of large trees. This reinforces that relationships between forest structure and ecosystem

function vary depending on which dimension of forest structure is considered (Felipe-Lucia et al. 2018). If the abundance of one or few species rather than the abundance or diversity of a whole functional group drive predation on insect herbivores, this has implications for the choice of which aspect of structural complexity should be promoted to strengthen this regulatory ecosystem service.

To more clearly determine the drivers of predation on caterpillars, future studies with artificial prey would profit from assigning predation to specific bird species. This cannot reliably be done by examining bite marks (Low et al. 2014), but approaches exist that enable identification of predators, such as camera-trapping (Muiruri et al. 2016; Akcali et al. 2019) or metabarcoding of eDNA from bite marks (Rößler et al. 2018, 2020). The latter method has not yet been used to identify avian predators of artificial caterpillars, but holds promise for this, having been recently employed to successfully identify predators of clay models of salamanders (Rößler et al. 2020; Pierson et al. 2022; Shaw et al. 2023) or fruits (Monge et al. 2020). It is also worth considering that the characteristics and position of artificial prey may be representative of only a subset of potential prey, and therefore favour certain predator types. Predatory insects and birds partition their foraging niches based on the size of caterpillar prey (Rommel et al. 2011; Singer et al. 2017), and likewise different species of foliage-gleaners exhibit niche partitioning based on prey sizes and foraging techniques (Robinson and Holmes 1982; Villard and Foppen 2018). In particular, the large size of our artificial caterpillars and their placement on branches may have

made them prone to attacks by *F. coelebs*, a relatively large species that forages by methodically walking and hopping on branches (Glutz von Blotzheim and Bauer 1985). This stands in contrast with the blue tit (*Cyanistes caeruleus*), for instance, which feeds by hanging from small twigs, being well-adapted to capture shelter-building and leaf-mining insects (Robinson and Holmes 1982; Connor et al. 1999). Thus, we propose that future studies place artificial caterpillars of different sizes and in different locations (e.g. trunk, branches, upper and lower leaf surfaces), to obtain a broader picture of tritrophic relationships between birds, insect herbivores and trees. Additionally, it is plausible that differences in cognitive abilities among bird species influence predation on artificial prey, as some species may more readily recognize unpalatable prey and avoid them, while others go on to bite multiple artificial caterpillars. This hypothesis has not been tested so far, but it is known that, for instance, *P. major* is a species with well-developed cognitive abilities (e.g. Estók et al. 2009; Cole et al. 2011; Brodin and Urhan 2014).

Bird predation on caterpillars across vertical strata

Although we found that bird attack rates on artificial caterpillars were on average higher on beech canopies than on the understorey, this was largely confounded by an observer effect. Thus, our findings may not reflect true differences in predation rates between vegetation layers, but rather differences in how the experiment was conducted by different field work teams, or between the sets of plots visited by each team. For instance, it is possible that teams differed in their interpretation of bird bite marks, or that tree climbers of different teams systematically differed in how they placed the caterpillars throughout the tree crown. The use of multiple observers is often unavoidable in artificial prey studies, but lends itself to observer biases (Rößler et al. 2018; Valdés-Correcher et al. 2022). In future studies, we recommend that these issues are addressed, for example by randomizing the composition of tree climber teams (if composed of more than one person), conducting trial runs where all field workers jointly check bite marks and establish clear criteria to identify them, or using a single separate (“neutral”) observer to identify all bite marks (Rößler et al. 2018). Differences in predation rates between the two field work teams could also not be fully explained by differences in the retrieval rate of caterpillars, or by the differences in plot-level predictors between the sets of plots visited by each team. An alternative explanation is that other environmental variables, unaccounted for in our study (e.g. local sun exposure, microclimate, and weather conditions during the experiment), differed between the plots visited by

each team, and affected predation pressure, particularly in the canopy.

Nevertheless, a pattern of higher predation rates in the canopy than in the understorey would be congruent with findings from heavily-shaded tropical forests (Loiselle and Farji-Brener 2002; Van Bael et al. 2003). Such studies indicate that higher plant productivity at the sun-exposed canopy compared to the understorey drives a trophic cascade of higher herbivore biomass, accompanied by higher predation pressure on herbivores. This is corroborated by multiple studies comparing situations of higher and lower plant productivity (e.g. gaps vs. shaded understorey, or fertilized vs. unfertilized plots), revealing a pattern of strengthened top-down pressures on herbivores wherever primary production is not otherwise limited by bottom-up factors, e.g. light, soil nutrients or precipitation (Forkner and Hunter 2000; Van Bael and Brawn 2005; Richards and Coley 2007; Bridgeland et al. 2010; Garibaldi et al. 2010). In our temperate forest plots, canopy closure was generally high (73% on average), as is typical of close-to-nature forestry systems (Gustafsson et al. 2020), strongly limiting light availability in the understorey, and thus its productivity (Axmanová et al. 2011; Landuyt et al. 2019; Dormann et al. 2020). In other temperate forests, it has been shown that activity of birds (Karpińska et al. 2023) and other natural enemies (e.g. predatory wasps and parasitoids, Sobek et al. 2009b) are concentrated in the canopy. Therefore, vertical patterns of predation pressure in closed-canopy Central European forests can be expected to parallel those of dense tropical forests. This has potential repercussions for future beech regeneration, if it translates to more leaf damage on beech saplings compared to the canopy (as in Stiegel et al. 2017), but the opposite pattern has also been reported (Gossner et al. 2014). Hence, future research should clarify the effect of bird predation on the vitality of beech trees and saplings, by measuring the extent of leaf damage alongside predation rates.

Bird predation on caterpillars across focal trees

Predation rates also varied strongly across focal trees, be it in the canopy or in the understorey, and appeared to be influenced by the species composition of surrounding trees and saplings, with no effect of canopy gaps or tree and crown size. In the canopy layer, our analysis suggests that predation was enhanced in the presence of monospecific neighbours (in most cases beech). In contrast to our findings, Muiruri et al. (2016) found increased predation rates with increased neighbouring tree diversity in a boreal forest, and attributed this to a more open structure in diverse stands, enhancing visibility of prey to birds (Groner and Ayal 2001; Anttonen et al. 2023). However, in Central Europe,

beech-dominated stands with a history of management typically display a more open, hall-like structure (Leuschner and Ellenberg 2017), compared to mixed stands with conifers (Pretzsch et al. 2016; Juchheim et al. 2020), which may facilitate detection of prey by birds and reduce the costs of foraging. In addition, beech trees may be subjected to more intense herbivory in the presence of conspecifics, due to a resource concentration effect (Root 1973; Guyot et al. 2016; Dekeukeleire et al. 2019; Jactel et al. 2021), which in turn can attract higher predation pressure. To clarify whether an increased share of beech in montane forests leads to resource concentration effects on herbivory, and to what degree bird predation compensates for those effects, future studies should compare leaf damage and the effect of bird removal (e.g. with exclosures) between trees surrounded by conspecifics and heterospecifics.

As for the understorey, our results suggest the opposite pattern—that predation rates are lower in a beech-dominated shrub layer. This is consistent with a previous study that found higher impact of leaf-chewing herbivores on beech stands with a species-poor understorey (Gossner et al. 2014). Possible explanations for this pattern are that birds are attracted by the presence of other deciduous species in the shrub layer, which host higher amounts of insect prey, such as sycamore maple (*Acer pseudoplatanus*) (Korňan 2000; Sobek et al. 2009a; Korňan and Adamík 2017), with a spill-over effect on adjacent beech saplings. Conifer saplings may also facilitate foraging in neighbouring deciduous vegetation, by providing close shelter from predators in their dense foliage. It is known that the selection of foraging microhabitats by birds can be influenced by predation risk and the proximity to dense vegetation cover (e.g. Lima 1990; Suhonen 1993; Camacho 2014).

A key caveat to our study is that we did not measure the background abundance of natural prey, and thus we could not assess its effects on predation rates. While we believe that reporting the results of our analyses without two highly influential focal trees revealed meaningful ecological patterns for the remaining trees, it remains unclear what characteristic makes those trees stand out from the overall patterns. Our tree-level predictors also explained only a small portion of the variability in predation rates. Such high unexplained variability may be related to patterns in the availability of natural prey, which is known to be highly variable over space (at both fine-grained and broader scales) and time (Nadolski et al. 2021; Molleman et al. 2022). Additionally, we sequenced our plot visits to follow as closely as we could the local phenology of beech, but we could not ensure that the artificial prey experiment matched with the peak in caterpillar abundance following bud burst. Previous

studies that measured both caterpillar abundances and bird predation rates on artificial prey often reported a positive relationship between the two, revealing a functional response of birds to natural prey availability (e.g. Bereczki et al. 2014; Molleman et al. 2016). Still, it is conceivable that high caterpillar availabilities may lead to birds avoiding artificial prey in favour of easily-accessible natural prey, making bite marks an unreliable indicator of predation pressure. Hence, to better contextualize and detect sources of variation in predation rates derived from artificial prey, we strongly recommend that future studies assess caterpillar abundance or biomass in parallel, e.g. through frass collectors, visual counting, branch beating or branch clipping (Zandt 1994; Hurlbert et al. 2019).

In part, unexplained variation in predation rates may also relate to the territoriality and breeding phenology of birds, producing a clumped spatial and temporal distribution of foraging effort. This is likely more pronounced if predation is driven by one or few bird species. Combining artificial prey experiments with territory mapping could help to match the scales at which predation pressure and bird activity are measured, overcoming this limitation. Furthermore, our artificial prey experiment covered only a small number of plots, due to issues with the material we initially used for artificial prey, weather conditions and the time and cost involved in placing caterpillars in the canopy using tree climbers. This, combined with the high variability in predation rates, made it difficult to identify with certainty the drivers of predation pressure at the plot level. Additionally, the spring of 2021 showed higher precipitation and lower temperature than average for our study area. These conditions lead to low caterpillar biomass and may alter the foraging behaviour of birds (Schöll et al. 2016), thus reducing the generalizability of our results. Researchers should ensure that future studies are carried out across multiple years (e.g. Vázquez-González et al. 2024b), thereby accounting for interannual variations in predator abundance and phenology, predation intensity, and weather conditions. For canopy studies, which frequently suffer from insufficient replication due to difficulty in accessing the canopy, new approaches are continuously being developed (Cannon et al. 2021). For instance, quicker and more cost-effective access to canopy could be achieved by throwing a line across the tree canopy and hoisting branches with artificial prey to the appropriate height.

Conclusions

Our findings lend only partial support to the natural enemies hypothesis within mixed montane forests. On one hand, they indicate that higher shares of broadleaf

trees and a more developed shrub layer are linked with higher abundances of foliage-gleaners, but this does not necessarily correspond with higher predation pressure by birds on insect herbivores. On the other hand, other aspects of structural complexity, including those favoured by retention forestry practices such as large-sized trees, can support higher abundances of individual bird species, which in turn may have a more important role in driving predation on caterpillars. Despite limitations in sample size and presence of observer effects, we were also able to detect variations in predation rates across individual trees and vegetation strata, which have only seldom been investigated in temperate forests (Muiruri et al. 2016; Staab and Schuldt 2020). Namely, our findings suggest that beech crowns surrounded by conspecifics (vs. higher neighbouring tree diversity) and saplings embedded in a mixed-species shrub-layer (vs. a pure beech shrub layer) witness stronger top-down pressures by birds on herbivores. Although more research is needed to confirm these relationships, clarify their mechanisms and consider additional sources of variability (namely ambient prey abundances), studies with small sample sizes such as ours are valuable to help formulate hypotheses and lay the groundwork for future studies (Bissonette 1999). Knowledge on fine-scale variations in top-down regulation of insect herbivores by birds is especially relevant as it can inform forest management actions at the scale of individual trees, now common in Central Europe (Gustafsson et al. 2020). Even low defoliation rates can have outsized effects on tree growth (Jacquet et al. 2012), and insect herbivory in beech is often overlooked, but nonetheless significant (Gossner et al. 2014). The effect of herbivory may also interact with other factors such as drought, which increasingly affects beech trees in Central Europe (Leuschner 2020). In summary, our study suggests that current management practices can contribute to increases predation pressure by birds on herbivores, but more attention is needed for the role of individual bird species in driving this process, and for variations in predation at finer scales.

Abbreviations

AICc	Akaike Information Criterion for small sample sizes
BCI	Bayesian credible interval
BM cover	Broadleaf and mixed forest cover
CET	Central European Time
ConFoBi	Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe
DAR	Daily attack rate
DBH	Diameter at breast height
GLM	Generalized Linear Model
GLMM	Generalized Linear Mixed Model
SD	Standard deviation

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-025-00638-5>.

Additional file 1

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Author contributions

JMCP and TS conceptualized the study; JMCP, TS, MB and GM collected the field data; JMCP carried out statistical analyses, with assistance from TS; IS secured funding for this study (through ConFoBi) and supervised the doctoral dissertation of JMCP, in which this study is included; GM supervised the doctoral dissertations of JMCP, TS and MB; JMCP wrote the first manuscript draft, and all authors reviewed and contributed critically to subsequent drafts.

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Data availability

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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