Global Ecology and Conservation 67 (2026) e04153

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Original Research Article

Humidity and gap history drive predation pressure on large carabids in a managed temperate forest

Jana Růžičková [a,b,*], Bence Kovács [c], Csaba Németh [c], Péter Ódor [c,d], Zoltán Elek [e,f]

[a] *HUN-REN-ELTE-MTM Integrative Ecology Research Group, Biological Institute, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, Budapest 1117, Hungary*
[b] *Department of Systematic Zoology and Ecology, Biological Institute, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, Budapest 1117, Hungary*
[c] *Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány út 2-4, Vácrátót 2163, Hungary*
[d] *Institute of Environmental Protection and Nature Conservation, Forestry Faculty, University of Sopron, Bajcsy-Zsilinszky utca 4, Sopron 9400, Hungary*
[e] *Department of Biostatistics, University of Veterinary Medicine Budapest, István utca 2, Budapest 1078, Hungary*
[f] *HUN-REN-DE Anthropocene Ecology Research Group, University of Debrecen, Egyetem tér 1, Debrecen 4032, Hungary*

ARTICLE INFO

Keywords:
Continuous cover forestry
Foraging behavior
Gap-cutting
Ground beetles
Microclimate
Sentinel method

ABSTRACT

Predation is one of the key ecological processes that shape animal communities and ecosystem functioning. However, its strength and variability across structurally heterogeneous forest habitats remain poorly understood, especially in ground-dwelling insects. Using 3D-printed decoys mimicking the large carabid beetle *Carabus coriaceus*, we investigated the predation pressure in a long-term monitored research system of managed oak-hornbeam forests in Hungary. We compared small-scale canopy gaps that differed in age and management history, either established in closed-canopy forest or stands after preparation cuts, and their unmanaged control plots. In addition, we tested whether the time of day and local microclimatic conditions (relative humidity, air temperature, and soil moisture) affected attack rates. Out of 2000 observations, 4.8% showed signs of predation in the form of turns, relocations, or broken parts of decoys. Regression tree analysis revealed that relative humidity was the strongest predictor of predation pressure. During very humid conditions, attack rates increased, particularly for gaps in preparation cuts. Soil moisture provided an additional effect in the other gap types and controls, while temperature and time of day did not affect predation events. Our results suggest that high humidity conditions may enhance the foraging activity of small-bodied predators, possibly due to relaxed physiological constraints or reduced availability of alternative prey. These findings underline the importance of considering management history, surrounding forest matrix, and fine-scale abiotic variation when assessing predator–prey interactions and the ecological consequences of silvicultural practices.

1. Introduction

By regulating prey abundance and mediating species interactions, predation contributes significantly to the organization of

---

* Corresponding author at: HUN-REN-ELTE-MTM Integrative Ecology Research Group, Biological Institute, ELTE Eötvös Loránd University, Pázmány Péter sétány 1/C, Budapest 1117, Hungary.

E-mail address: jr.tracey@seznam.cz (J. Růžičková).

https://doi.org/10.1016/j.gecco.2026.e04153
Received 21 October 2025; Received in revised form 9 January 2026; Accepted 5 March 2026

communities and ecosystem functioning (Hairston et al., 1960). Predators not only reduce prey populations directly but also indirectly affect prey behavior and spatial distribution through the risk of predation (Sih et al., 1985; Lima and Dill, 1990). These trait-mediated effects can cascade across trophic levels, affecting key ecosystem functions such as herbivory, decomposition, and pest control (Schmitz et al., 2004). However, the strength and consequences of predation can vary considerably across ecosystems, depending on habitat complexity and species interactions within food webs (Tablado et al., 2014; Klecka and Boukal, 2014; Chang and Todd, 2023). Understanding how these dynamics in foraging activity manifest in different environments, especially those modified by land-use, is essential for predicting the broader ecological impacts of habitat alteration.

Forests are particularly interesting in this context because their vertically and horizontally complex structure supports the development of diverse microhabitats that strongly influence predator–prey dynamics (Roslin et al., 2017). Dense forest vegetation can decrease predation risk because it provides refuges for prey and obstacles for foraging predators (Chalfound and Martin, 2009; Šipoš and Kindlmann, 2013; Goßmann et al., 2023). On the other hand, such habitats may benefit ambush predators by providing cover and thereby increasing prey predation (Langellotto and Denno, 2004). In addition to structural complexity, forest microclimate plays a crucial role in shaping these interactions. Canopy openness and the arrangement of vertical layers can alter local soil and air temperature, air humidity, and soil moisture, thereby modifying the below-canopy microclimate within forest stands (Chen et al., 1999; Kovács et al., 2017; De Frenne et al., 2021; Horváth et al., 2023). Temperature changes can alter the behavior and metabolic demands of predators and prey independently, thereby affecting predation (Dell et al., 2011, 2014; Vucic-Pestic et al., 2011). This is particularly important for small-bodied animals, which are more vulnerable to thermal stress due to their high body surface area relative to volume (Vickery and Bider, 1981; Wróbel and Bogdziewicz, 2015). Similarly, air humidity and soil moisture can affect microhabitat use, as smaller prey species may aggregate in wetter patches to avoid desiccation but may face increased exposure to predators as a result (Verdeny-Vilalta and Moya-Laraño, 2014).

In temperate deciduous forests, predation studies have predominantly focused on herbivorous insects, often using plasticine caterpillars as artificial prey to quantify attack rates (Lövei and Ferrante, 2017; Roslin et al., 2017; Ferrante and Lövei, 2025). Several factors have been shown to affect predation pressure in these systems, including forest fragmentation (Maguire et al., 2015), urbanization (Ferrante et al., 2014), topography (Nakatsuji et al., 2024), and forest edges (Drozdová et al., 2013). Tree species (Nakatsuji et al., 2024), canopy height (Aikens et al., 2013), canopy openness (Šipoš et al., 2011), and the type of tree-related microhabitats (Šipoš et al., 2013; Gossner et al., 2020) have also been linked to variation in predation pressure on herbivorous insects. While these studies emphasize forest structure as a key driver of predator–prey dynamics on herbivorous insects, much less is known about how natural disturbances and forest management shape predation risk (Goßmann et al., 2023).

The majority of published research also focuses on a narrow group of predators, primarily birds and ants, which are abundant and highly active in temperate forests, and on a single prey type, typically caterpillars. This bias likely reflects the long-standing focus on the gypsy moth, one of the most intensively monitored forest pests after bark beetles (Liebhold, 2012). As a result, the role of other insect groups as prey remains relatively poorly understood (Goßmann et al., 2023). Ground beetles (Coleoptera: Carabidae), for example, are key components of temperate forest ecosystems (Lövei and Sunderland, 1996; Rainio and Niemelä, 2003). Although they are well studied as predators and contributors to pest control (Kotze et al., 2011; Schowalter et al., 2018), their role as prey is often overlooked, despite being targeted by a wide range of vertebrate predators (e.g., Graclik and Wasielewski, 2012; Fukuda and Konuma, 2019). As mesopredators, carabids occupy an intermediate trophic position, and changes in their predation risk may have cascading effects both upward to vertebrate predators and downward to lower trophic levels. Evidence from forested islands and vertebrate exclusions in woodlands shows that predation by small-bodied mammals, such as rodents, can substantially suppress carabid populations, with rapid recovery following predator removal or exclusion (Marris, 2000; Watts et al., 2020; Vergara et al., 2021). Consequently, variation in predation pressure can influence carabid abundance and alter their regulatory role within insect communities. Forest management practices that modify habitat structure and microclimate may therefore affect ecosystem functioning not only directly, but also indirectly, by increasing the exposure and vulnerability of carabids to predation (Růžičková and Elek, 2021).

In this study, we used 3D-printed decoys mimicking the largest local carabid beetle, *Carabus coriaceus* L., 1758, to investigate predation pressure across artificial canopy gaps in a managed temperate forest in Hungary. These gaps were created as part of continuous cover forestry, a silvicultural system that seeks to emulate natural disturbance regimes in temperate deciduous forests through low-intensity interventions, including small-scale gap cutting (single-tree and group selection) or aggregated upper canopy thinning (Pommerening and Murphy, 2004; Raymond et al., 2009). Such management results in uneven-aged, vertically multi-layered, and horizontally heterogeneous stands (Nagel et al., 2014; Aszalós et al., 2022). In contrast, rotation forestry systems, such as clear-cutting or regular shelterwood systems, substantially reduce structural heterogeneity and create even-aged stands with simplified canopy structure (Matthews, 1991).

We selected artificial canopy gaps created by group selection, which is the primary tool of continuous cover forestry in this region. These gaps modify forest structure and microclimate by locally increasing canopy openness, altering vertical layering, and promoting understory development, while on the stand scale, they maintain the abiotic conditions of a closed forest matrix (Kovács et al., 2020; Horváth et al., 2023). By mimicking the natural disturbance dynamics of Central European temperate forests (i.e., gap dynamics), they are expected to support ecosystem services and biodiversity more effectively than large-scale rotation forestry practices (Bengtsson et al., 2000; Pommerening and Murphy, 2004; Mason et al., 2022). We examined artificial gaps of different ages (new vs. 10 years old) and formation histories, created either in closed-canopy forests or more open forest matrix formed by upper canopy thinning (preparation cutting). Our previous research showed that gap shape (circular vs. elongated) and size ($\sim$150 m^2 vs. $\sim$300 m^2) did not significantly affect predation pressure, likely because vertebrate predators of large carabids did not perceive these small-scale openings as distinct habitats, resulting in relatively uniform foraging behavior (Růžičková et al., 2024). Similarly, local microhabitat characteristics at the ground level, such as the cover of bare soil, leaf litter, or the herb layer, did not affect attack rates. In contrast, coarse-scale forestry treatments, particularly (micro)clear-cuts and preparation cuts, significantly increased predation pressure, suggesting negative effects on the forest food web (Růžičková and Elek, 2021). Thus, the adjacent forest matrix and management history, rather than gap geometry alone, could be important determinants of predation risk in small canopy openings. Finally, predation pressure may also vary over the diel cycle, as many vertebrate predators exhibit distinct diurnal or nocturnal foraging patterns constrained by temperature, humidity, and light conditions (e.g., Dell et al., 2011; Wróbel and Bogdziewicz, 2015). Diurnal variation in microclimate may therefore interact with forest structure to further modulate predation pressure on carabids.

Based on these findings, we hypothesized that small-scale canopy gaps differ in predation pressure depending on their formation history in the surrounding forest matrix compared to control plots. Gaps created within former preparation cuts (more open/less closed stands) are expected to exhibit higher predation pressure because their structurally complex understory and modified microclimate may facilitate predator activity and alter prey accessibility. In contrast, newly created gaps in closed-canopy forests mostly retain characteristics of the original forest, including lower light availability and weaker structural contrast (compared to preparation cuts), making them less distinct to predators and resulting in lower predation rates. Old gaps in closed-canopy forests may partially deviate from these conditions as vegetation regeneration alters local structure and microclimate, potentially leading to modest increases in predation pressure. Additionally, we examined the role of time of day and microclimate, including soil moisture, air temperature, and relative humidity, as these factors can constrain predator foraging activity through physiological and behavioral mechanisms. Specifically, we tested: (1) whether predation pressure on large carabids varies among canopy gaps of different ages and management histories, and (2) whether diurnal foraging patterns of predators and microclimatic conditions contribute to variability in predation pressure.

2. Material and methods

2.1. Study site and forestry treatments

The experimental site is located near the village of Pilisszántó on the northern slope of Hosszú-hegy in the Pilis Mountains, Hungary (47.6747°N, 18.9094°E; Figs. 1a and 1b), and it is a part of the Pilis Forestry Systems Experiment (project website: https://piliskiserlet.ecolres.hu/en). This project aims to examine how various forestry treatments affect forest site conditions (including soil and litter characteristics and microclimate), multi-taxon biodiversity, and natural regeneration (Elek et al., 2018; 2022; Boros et al., 2019; Tinya et al., 2019; Kovács et al., 2020; Samu et al., 2021; Aszalós et al., 2023). The site is an approximately 90-year-old managed oak-hornbeam forest, with sessile oak (*Quercus petraea* (Matt.) Liebl., 1784) dominating the canopy layer and hornbeam (*Carpinus betulus* L., 1753) forming the secondary canopy layer. Other admixed tree species include Turkey oak (*Quercus cerris* L., 1753), beech (*Fagus sylvatica* L., 1753), wild cherry (*Prunus avium* L., 1755), and manna ash (*Fraxinus ornus* L., 1753). The sparse shrub layer consists

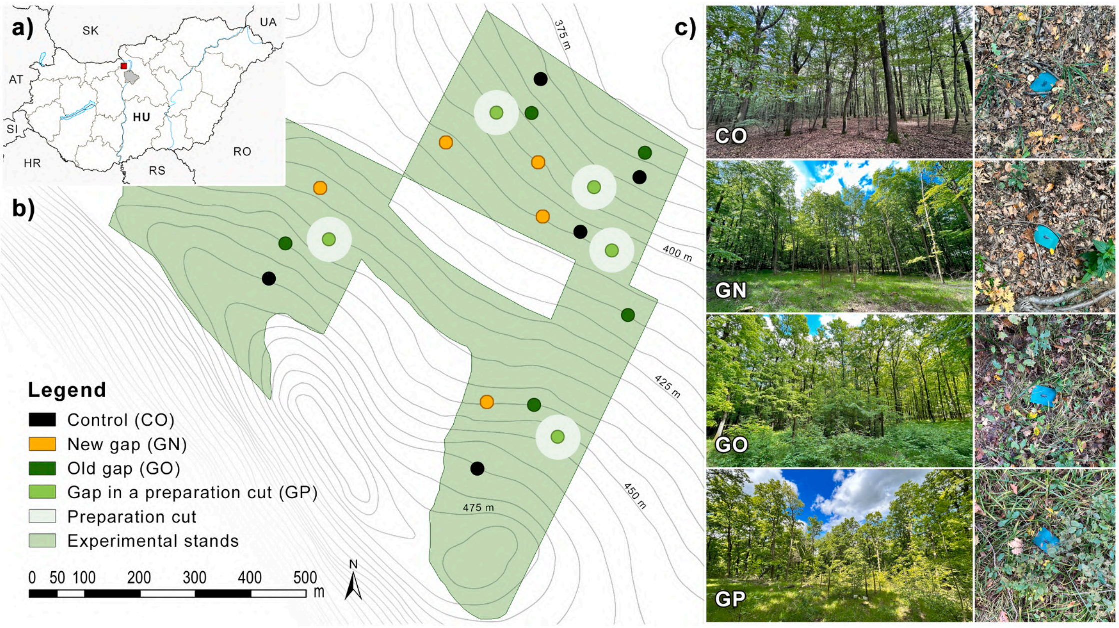

Fig. 1. (a) Location of the study area in the Pilis Mountains in northern Hungary (red square); countries are Hungary (HU), Slovakia (SK), Ukraine (UA), Romania (RO), Serbia (RS), Croatia (HR), Slovenia (SI), and Austria (AT). (b) The overview of the Pilis Forestry Systems Experiment design. (c) Photos of small-scale forestry treatments included in the study, with detailed views of ground vegetation showing a decoy placed at the center of each plot: control closed-canopy forest stand (CO); newly created gap in a closed-canopy forest (GN); 10-year-old gap in a closed-canopy forest (GO); and gap created in a preparation cut following upper canopy thinning (GP).

primarily of hornbeam and manna ash seedlings, along with mesic forest herbaceous species, such as *Carex pilosa* Scopoli, 1772, and *Melica uniflora* Retz, 1779.

We focused on small, circular canopy gaps (~300 m^2) with a 1:1 ratio of gap diameter to surrounding canopy height (approximately 10 m in radius), created within both closed and partially open stands (Fig. 1c). Unmanaged closed-canopy forest stands served as controls (CO). The applied gap types included new gaps in closed stands (GN), old gaps in closed stands (GO), and new gaps in preparation cuts (GP). New gaps were established in the winter of 2023/2024 (one year before this investigation), while old gaps were created in the winter of 2014/2015 (ten years before this investigation). The preparation cuts were originally implemented in the winter of 2014/2015 by removing approximately 30% of the upper canopy and the entire secondary canopy layer within circular areas of 0.5 ha with a radius of 40 m (Elek et al., 2018). This partial cutting increased canopy openness, promoting the development of a dense and structurally complex understory. Similarly, old gaps (GO) now contain a well-developed understory and regeneration layer (Aszalós et al., 2023). In contrast, newly created gaps (GN) in closed-canopy forests retain the original sparse herbaceous layer and are bordered by a dense canopy, creating pronounced light contrasts. All treatments and controls were replicated across five blocks to ensure robust comparisons, resulting in 20 sampling plots in total (Fig. 1b).

2.2. 3D-printed decoys and data sampling

As a model species for the predation pressure experiment, we selected the largest ground beetle species in the area, the approximately 4-cm long, black-colored *Carabus coriaceus* without iridescence (Fig. 2). The 3D model of the species was printed as a single piece using black polylactic acid (PLA) filament (for the technical details about 3D printing, see Růžičková and Elek, 2021). While the use of artificial decoys inevitably cannot reproduce the full range of cues provided by the living prey, they remain a useful tool for assessing relative patterns of predation pressure, providing standardized and comparable estimates that are well suited for detecting treatment effects (Ferrante et al., 2024; Ferrante and Lövei, 2025).

In each sampling plot, we installed 10 decoys approximately in a circular arrangement to ensure that all decoys had the same distance from the plot center. Each decoy was positioned in the center of the green heavy paper sheet (density 200 g/m^2), at the intersection of two perpendicular lines (Figs. 2a and 2b). To prevent unwanted movement from wind or rain, the decoys were secured in the intersection using a very small amount of moisture- and UV-resistant glue (UHU Patafix glue pads; UHU GmbH, Bühl/Baden, Germany) applied at one point on the ventral side of the decoy's abdomen. The paper sheets were fixed to the ground by branches or stones. This arrangement allowed us to record even the subtle movements of the decoy made by small predators when investigating the decoy's edibility under changing weather conditions. In total, we installed 200 decoys. They were installed in October 2024 and checked twice a day, in the morning (around 7:00) and evening (around 19:00) for five consecutive days (10 observation events), leading to a total of 2000 observations during the experiment. If the decoy was turned (Fig. 2c), damaged (Fig. 2d), or relocated

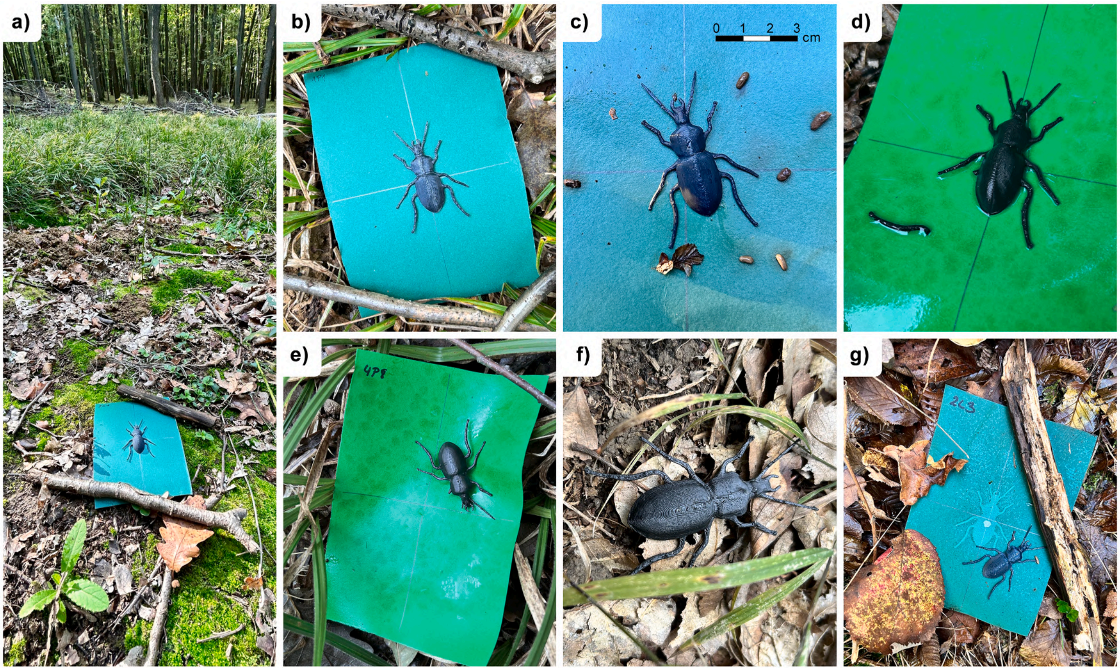

Fig. 2. 3D-printed decoys resembling *Carabus coriaceus* installed on a green heavy paper sheet (a) at the intersection of two perpendicular lines (b). The decoys were regularly monitored for signs of turning (c, here also with the droppings of a small mammalian predator, probably a rodent or a bat), damage or broken parts (d, e), and relocation (e, f, g). The length of each decoy was approximately 4 cm, measured from the top of the head to the end of the abdomen, see scale in panel c).

(Fig. 2e, f, g), this was considered to be a result of a predation attempt. After measurements, decoys were placed in their original position or replaced if damaged. The same applies to paper sheets. Moreover, for a qualitative assessment of predator species identity foraging in the area and interacting with the decoys, we deployed one camera trap per treatment in a single block (EVOLVEO StrongVision Mini, Abacus Electric Ltd., Czech Republic), resulting in four camera traps in total. The camera traps were active throughout the entire experiment.

2.3. Microclimate and variable selection

Microclimate variables were measured in the centers of each plot using Voltcraft DL-210TH loggers (Conrad Electronic SE, Germany) and TMS-4 dataloggers (TOMST Ltd., Czech Republic), operated simultaneously. Temperature (°C) was recorded at four levels: 130 cm and 15 cm above the ground layer, directly on the soil surface, and 8 cm below ground. Relative humidity (RH, %) was measured at 130 cm. Soil moisture was recorded as volumetric water content (VWC, %) in the upper soil layer at a depth of 8–14 cm (for technical details, see Wild et al., 2019). During the experimental period (October 9–13, 2024), these variables were recorded at 15-minute intervals. For each day, we calculated mean values for each microclimate variable separately for daytime (07:00–18:45 local time) and nighttime (19:00–06:45 local time) to match the temporal resolution of our predation data sampling and subsequent analyses.

To reduce multicollinearity among the seven measured microclimate variables, we combined random forest variable importance and Spearman correlation analysis. We applied a conditional random forest using the *cforest* function from the 'party' package (Hothorn et al., 2006; Strobl et al., 2007) to assess the relative importance of each microclimate variable in relation to the predation pressure. We also calculated Spearman pairwise correlations via the *corr_coef* function from the 'metan' package (Olivoto and Lúcio, 2020). Based on these combined results (see Supplementary Figure A1), we selected three uncorrelated microclimate variables for further analysis: relative humidity, soil moisture, and air temperature at 15 cm above the ground. Although surface temperature showed a slightly higher importance, we chose the 15 cm temperature because it better represents the thermal conditions experienced by larger, ground-active predators of carabids that move slightly above the soil surface. An overview of the dynamics in these microclimatic conditions during the experimental period is shown in Supplementary Figure A2.

2.4. Data analysis

To assess overall differences in predation attempts among treatments, we analyzed the cumulative counts of different predation signs (turns, relocations, and damages) per treatment across the entire experimental period. We used a generalized linear model with a Poisson distribution and log link function (the *glm* function from the 'stats' package, R Core Team, 2023), treating the total number of observed signs as the response variable. Treatment, sign type, and their interaction were included as predictors. Model significance was assessed using the *Anova* function with type III estimates from the 'car' package (Fox and Weisberg, 2018).

For further analysis, predation pressure was quantified as the proportion of attacked decoys out of the total number of decoys (attack / [attack + no attack]) within each sampling plot and measurement session and was used as a response variable. The observed complexity in the data suggested the presence of nonlinearity and interaction between explanatory variables, and potential threshold responses that standard generalized linear mixed models are not well-suited to capture (De'ath and Fabricius, 2000). Therefore, we applied univariate regression tree analysis, which is more effective in handling ecological datasets with complex response patterns (De'ath and Fabricius, 2000; Zuur et al., 2007).

The regression tree analysis included the following explanatory variables: forestry treatment (four-level factor), time of the day (two-level factor: nighttime and daytime), relative humidity (continuous), temperature at 15 cm above ground (continuous), and soil moisture, measured as volumetric water content (continuous). Trees were fitted using the *rpart* function from the 'rpart' package (Therneau et al., 2025), applying the "anova" method. To control model complexity, we set the minimum complexity parameter to 0.01, required at least 20 observations to attempt a split, and set a minimum of 7 observations per terminal node. Model performance was internally validated using 10-fold cross-validation to estimate the cross-validated error. Because regression trees are sensitive to random data partitioning during cross-validation, we assessed model stability by generating 1000 trees using varying random seeds. For each tree, we selected the complexity parameter that minimized cross-validated error and pruned the tree accordingly to prevent overfitting.

Although Breiman et al. (1984) recommend selecting the smallest tree within one standard error of the minimum cross-validated error (the "1-SE rule") to prioritize parsimony, we found that applying this rule consistently resulted in trees that were too simplistic to capture the ecological patterns of interest (De'ath and Fabricius, 2000). Therefore, we selected the best tree as the one with the absolute lowest cross-validated error across all iterations to prioritize predictive performance over tree simplicity. We evaluated model stability by examining the distribution of variable importance scores, tree sizes, and cross-validated errors across all trees (see Supplementary Figure A3). To further interpret the marginal effects of individual predictors on predation pressure, we generated partial dependence plots using the 'pdp' package (Greenwell, 2017). All statistical analyses were performed in R version 4.3.2 (R Core Team, 2023).

3. Results

Out of 2000 observations, we have recorded 96 predation events and thus an overall predation rate of 4.8%. The three types of predation differed significantly in overall counts ($\chi^2 = 12.23$, df = 2, $p < 0.002$), with turnings observed most often (61 cases), followed by relocations (23) and damages, such as missing legs and/or antennae (12). Predation attempts only marginally varied across treatments ($\chi^2 = 7.40$, df = 3, p = 0.060). Although signs of damage were not recorded in control plots (CO, Fig. 3), the relative proportions of sign types did not differ significantly among treatments (interaction term: $\chi^2 = 8.76$, df = 6, p = 0.187). In two relocation cases, missing legs were additionally observed. Relocation distances ranged from 1 to 100 cm, with a mean of 12.6 cm. Regarding predator species identity, the camera traps did not capture any large-bodied predators interacting with the decoys, indicating that the predation events may have been caused primarily by small animals below the detection threshold of the camera traps. On one occasion, the decoy was found with the droppings of a small mammalian predator, probably a rodent or bat (Fig. 2c).

Across 1000 regression trees generated using varying random seeds, the most frequent tree structure involved sequential splits on relative humidity, treatment, and soil moisture (42% of runs), followed by trees splitting on relative humidity and treatment (30%), single-node trees with no splits (27%), and simple trees splitting only on relative humidity (1%). The best-performing model had four terminal nodes (Fig. 4a) with a cross-validated error of 0.895 (SE = 0.120). For the additional diagnostics, see Supplementary Figure A3. Relative humidity was the most important predictor of predation pressure (importance score: 40), followed by forestry treatment (27) and soil moisture (21). Time of the day and temperature at 15 cm above ground showed no detectable effect on predation pressure and were not included in the final regression tree.

In this tree, the primary split occurred at a relative humidity threshold of 96%. When relative humidity was below 96% (78% of observations, Fig. 4a), predation pressure remained uniformly low (mean = 0.038). In contrast, under conditions close to the dew point (RH ≥ 96%), the model further divided responses based on forestry treatment. Specifically, canopy gaps created in preparation cuts (GP) were associated with the highest attack rates (mean = 0.120). In other gap treatments (GN and GO) and control plots, attack rates were moderate (mean = 0.052) and further affected by soil volumetric water content. Partial dependence plots, which illustrate the marginal effect of each predictor while averaging the effects of all other variables in the model, reflect the same structure; they show an increase in predation pressure above the 96% humidity threshold (Fig. 4b), forestry treatment differences between GP and other treatments (Fig. 4c), and the effect of soil moisture (Fig. 4d).

4. Discussion

Using 3D-printed decoys, we found that predation pressure on large carabids varied, depending locally on the forest matrix. Although only short-term, our results support the first hypothesis that predation risk differs among canopy gaps: the highest attack rates occurred in gaps created in preparation cuts (GP), whereas other gap types (GN and GO) and control plots exhibited lower and more variable predation risks. We also found partial support for the second hypothesis regarding diurnal patterns and microclimatic conditions. While temperature and time of day had no detectable effect, high relative humidity strongly increased predation pressure, and soil moisture further modulated risk within certain forestry treatments. These findings highlight the combined effects of gap formation history and local abiotic variation in shaping predator–prey interactions on the forest floor.

Increased predation pressure during periods of very high humidity may result from altered prey availability and changes in predator behavior. Rain and elevated moisture levels often reduce the activity of many insect species, leading to a temporary decline in available prey for generalist predators (Bider, 1968). In response, predators may switch to alternative food sources (Murdoch, 1969; Van Baalen et al., 2001). Our decoys, positioned in relatively exposed locations on paper sheets on the ground, may have appeared as easy targets under such conditions. As no large-bodied predators (e.g., wild boars) were captured by camera traps, we assume that the majority of attacks were carried out by small predators, such as hedgehogs, shrews, some other rodents, frogs, or birds. These small-bodied animals are often sensitive to environmental conditions and adjust their foraging behavior accordingly (Wróbel and Bogdziewicz, 2015). Previous research showed that predation pressure on small mammals decreases during rainy nights (Vickery and Bider, 1981; Orrock et al., 2004), suggesting that their increased activity during rainfall can be a strategy to avoid predation themselves while foraging, since the sound of rainfall masks movement and olfactory cues are rapidly diluted or washed away (Vickery and Bider, 1981; Vickery and Rivest, 1992). Some forest-dwelling rodents, such as *Apodemus* spp., are primarily granivorous but increase their intake of animal prey, including large beetles, when seeds become scarce in autumn (Rogers and Gorman, 1995). Similarly,

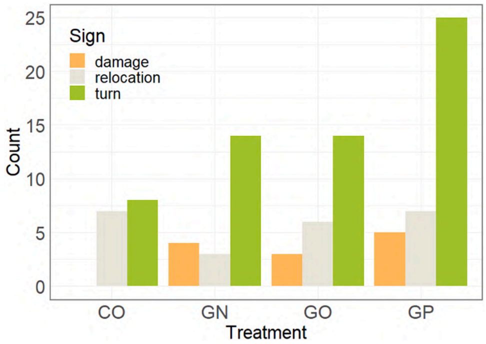

Fig. 3. Different types of recorded predation attempts in the studied forestry treatments. Treatment abbreviations: CO = control, GN = new gap, GO = old gap, GP = gap in a preparation cut.

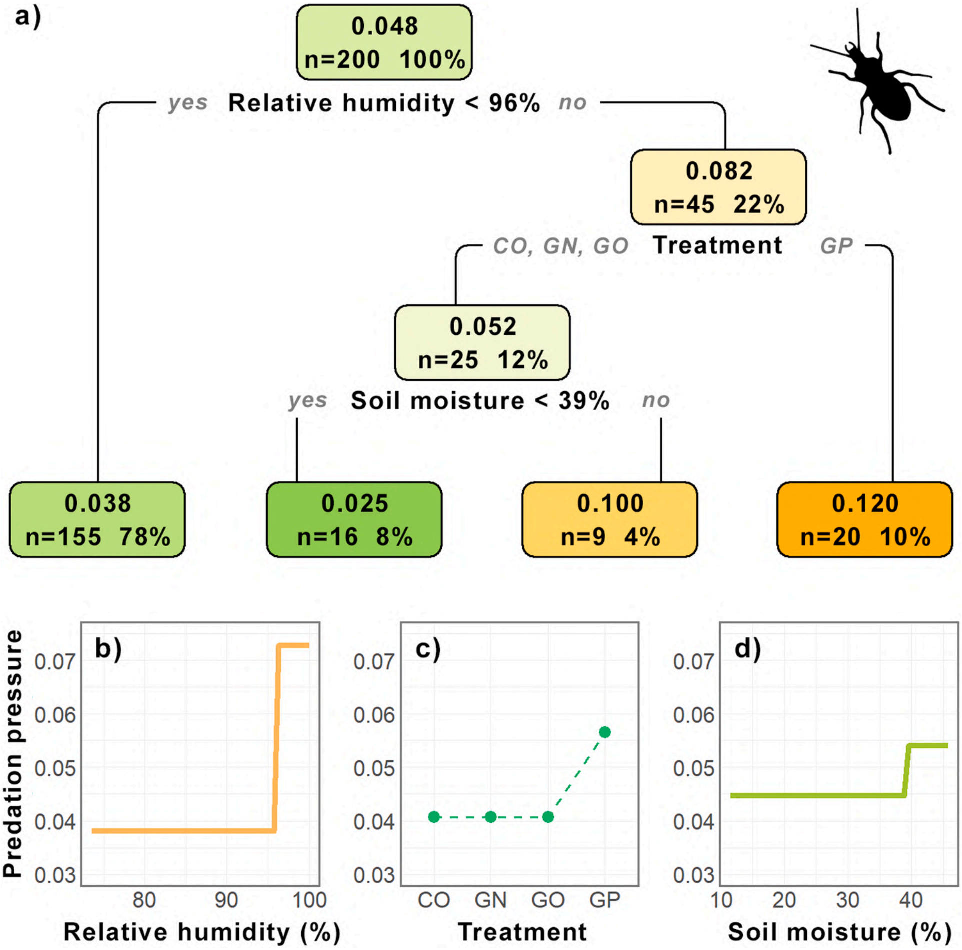

Fig. 4. Summary of the regression tree analysis predicting predation pressure on large carabids. The best regression tree (a) was selected from 1000 competing trees based on minimal cross-validated error. Each node shows the mean predation pressure, sample size, and the proportion of observations. Partial dependence plots illustrate the marginal effects of relative humidity (b), forestry treatment (c), and soil moisture (volumetric water content, d) on predation pressure while accounting for the effects of other predictors. Treatment abbreviations: CO = control, GN = new gap, GO = old gap, GP = gap in a preparation cut.

shrews (*Sorex* spp.) preferentially consume larger beetles, with a positive correlation between beetle availability and consumption rate (Churchfield, 1982). The observed signs of predation on the decoys, including broken legs and antennae, can be consistent with bites from rodents or insectivores, supporting the clue that predation was predominantly carried out by small predators targeting easily accessible, though suboptimal, food sources. Taken together, high humidity may act as an ecological trigger, altering predator foraging behavior and increasing predation pressure on otherwise well-defended prey, such as large carabids.

Forestry treatments emerged as the second most important variable explaining predation pressure, with clear differences among gap types. The highest attack rates occurred in newly established gaps created in preparation cuts, whereas new and old gaps in closed-canopy stands, as well as closed-canopy controls, showed lower and more uniform predation levels. This suggests that the surrounding forest matrix, and not just the current stand structure, can leave a lasting imprint on trophic interactions. Gaps created in preparation cuts resemble the already thinned surrounding forest in terms of habitat structure. Increased canopy openness compared to closed-canopy stands promotes dense understory vegetation and microhabitat heterogeneity (Aszalós et al., 2023). Such conditions support oak regeneration, which benefits from increased light availability and growth while maintaining acorn production through the presence of mature trees in the surrounding forest matrix. The existing understory also contributes to a buffered microclimate that is similar to the below-canopy conditions in closed forests, even with increased solar radiation. This combination of higher structural heterogeneity, ongoing tree regeneration, and reduced canopy cover may cause predators to perceive these areas as distinct habitats offering different foraging opportunities (Lloyd, 1980; Riber, 2006). However, dense understory layers may restrict predator movement and reduce foraging efficiency on the soil surface, limiting access to otherwise abundant prey such as earthworms (Kowalczyk et al., 2003; Boros et al., 2019). When preferred prey becomes less accessible, predators may switch to more exposed and easily detected alternatives, such as the carabid decoys used in this study. In addition, improved light conditions in these thinned stands could indirectly affect foraging activity, especially under low-light conditions such as dusk or dawn. Together, these changes in habitat structure and foraging behavior likely lead to higher predation pressure, supporting our previous findings from preparation cuts (Růžičková and Elek, 2021). In contrast, old gaps created in closed-canopy stands also had a well-developed understory layer compared to new gaps. However, despite their more complex structure, predation pressure remained low and similar to that observed in new gaps and controls. It seems that gaps originating from closed-canopy forests are not perceived by predators as distinct habitats, likely due to their relatively small size and limited light conditions. Our findings are consistent with previous work showing that predators of large carabids may not recognize small canopy openings as separate habitat types within a forest matrix, resulting in uniform predation pressure (Růžičková et al., 2024).

Soil moisture also contributed to predation risk, but only under humid conditions and within certain treatments. Moist soil patches may attract both predators and prey, as smaller prey, including insects, often aggregate in such microhabitats to avoid desiccation, creating predictable prey hotspots (Tauber et al., 1998; Verdeny-Vilalta and Moya-Laraño, 2014). Predators may exploit these patches, particularly if prey trade off safety for hydration. Such microhabitat-level processes likely explain why specific combinations of humidity and soil moisture were associated with higher attack rates. By contrast, the temperature measured 15 cm above the ground had no detectable effect. Although temperature is generally an important factor influencing insect activity and their predators (Bider, 1968; Dowding et al., 2010), the lack of effect in our study may reflect the narrow thermal range during the short-term experiment or the thermal buffering provided by forest vegetation and leaf litter (Kovács et al., 2020; De Frenne et al., 2021; Verdonck et al., 2025). Similarly, the lack of a day–night effect could be explained by overlapping activity patterns of different predators and their high, continuous energy demands, likely due to the accumulation of fat reserves for the winter.

Finally, we recognize some limitations of using artificial 3D-printed decoys to quantify predation pressure. Decoy-based approaches cannot provide precise information on the identity of predator species, but only major taxonomic categories, such as birds, rodents, and large mammals. Signs in the form of displacement, turning, or damage indicate predation attempts but cannot be unambiguously assigned to a specific species, especially if multiple predator groups are present at a site. These limitations could theoretically be addressed by placing a camera trap at each decoy to capture the full range of predators, but in our case, this was not feasible due to logistical constraints. Since camera traps are primarily designed to detect moderate-sized or large-bodied animals, micro and mesopredators can be on the edge or under the detection range of these devices, or can be detected by a very high number of erroneous video captures. Detection sensitivity can also be constrained by vegetation structure and by the number of devices that can be feasibly installed, taking into account lighting conditions and the field of view of the lenses and sensors. Moreover, artificial decoys cannot fully mimic the behavioral, chemical, or thermal signals of the living prey, which can influence predator responses and lead to conservative estimates of predation rates. Despite these limitations, this method remains a valuable and widely used tool for standardized comparisons of relative predation pressure across different treatments (Ferrante et al., 2024; Ferrante and Lövei, 2025).

5. Conclusions

Small canopy gaps are widely promoted as biodiversity-friendly alternatives to large-scale logging, as they mimic natural disturbances and can maintain structural complexity in uneven-aged forests. This study highlights that the ecological consequences of such gaps also depend on the surrounding forest matrix and microhabitat complexity. Even subtle differences in canopy openness, understory structure, and microclimatic buffering can influence predator–prey interactions and the accessibility of prey resources, shaping the spatial distribution of predation pressure. While moderate predation is a natural component of ecosystem functioning, increased and spatially predictable risk could contribute to ecological traps, creating habitats that appear suitable but reduce survival or reproduction.

CRediT authorship contribution statement

Jana Růžičková: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Csaba Németh:** Investigation. **Bence Kovács:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Zoltán Elek:** Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Péter Ódor:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

Funding

The study was supported by the Hungarian National Research Development and Innovation Fund (PD 146480, PD 146325, K 143270) and the #oakadapt project of the Interreg VI-A Hungary-Slovakia Program (HUSK/2302/1.2/168). It has also received funding from the HUN-REN Hungarian Research Network.

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.

Acknowledgements

We thank foresters from Pilisi Parkerdő Ltd. (Péter Csépányi, Viktor Farkas, and László Simon) for the maintenance of the experimental site.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04153.

Data Availability

Data will be made available on request.

References

Aikens, K.R., Timms, L.L., Buddle, C.M., 2013. Vertical heterogeneity in predation pressure in a temperate forest canopy. PeerJ 1, e138.

Aszalós, R., Kovács, B., Tinya, F., Németh, C., Horváth, C.V., Ódor, P., 2023. Canopy gaps are less susceptible to disturbance-related and invasive herbs than clear-cuts: temporal changes in the understorey after experimental silvicultural treatments. For. Ecol. Manag. 549, 121438.

Aszalós, R., Thom, D., Aakala, T., Angelstam, P., Brūmelis, G., Gálhidy, L., Gratzer, G., Hlásny, T., Katzensteiner, K., Kovács, B., Knoke, T., Larrieu, L., Motta, R., Müller, J., Ódor, P., Roženbergar, D., Paillet, Y., Pitar, D., Standovár, T., Svoboda, M., Szwagrzyk, J., Toscani, P., Keeton, W.S., 2022. Natural disturbance regimes as a guide for sustainable forest management in Europe. Ecol. Appl. 32, e2596.

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

Bider, J.R., 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. Ecol. Monogr. 38, 269–308.

Boros, G., Kovács, B., Ódor, P., 2019. Green tree retention enhances negative short-term effects of clear-cutting on enchytraeid assemblages in a temperate forest. Appl. Soil Ecol. 136, 106–115.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.G., 1984. Classification and regression trees. Wadsworth International Group, Belmont, CA.

Chalfound, A.D., Martin, T.E., 2009. Habitat structure mediates predation risk for sedentary prey: Experimental tests of alternative hypotheses. J. Anim. Ecol. 78, 497–503.

Chang, C.C., Todd, P.A., 2023. Reduced predation pressure as a potential driver of prey diversity and abundance in complex habitats. npj Biodivers. 2 (1).

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. BioScience 49, 288–297.

Churchfield, S., 1982. Food availability and the diet of the common shrew, Sorex araneus, in Britain. J. Anim. Ecol. 51, 15–28.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Change Biol. 27, 2279–2297.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

Dell, A.I., Pawar, S., Savage, V.M., 2011. Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. 108, 10591–10596.

Dell, A.I., Pawar, S., Savage, V.M., 2014. Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. J. Anim. Ecol. 83, 70–84.

Dowding, C.V., Harris, S., Poulton, S., Baker, P.J., 2010. Nocturnal ranging behaviour of urban hedgehogs, Erinaceus europaeus, in relation to risk and reward. Anim. Behav. 80, 13–21.

Drozdová, M., Šipoš, J., Drozd, P., 2013. Key factors affecting the predation risk on insects on leaves in temperate floodplain forest. Eur. J. Entomol. 110, 469–476.

Elek, Z., Kovács, B., Aszalós, R., Boros, G., Samu, F., Tinya, F., Ódor, P., 2018. Taxon-specific responses to different forestry treatments in a temperate forest. Sci. Rep. 8, 16990.

Elek, Z., Růžičková, J., Ódor, P., 2022. Functional plasticity of carabids can presume better the changes in community composition than taxon-based descriptors. Ecol. Appl. 32, e02460.

Ferrante, M., Howe, A.G., Lövei, G.L., 2024. Experimental considerations support the use of artificial sentinel prey—a comment on Rodriguez-Campbell et al. J. Biogeogr. 51, 2152–2155.

Ferrante, M., Lo Cacciato, A., Lövei, G.L., 2014. Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. Eur. J. Entomol. 111, 663–670.

Ferrante, M., Lövei, G.L., 2025. The sentinel approach to quantify ecosystem function intensities. Methods Ecol. Evol. 1–13.

Fox, J., Weisberg, S., 2018. An R Companion to Applied Regression. Sage publications.

Fukuda, S., Konuma, J., 2019. Using three-dimensional printed models to test for aposematism in a carabid beetle. Biol. J. Linn. Soc. 128, 735–741.

Goßmann, A., Ambrožová, L., Cizek, L., Drag, L., Georgiev, K., Neudam, L., Perlík, M., Seidel, D., Thorn, S., 2023. Habitat openness and predator abundance determine predation risk of warningly colored longhorn beetles (Cerambycidae) in temperate forest. J. Insect Sci. 23, 16.

Gossner, M.M., Gazzea, E., Diedus, V., Jonker, M., Yaremchuk, M., 2020. Using sentinel prey to assess predation pressure from terrestrial predators in water-filled tree holes. Eur. J. Entomol. 117, 226–234.

Graclik, A., Wasielewski, O., 2012. Diet composition of Myotis myotis (Chiroptera, Vespertilionidae) in western Poland: results of fecal analyses. Turk. J. Zool. 36, 209–213.

Greenwell, B.M., 2017. pdp: An R package for constructing partial dependence plots. R. J. 9, 421–436.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. Am. Nat. 94, 421–425.

Horváth, C.V., Kovács, B., Tinya, F., Locatelli, J.S., Németh, C., Crecco, L., Illés, G., Csépányi, P., Ódor, P., 2023. A matter of size and shape: microclimatic changes induced by experimental gap openings in a sessile oak–hornbeam forest. Sci. Total Environ. 873, 162302.

Hothorn, T., Hornik, K., Zeileis, A., 2006. Unbiased recursive partitioning: a conditional inference framework. J. Comput. Graph. Stat. 15, 651–674.

Klecka, J., Boukal, D.S., 2014. The effect of habitat structure on prey mortality depends on predator and prey microhabitat use. Oecologia 176, 183–191.

Kotze, D.J., Brandmayr, P., Casale, A., Dauffy-Richard, E., Dekoninck, W., Koivula, M.J., Lövei, G.L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R., Zetto, T., 2011. Forty years of carabid beetle research in Europe - from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. ZooKeys (100), 55–148.

Kovács, B., Tinya, F., Ódor, P., 2017. Stand structural drivers of microclimate in mature temperate mixed forests. Agric. For. Meteorol. 234, 11–21.

Kovács, B., Tinya, F., Németh, C., Ódor, P., 2020. Unfolding the effects of different forestry treatments on microclimate in oak forests: results of a 4-yr experiment. Ecol. Appl. 30, e02043.

Kowalczyk, R., Zalewski, A., Jedrzejewska, B., Jedrzejewski, W., 2003. Spatial organization and demography of badgers (Meles meles) in Bialowieza Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe. Can. J. Zool. 81, 74–87.

Langellotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. Oecologia 139, 1–10.

Liebhold, A.M., 2012. Forest pest management in a changing world. Int. J. Pest Manag. 58 (3), 289–295.

Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Can. J. Zool. 68, 619–640.

Lloyd, H.G., 1980. Habitat requirements of the red fox. In The red fox: symposium on behaviour and ecology. Springer Netherlands, Dordrecht, pp. 7–25.

Lövei, G.L., Ferrante, M., 2017. A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. Insect Sci. 24, 528–542.

Lövei, G.L., Sunderland, K.D., 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. 41, 231–256.

Maguire, D.Y., Nicole, T., Buddle, C.M., Bennett, E.M., 2015. Effect of fragmentation on predation pressure of insect herbivores in a north temperate deciduous forest ecosystem. Ecol. Entomol. 40, 182–186.

Marris, J.W.M., 2000. The beetle (Coleoptera) fauna of the Antipodes Islands, with comments on the impact of mice; and an annotated checklist of the insect and arachnid fauna. J. R. Soc. N. Z. 30 (2), 169–195.

Mason, W.L., Diaci, J., Carvalho, J., Valkonen, S., 2022. Continuous cover forestry in Europe: Usage and the knowledge gaps and challenges to wider adoption. For. Int. J. For. Res. 95, 1–12.

Matthews, J.D., 1991. Silvicultural systems. Oxford University Press.

Murdoch, W.W., 1969. Switching in general predators: Experiments on predator specificity and stability of prey populations. Ecol. Monogr. 39, 335–354.

Nagel, T.A., Svoboda, M., Kobal, M., 2014. Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. Ecol. Appl. 24, 663–679.

Nakatsuji, K., Kobayashi, Y., Yoshida, T., 2024. Microtopography and vegetation generate uneven predation pressure on forest insects. Acta Oecologica 125, 104031.

Olivoto, T., Lúcio, A.D., 2020. metan: An R package for multi-environment trial analysis. Methods Ecol. Evol. 11, 783–789.

Orrock, J.L., Danielson, B.J., Brinkerhoff, R.J., 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behav. Ecol. 15, 433–437.

Pommerening, A., Murphy, S.T., 2004. A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77, 27–44.

R Core Team, 2023. R: a language and environment for statistical computing. Vienna Austria. R. Found. Stat. Comput. ⟨https://www.R-project.org/⟩.

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodivers. & Conserv. 12, 487–506.

Raymond, P., Bédard, S., Roy, V., Larouche, C., Tremblay, S., 2009. The irregular shelterwood system: review, classification, and potential application to forests affected by partial disturbances. J. For. 107, 405–413.

Riber, A.B., 2006. Habitat use and behaviour of European hedgehog Erinaceus europaeus in a Danish rural area. Acta Theriol. 51, 363–371.

Rogers, L.M., Gorman, M.L., 1995. The home-range size of wood mice Apodemus sylvaticus living in set-aside and surrounding semi-natural and crop land. J. Zool. 237, 675–678.

Roslin, T., Hardwick, B., Novotny, V., Petry, W.K., Andrew, N.R., Asmus, A., Barrio, I.C., Basset, Y., Boesing, A.L., Bonebrake, T.C., Cameron, E.K., Dáttilo, W., Donoso, D.A., Drozd, P., Gray, C.L., Hik, D.S., Hill, S.J., Hopkins, T., Huang, S., Koane, B., Laird-Hopkins, B., Laukkanen, L., Lewis, O.T., Milne, S., Mwesige, I., Nakamura, A., Nell, C.S., Nichols, E., Prokurat, A., Sam, K., Schmidt, N.M., Slade, A., Slade, V., Suchanková, A., Teder, T., van Nouhuys, S., Vandvik, V., Weissflog, A., Zhukovich, V., Slade, E.M., 2017. Higher predation risk for insect prey at low latitudes and elevations. Science 356, 742–744.

Růžičková, J., Elek, Z., 2021. Unequivocal differences in predation pressure on large carabid beetles between forestry treatments. Diversity 13, 484.

Růžičková, J., Harnos, A., Elek, Z., 2024. Small canopy gaps do not affect the predation pressure on large ground beetles (Coleoptera: Carabidae) in a managed forest. Eur. J. Entomol. 121, 369–373.

Samu, F., Elek, Z., Kovács, B., Fülöp, D., Botos, E., Schmera, D., Aszalós, R., Bidló, A., Németh, C., Sass, V., Tinya, F., Ódor, P., 2021. Resilience of spider communities affected by a range of silvicultural treatments in a temperate deciduous forest stand. Sci. Rep. 11, 20520.

Schmitz, O.J., Krivan, V., Ovadia, O., 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. Ecol. Lett. 7, 153–163.

Schowalter, T.D., Noriega, J.A., Tscharntke, T., 2018. Insect effects on ecosystem services—Introduction. Basic Appl. Ecol. 26, 1–7.

Sih, A., Crowley, P., McPeek, M., Petranka, J., Strohmeier, K., 1985. Predation, competition, and prey communities: A review of field experiments. Ecology 66, 269–311.

Šipoš, J., Drozdová, M., Drozd, P., 2011. Effect of canopy openness on the pressure of predatory arthropods and birds on epigeic insects. Cent. Eur. J. Biol. 7, 1021–1029.

Šipoš, J., Drozdová, M., Drozd, P., 2013. Assessment of trends in predation pressure on insects across temperate forest microhabitats. Agric. For. Entomol. 15, 255–261.

Šipoš, J., Kindlmann, P., 2013. Effect of the canopy complexity of trees on the rate of predation of insects. J. Appl. Entomol. 137, 445–451.

Strobl, C., Boulesteix, A., Zeileis, A., Hothorn, T., 2007. Bias in random forest variable importance measures: Illustrations, sources and a solution. BMC Bioinforma. 8, 25.

Tablado, Z., Fauchald, P., Mabille, G., Stien, A., Tveraa, T., 2014. Environmental variation as a driver of predator-prey interactions. Ecosphere 5, 1–13.

Tauber, M.J., Tauber, C.A., Nyrop, J.P., Villani, M.G., 1998. Moisture, a vital but neglected factor in the seasonal ecology of insects: Hypotheses and tests of mechanisms. Environ. Entomol. 27, 523–530.

Therneau, T., Atkinson, B., Ripley, B., 2025. rpart Recursive Partit. R. Package. ⟨http://CRAN.R-project.org/package=rpart⟩.

Tinya, F., Kovács, B., Prättälä, A., Farkas, P., Aszalós, R., Ódor, P., 2019. Initial understory response to experimental silvicultural treatments in a temperate oak-dominated forest. Eur. J. For. Res. 138, 65–77.

Van Baalen, M., Křivan, V., van Rijn, P.C., Sabelis, M.W., 2001. Alternative food, switching predators, and the persistence of predator-prey systems. Am. Nat. 157, 512–524.

Verdeny-Vilalta, O., Moya-Laraño, J., 2014. Seeking water while avoiding predators: Moisture gradients can affect predator–prey interactions. Anim. Behav. 90, 101–108.

Verdonck, S., De Win, Y., Nutter, T., Van Meerbeek, K., Thomaes, A., De Smedt, P., Dekoninck, W., Hendrickx, F., Muys, B., 2025. Managing canopy cover to preserve forest microclimate and diverse macroarthropod communities in times of drought. J. Appl. Ecol. 1, 12.

Vergara, O.E., Nelson, N., Hartley, S., 2021. Effects of mammal exclusion on invertebrate communities in New Zealand. Austral Ecol. 46 (5), 776–791.

Vickery, W.L., Bider, J.R., 1981. The influence of weather on rodent activity. J. Mammal. 62, 140–145.

Vickery, W.L., Rivest, D., 1992. The influence of weather on habitat use by small mammals. Ecography 15, 205–211.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C., Brose, U., 2011. Warming up the system: Higher predator feeding rates but lower energetic efficiencies. Glob. Change Biol. 17, 1301–1310.

Watts, C., Innes, J., Cave, V., Thornburrow, D., Thorpe, S., 2020. Beetle and wētā community responses to mammal eradication on Maungatautari, Waikato, New Zealand. N. Z. J. Zool. 47 (4), 272–290.

Wild, J., Kopecký, M., Macek, M., Šanda, M., Jankovec, J., Haase, T., 2019. Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agric. For. Meteorol. 268, 40–47.

Wróbel, A., Bogdziewicz, M., 2015. It is raining mice and voles: which weather conditions influence the activity of Apodemus flavicollis and Myodes glareolus? Eur. J. Wildl. Res. 61, 475–478.

Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. Analysing ecological data, 680. Springer, New York, NY.