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Long-term effects of clear-cut forestry on predation of artificial caterpillars in boreal forests of southeastern Norway
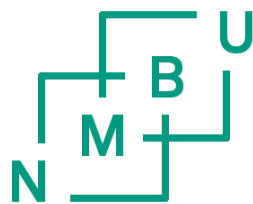
Ingvild Skjelle Fimreite

Master of Biology

Preface

This is my final Master's thesis in Biology within the Faculty of Biosciences, but written and with supervisors at the Faculty of Environmental Sciences and Natural Resource Management. The field of study is Animal Biology, with specialization in interactions between insects and plants.

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Ås, May 15th, 2023

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Ingvild Skjelle Fimreite

Abstract

Predator-prey interactions are one of the key ecological interactions contributing to ecosystem structure and stability within complex forest ecosystems. Intact forest ecosystems contain high abundances and diversity of prey and natural enemies, but impact from forest management intensities could potentially threaten these interactions. I used 640 artificial caterpillars made from brown or green plasticine to compare predation rates between 10 pairs of boreal near-natural (NN) forests and former clear-cut (CC) forests in the southeastern parts of Norway. Half of them were placed on tree stems, and the other half on bilberry bushes. Artificial caterpillars were placed out in two periods, from late May to late June 2022. Predation was measured in two ways: by recording the presence or absence of attack marks on caterpillars, which could indicate predation rates by arthropods, mammals, or birds; and by counting the number of arthropod attack marks per caterpillar. I also assessed the abundance of predatory beetles in traps and the occurrence of anthills in late June.

108 caterpillars were fully removed by unknown predators. From the remaining caterpillars, were 88% attacked by arthropods, 46% by mammals, and 14% by birds. Almost twice as many caterpillars were removed from the former clear-cut forests as near-natural forests (21% vs. 13%), especially on bilberry bushes, and during the second period. Forest type was a significant predictor of both presence of arthropod predation, and number of arthropod attack marks per caterpillar. The arthropod predation rates of caterpillars were highest in the near-natural forests, especially the first period, but caterpillars in clear-cut forests suffered more attack marks per caterpillar, specifically brown ones. Arthropod predators significantly preferred caterpillars on tree stems, particularly the first period. The colour preference of arthropods was only pronounced the second period, with significantly less predated green caterpillars. Both anthills and predatory beetles significantly increased arthropod attack marks per caterpillar. Bird and mammal predation did not differ significantly between the two forest types, they only showed a preference for caterpillars placed on bilberry bushes. My results indicate that different predators react differently to forest management regimes, caterpillar colour, and placement, highlighting the importance of further investigations towards impacts from forest type and other potential ecological interactions on predation rates.

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1 Introduction

Predator-prey interactions is a key ecological contributor to ecosystem structure and stability within complex forest ecosystems (Bailey et al., 2006; Muchula et al., 2019). Intact forests with higher structural complexity and tree diversity support higher abundances and species richness of prey and predators through increased microhabitats, offering shelter and food (Wetherbee et al., 2020). Unfortunately, many forests have deviated from their original forest state (Artsdatabanken, 2021a; Jacobsen et al., 2020), with a lack of appropriate tree age and structure required to support these species. Such changes in forest structure and composition can cause changes in whole forest species communities (Paillet et al., 2010). Prevailing forests that have not undergone intensive forest management practices like clear-cutting, still retain forest structures and microhabitats similar to old-growth forests, making them vital refuges for many threatened and endangered species (Jacobsen et al., 2020). Such forests are called near-natural forests.

Norway is covered by 37.4% forests (SSB, 2021). Approximately 48% of the threatened species in the Norwegian Red List 2021 inhabit forest ecosystems, and 84% of these threatened forest species are presumed to be found in older or high-productivity forests, like near-natural forests. Of the threatened species found in Norwegian forests, most of them are beetles (232 Coleoptera species) and flies (137 Diptera species) (Artsdatabanken, 2021b). Many of these species are saproxylic, dependent on dead wood for their survival (Artsdatabanken, 2021b; Stokland et al., 2005), a resource that is much more abundant and varied in older forests like near-natural forests, but have been depleted by forest management practices (Jacobsen et al., 2020).

Intensive forest management of 90% of Fenno-Scandinavian boreal forests have led to significant loss in biodiversity. The removal of older forests through the clear-cutting practice, reduces structural attributes crucial to forest communities, such as cavity shelters in large trees, heterogeneity in the forest cover, and dead wood abundances (Jacobsen et al., 2020). As a result, formerly clear-cut forest stands are less biologically and structurally diverse, with higher proportions of early-successional regenerated stands (Gauthier et al., 2015). This loss of structural diversity poses a significant threat to many forest-dwelling species.

Previous studies comparing near-natural and former clear-cut forests have found higher species richness of saproxylic beetle species in near-natural forests, due to its higher dead wood availability (Jacobsen et al., 2020; Martikainen et al., 2000). Older trees, like veteran oaks, are keystone structures for predatory beetle diversity compared to young trees (Wetherbee et al., 2020). Such old trees are expected to contain higher stand biomass, which also has positive correlations on herbivore abundances (Leidinger et al., 2019). Saproxylic beetles are dependent on dead or decaying wood for survival, and a reduction in large woody debris, along with the loss of open canopy, increases the vulnerability of saproxylic beetles to population declines and local extirpation (Seibold et al., 2015). Thus are there expected many decreasing structures and environmental variables preferable for arthropods through clear-cutting.

Predation rates in predator-prey interactions are primarily influenced by the density of both the prey and predator (Kollberg et al., 2014). Boreal forests harbour many herbivorous insects, including caterpillars (Zvereva et al., 2020). Such herbivores contribute to complex forest communities as a food source for higher trophic levels, like predatory arthropods, birds, and mammals.

Predators such as insectivorous species are important chains in ecological processes, reducing herbivore abundances in forests through predation (Poch & Simonetti, 2013). Structurally complex habitats, similar to near-natural forests, are predicted to maintain high abundances and species richness of caterpillar predators (Tvardikova & Novotny, 2012; Weissflog et al., 2022; Wetherbee et al., 2020).

Birds and small mammals are highly mobile and visual-predating species, and hence efficient in detecting prey (Gossner et al., 2020). Mammals are often ground-dwelling (Bogdziewicz & Zwolak, 2014), while birds often forage in the canopy (Sipos & Kindlmann, 2013)

Forests with high structural complexity, characterized by larger tree stem diameters, dense forest cover, and vegetation close to the ground, have been shown to promote both bird species richness and predation (Hohlenwerger et al., 2022; Klein et al., 2020), for all vertical strata (Kwok, 2009). Insectivorous birds, as important predators in these forests, primarily search for prey within microhabitats like small branches and leaves, and exhibit a preference for gleaning (carefully inspecting surfaces) as their foraging strategy. This strategy has a strong correlation with tree species preference (Holmes & Robinson, 1981; Kwok, 2009), and bird species with this strategy are therefore expected to be reduced in forests lacking their preferred tree species.

A study on predatory beetles' substrate preference found that stand type, dead wood availability, and prey abundance were all important factors in determining the abundance and distribution of 10 common predatory beetle species that are natural enemies of saproxylic beetles (Johansson et al., 2007). The responses varied among the species, where some species were more abundant in clear-cuts, while other had higher abundances in mature manged and old-growth stands. Such findings highlight the complex relationships between predators, prey, and environment, and underscore the importance of considering the impacts of forest management on natural enemies and predators when developing sustainable forest management practices.

Identifying natural enemies is important in measuring predation rates, and using artificial prey, such as dummy caterpillars, is a simple method to do so. The use of plasticine models in predation studies was first introduced in the 1980s and 90s. Some researchers have used artificial eggs to study predation within nests, while others have explored predation rates on mimicked prey like lizards, snakes and small mammals (Bateman et al., 2017). The study method of using artificial prey made from plasticine allow researchers to manipulate the morphology of the prey to suit the potential predators' preferences, as well as altering the prey size to mimic both juveniles and adults.

Artificial caterpillars are commonly used as models of invertebrates to study foraging behaviours (Bateman et al., 2017; Liu et al., 2020; Roeder et al., 2023). They are a valid proxy for live prey, as demonstrated by Ferrante et al. (2017), who compared the predation attractiveness of artificial caterpillars versus live cabbage moth larvae (*Mamestra brassicae*) for the carabid predator *Pterostichus melanrius*, and found that the predators were not more attracted to the live caterpillars than the artificial ones. Overall, the use of artificial prey, particularly artificial caterpillars, is a valuable method for studying predator-prey interactions. By providing a standardized way to measure predation rates and investigate the factors that influence foraging behaviour, this method allows researchers to gain insight into the complex dynamics that shape ecological communities.

The relationship between diversity and biotic interactions, such as predation rates, remains uncertain in former clear-cut forests. This study provides a unique opportunity to better understand patterns in

ecosystem processes, and how environmental change may affect biodiversity, specifically natural enemies. Predation of herbivores by natural enemies can have significant ecological and evolutionary effects, affecting the abundance and traits of both herbivores and plants through trophic cascades. By studying predation rates, we can gain a better understanding of the complex interactions that shape forest ecosystems and how they respond to environmental change.

Artificial prey can be used to assess predation pressure in different forest ecosystems, with the opportunity to alter prey colour, size and placement. The aim of this thesis is to (1) compare predation on artificial caterpillars between near-natural and former clear-cut forests, (2) identify and compare these predation rates between three predator groups (arthropods, mammal, bird), (3) identify other relevant explanatory variables influencing predation rates (caterpillar colour, placement and exposure period), and (4) elaborate further on arthropod predation, using number of arthropod attack marks per caterpillar and including additional explanatory variables (anthills and predatory beetles). I predict higher predation rates of all three predator groups in the near-natural forests due to more complex forest structures.

2 Materials and methods

2.1 Study area and site selection

This Master's thesis is part of project "EcoForest", which focuses on the long-term effects of forest management on insect biodiversity and biomass by comparing near-natural (NN) forests with former clear-cut (CC) but now mature forests. The study sites are located in the south-eastern parts of Norway and my study comprises 20 paired forest stands. Each forest-pair consists of one near-natural forest, and one mature former clear-cut forest in close geographical proximity to each other (Figure 1).
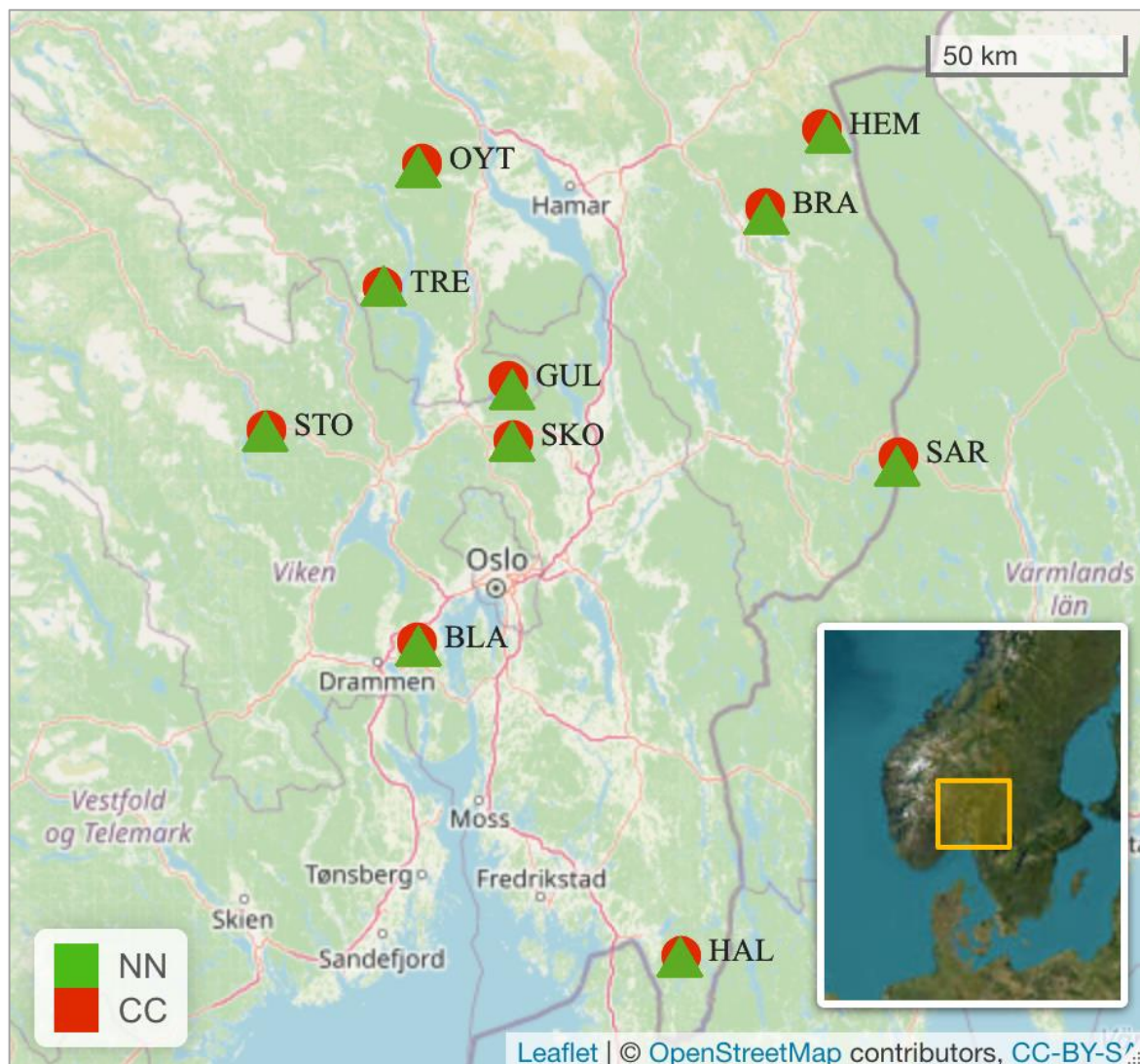
Figure 1. Locations of all 20 forest stands in the south-eastern parts of Norway. Every forest-pair consists of one near-natural (NN) forest, and one former clear-cut (CC) now matured forest.

All forest stands fall within the boreal zone between 59.8° and 60.9° north, spanning from 205 to 667 metres above sea level (Appendix). All 20 designated forest stands were dominated (>70%) by Norway spruce (*Picea abies*) and bilberry (*Vaccinium myrtillus*) bushes. Each forest stand contained a

225 m^2 squared main plot (where other EcoForest studies were conducted) in the centre of the designated forest stand. The fieldwork for this study was conducted on the outer parts of the main plot (Figure 2). The selection criteria for the near-natural forest stands were that they never had been clear-cut, but might have included other logging activities earlier, while the corresponding former clear-cut forest stands had to be within 1 to 5 km close to the near-natural forest. The former clear-cut forests had been clear-cut, spruce trees planted, not thinned or ditched, and have now grown to a mature phase. For each individual forest pair, the soil conditions had to be equal or similar. These conditions included soil depth, soil horizon (similar mineral compositions), the amount of stones, hydrological conditions, and relatively dry ground with no direct water stream. The paired sites also needed similar altitude, slope, aspect, and sun exposure (excluding sun exposure caused by trees).

2.2 Study design

The fieldwork was conducted during the Summer of 2022 from late May to late June, and included two collection rounds (period 1 = May 22nd – June 13th; period 2 = June 6th – June 27th). During a collection round, each of the 20 forest stands received four standard insect window traps for arthropod collection, and 16 artificial caterpillars to estimate predation rates (Figure 2).
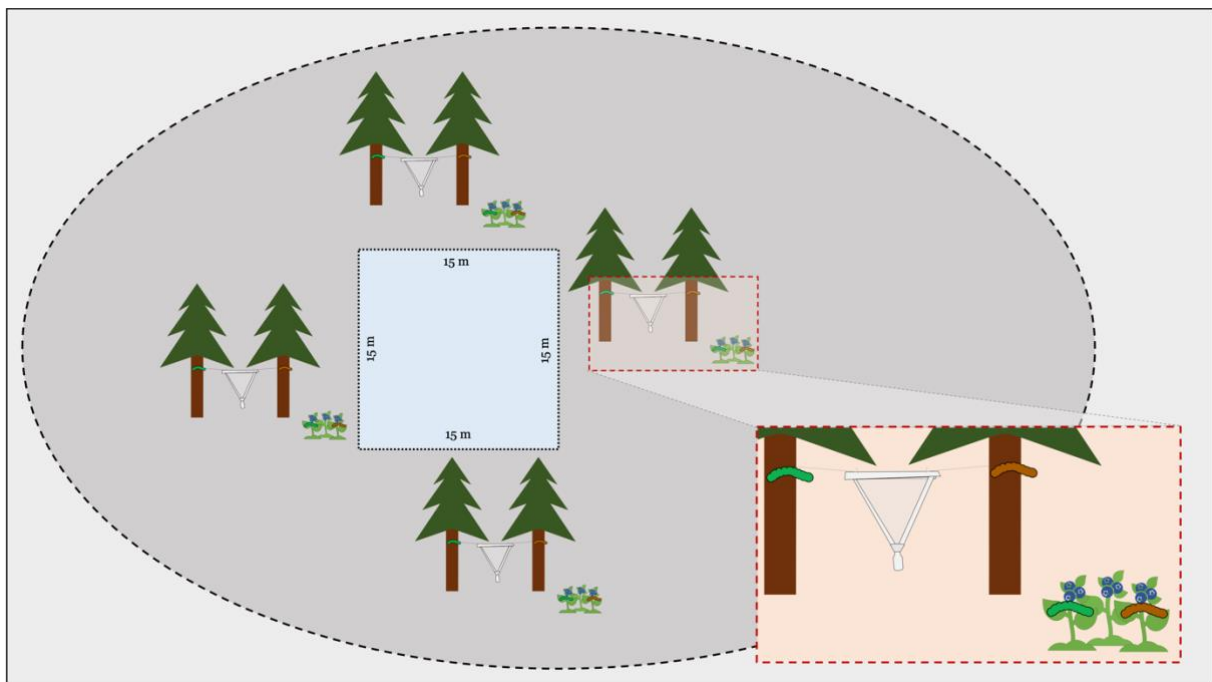
Figure 2. The figure shows the placement of the four window traps and the 16 artificial caterpillars within each of my 2 × 10 study sites.

2.2.1 Insect collection
Arthropods were collected using four flight intercepting IBL-2 window traps (Figure 3a) positioned at the outer edges of each central plot; one towards north, one towards south, one towards east, and one towards west (Figure 2). The traps were hung approximately 1-2 metres above the ground, and each contained a bottle filled with conservational mixture of 70% propylene-glycol, 30% water, and a drop

of Zalo to break the water membrane. Each bottle was fitted with a pair of small holes at the sides located just above the middle to prevent overflowing by water after rainfall. Insects and other arthropods collected in the traps were poured through filtering cups to remove the liquids and placed in freezers at –20°C for later analysis, and the bottles were refilled. The trap contents were collected twice (period 1 = May-June; period 2 = late June) after a 14-day exposure for each period.

We collected a total of 160 samples from the window traps after the two sampling periods, but only the beetles caught in the traps during the second period (late June) were used in this study. I also recorded the presence of anthills in each plot; no anthills in and around the plot (0), anthills present in and around plot, but not closest to the specific window trap with corresponding artificial caterpillars (1), and anthills present in and around plot and also closest to that specific window trap with corresponding artificial caterpillars (2). The anthill proximity to caterpillars could vary much, expanding from approximately 1-20 meters.

Figure 3. The free hanging IBL-2 window trap used in the study (a), and the artificial caterpillars with examples of bite marks from different taxa (b-e); (b) green artificial caterpillar attached to a tree stem with only the metal wire left, indicating a removed caterpillar, (c) brown artificial caterpillar on a tree stem with 'arthropod' bite marks, (d) green caterpillar attached to bilberry bush with 'bird' bite marks, and (e) brown artificial caterpillar on a bilberry bush with 'mammal' bite marks.

2.2.2 Artificial caterpillars

Predation rates were measured by using a balanced experimental design with standardized artificial caterpillars made by plasticine. The plasticine was rolled by hand into 20-30 mm long and 5 mm thick cylinders, with a metal wire through the core for attachment. To mimic common Scandinavian Lepidoptera larvae (Wetherbee et al., 2020), 320 of the artificial caterpillars were green and 320 were brown (Figure 3b-e).

The caterpillars were attached near each window trap with the metal wire: one brown and one green caterpillar on tree trunks (~1-2 metres high, often on thin branches), and one brown and one green caterpillar attached to bilberry bushes on tufts close by (~10-30 cm above the ground; either two separate tufts, or on the same tuft, but not too close to each other) (Figure 2). This added up to 16 artificial caterpillars within each forest stand, with an exposure period of approximately 14 days for two rounds. The reasoning for placing four specific caterpillars near a specific window trap, was to be able to compare the number of predatory beetles within each trap, with number of arthropod bite marks per artificial caterpillar close by. The caterpillar colours were randomized the first exposure period, and then the placement of the green and the brown caterpillars were swapped for the second period.

In total, I had four brown and four green caterpillars placed out on bilberry bushes, and four brown and four green caterpillars on tree stems in each forest stand for both periods. With this experimental design, the artificial caterpillars added up to a total of 640 (2 forest types × 10 sites × 16 artificial caterpillars × 2 time periods). Six artificial caterpillars and their wires were missing the second collection period (late June) and thus were excluded from the data analyses (CC: 1 green on tree stem, and 1 green on bilberry bush; NN: 1 brown and 1 green on tree stem, and the same on bilberry bush). This added up to as many as 634 plasteline caterpillars or wires to retrieved after exposure.

To make sure that the marks on the caterpillars would not be confused with those that were not made by predators (e.g., marks from the bilberry bush or tree stem), pictures were taken of the caterpillars before collection. To further prevent accidental marks during collecting, the caterpillars were placed inside cotton pads and stored in boxes. It is also important to note that the plasticine could have marks from humans (nail marks etc.), contain debris from the environment, have cracks from sun exposure, and could have somewhat dissolved when placed and/or collected during rainy weather.

2.3 Laboratory processing

The collected arthropods from the window traps were sorted to 'beetles' and 'other arthropods' in the lab and sent for further morphological identification of the beetle species by Sindre Ligaard (UiO). I only used data on the *predatory* beetles in the analyses for this study.

All artificial caterpillars were examined in the lab for identification of attack marks. The marks were categorized to come from either arthropod, bird, mammal, or unknown, based on a key provided by Low et al. (2014). Most studies using artificial prey do not identify predators to the species level, they rather broadly classify them (Bateman et al., 2017). There are nine different types of arthropod marks, including scratches, paired marks, pricks, deep distortions, disturbed surfaces, detached segments, granulated surfaces, dents, and elongated scratches, with scratches and paired marks being the most common (Khan, F. Z. A. & Joseph, S. V., 2021). Typical attack marks from 'arthropods' in this study

were paired "pinches", scratches, and pricks or holes. Marks registered as 'birds' were beak-marks, while marks from 'mammals' were "chunks" caused by their teeth. Cases where all the plasticine was fully removed from the wire in the field were categorized as 'removed', and these were caused by unidentifiable predators, but one can assume they were removed by birds (Low et al., 2014). The number of attack marks from arthropods were counted for each caterpillar exposed the second field period (late June). Attack marks from arthropods were mostly caused by insects, but could also have been caused by other arthropod taxa (e.g., spiders).

2.4 Data analysis

To analyse the data, I used R version 4.1.1 (R Core Team, 2021) and RStudio version 2022.07.1 (RStudio Team, 2022), and a range of packages, including 'readxl' (Wickham, 2022), 'ggplot2' (Wickham, 2016), 'lme4' (Bates et al., 2015), and 'effects' (Fox, 2003; Fox, 2019). Specifically, the 'glmer' function from the lme4 package (Bates et al., 2015) was used to fit five Generalized Linear Mixed Models (GLMM) to the data, with various fixed factors, and site as a random effect to take account for potential sources of variation in the data.

The dataset comprises binary and count data as response variables. The final models included four GLMMs of binary data with binomial distribution: the presence of (1) 'removed' caterpillars, and caterpillars with the presence of (2) 'arthropod', (3) 'bird', and (4) 'mammal' attack marks as the response variables. The fifth GLMM was of count data with negative binomial distribution, due to overdispersion when using Poisson distribution. This model had 'number of arthropod attack marks' per caterpillar as its response variable.

All models included several predictor variables, such as forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement (bilberry bush; tree stem), and caterpillar colour (brown; green). The four models with binary data also included the period of field exposure (1 = May-June; 2 = late June) as a predictor variable, but 'number of arthropod attack marks' per caterpillar was only counted for the second period (late June). All models, except 'mammal' and 'bird', included interactions between some predictor variables. The 'removed' model included interactions between forest type and placement, forest type and period, placement and colour, and placement and period. The 'arthropod' model included three interactions with period: forest type, placement, and colour. 'Number of arthropod attack marks' per caterpillar included an interaction between forest type and colour, in addition to an anthill variable, number of predatory beetle individuals, and number of predatory beetle species as predictor variables. The choices of the best fitting models are based on the Akaike Information Criterion (AIC) scores (Akaike, 1998), with subsequent models building on the previous ones by adding or removing terms that were deemed non-significant.

Finally, to illustrate the results, the 'ggplot2' package (Wickham, 2016) was used to make bar- and boxplots, and the effects was shown using the 'effects' package (Fox, 2003; Fox, 2019) with the 'allEffects' function on the respective GLMMs. The map was created by the 'leaflet' package (Cheng, 2022), and all icons in the figures are adapted from Flaticon (Flaticon, 2023a; Flaticon, 2023b; Flaticon, 2023c).

3 Results

3.1 Removed caterpillars

Out of the 634 artificial caterpillars collected from the field, a total of 108 (17%) had their plasticine completely removed with only the wire left (Table A2).

Forest type had a significant impact on the number of removed caterpillars (Table 1). Caterpillars in the former clear-cut forests were almost twice as likely to be removed compared to those in the near-natural forests (Figure 4a) (Supporting information in Appendix: Figure A1; Table A2). Removal rates within the forest types also showed a trend towards increasing during the second period (p = 0.093, Table 1), especially in the former clear-cut forests with almost doubled removal rates (Figure 4h).

Table 1. Generalized Linear Mixed Model (GLMM) of removed caterpillars, fit by maximum likelihood. The table shows the estimates and standard errors for the fixed effects (site as random effect), as well as their associated p-values. Note: Only the significant two-way interactions are included in the final model (indicated with '*').

Model	Variable	Estimate	Std. Error	Z value	Pr(>|z|)
Removed caterpillars	(Intercept)	–3.023	1.063	–2.844	0.005
	Forest type	–1.489	0.591	–2.520	**0.012**
	Placement	–1.542	0.661	–2.334	**0.020**
	Colour	–0.768	0.466	–1.649	0.099
	Period	1.063	0.546	1.945	**0.052**
	Forest type*placement	1.392	0.659	2.112	**0.035**
	Forest type*period	–1.166	0.654	–1.783	0.075
	Placement*colour	1.088	0.640	1.699	0.093
	Placement*period	1.796	0.664	2.706	**0.007**

Caterpillars placed on bilberry bushes in near-natural forests had the significantly lowest removal rates (Table 1), while removal within clear-cut forests showed no significant difference between tree stems and bilberry bushes (Table 1; Figure 4b). Number of removed caterpillars were generally significantly higher on tree stems compared to bilberry bushes (Table 1; Figure 4c), specifically during the second period (Table 1; Figure 4d).

Brown caterpillars showed a trend towards higher removal rates than green ones (p = 0.099, Table 1; Figure 4e). This colour preference trend was more apparent on bilberry bushes (p = 0.093, Table 1), with less removed green than brown caterpillars. In contrary to this, tree stems had higher removal rates of green than brown caterpillars (Table 1; Figure 4g).

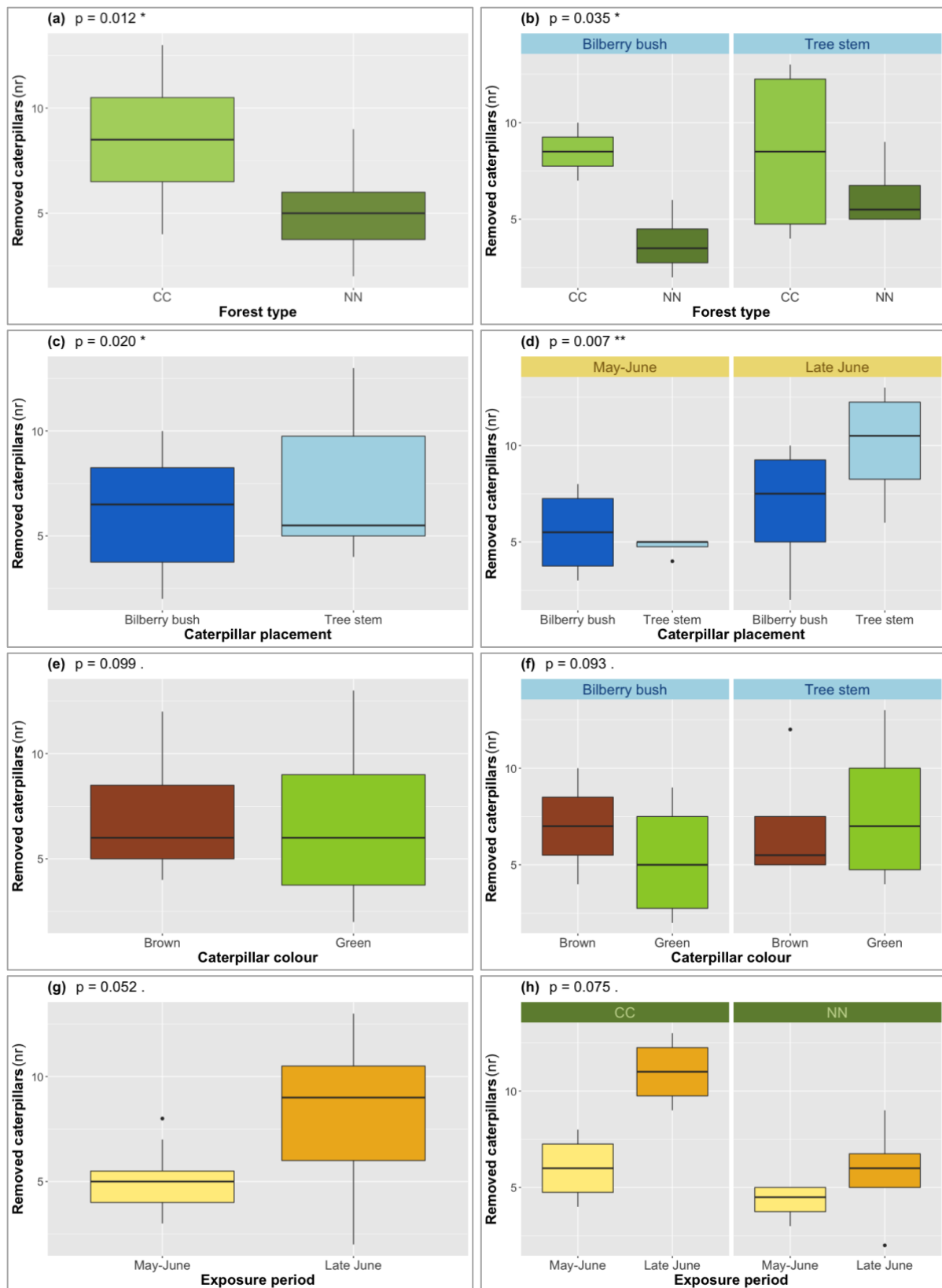**Figure 4.** Number of removed caterpillars according to (a) forest type (NN = near-natural forest; CC = former clear-cut forest), (b) forest type and caterpillar placement, (c) caterpillar placement, (d) caterpillar placement and exposure period (1 = May-June; 2 = late June), (e) caterpillar colour, (f) caterpillar colour and placement, (g) exposure period, and (h) forest type and exposure period.

3.2 Presence of attack marks by birds, mammals, and arthropods

A total of 526 artificial caterpillars were left in the field with the possibility to detect traces of predators. The majority of the caterpillars were attacked by arthropods (85.7%, 451 caterpillars, Table A3). Mammals attacked 46.2% (243, Table A4) of the artificial caterpillars, while birds attacked 13.9% (73, Table A5). Only 14 artificial caterpillars (2.2% of the total number of caterpillars, or 2.7% of the remaining caterpillars) showed no signs of attacks (NN: 6 caterpillars; CC: 8 caterpillars).

Forest type was a significant predictor of arthropod predation (Table 2), with higher predation rates in the near-natural forests compared to former clear-cut forests (Figure 5a) (Supporting information in Appendix: Figure A2; Table A3). This effect of forest type did also show a significant trend towards decreasing the second period of field exposure (p = 0.066, Table 2; Figure 5e). Arthropod predation rates were highest the first period, for both forest types, but even higher in the near-natural forests than in the former clear-cuts (Figure 5e).

Table 2. Summary of selected Generalized Linear Mixed Models (GLMM) of caterpillars attacked by arthropods, mammals, and birds, fit by maximum likelihood. The table shows the estimates and standard errors for the fixed effects (site as random effect), as well as their associated p-values. Note: Only the significant two-way interactions are included in the final arthropod model (indicated with '*').

Model	Variable	Estimate	Std. Error	Z value	Pr(>|z|)
Arthropods	(Intercept)	0.960	0.410	2.345	0.019
	Forest type	1.143	0.386	2.958	**0.003**
	Placement	1.280	0.395	3.243	**0.001**
	Colour	–0.014	0.366	–0.038	0.969
	Period	1.370	0.527	2.597	**0.009**
	Forest type*period	–0.987	0.538	–1.836	0.066
	Placement*period	–1.214	0.547	–2.219	**0.027**
	Colour*period	–0.991	0.537	–1.846	0.065
Mammals	(Intercept)	0.811	0.246	3.290	<0.001
	Forest type	0.224	0.205	1.093	0.274
	Placement	–2.251	0.212	–10.613	**<0.001**
	Colour	0.275	0.204	1.347	0.178
	Period	–0.385	0.206	–1.865	0.062
Birds	(Intercept)	–1.194	0.315	–3.792	<0.001
	Forest type	–0.130	0.265	–0.492	0.623
	Placement	–1.516	0.307	–4.933	**<0.001**
	Colour	–0.290	0.264	–1.101	0.271
	Period	0.244	0.264	0.924	0.356

Caterpillar placement also significantly affected arthropod predation rates (Table 2), with overall more attacked caterpillars on tree stems than on bilberry bushes (Figure 5b). This tree stem preference was only apparent during the first period (Table 2; Figure 5f).

Arthropods did not significantly prefer any caterpillar colour (Figure 5c), except for a trend towards significance when also taking account for the exposure period (p = 0.065, Table 2). Specifically, green caterpillars were predated less by arthropods than brown ones during the second period (Figure 5g).

Figure 5. Number of caterpillars attacked by arthropods according to (a) forest type (NN = near-natural forest; CC = former clear-cut forest), (b) forest type and exposure period (1 = May-June; 2 = late June), (c) caterpillar placement, (d) caterpillar placement and period, (e) caterpillar colour, (f) caterpillar colour and period, and (g) exposure period. The icon is adapted from Flaticon (2023b).

Neither birds nor mammals showed significant differences in predation rates between the two forest types (Table 2: Figure 6a-b) (Supporting information in Appendix: Figure A3-4; Table A4-5). Similarly, there were no significant preferences for caterpillar colour, as predation rates did not differ

significantly between brown and green caterpillars (Figure 6e-f). However, the placement of the caterpillar had a significant effect on predation by both birds and mammals. Predation rates were higher on bilberry bushes compared to tree stems for both taxa (Figure 6-c-d). Additionally, mammals exhibited a significant trend of higher predation rates during the first period compared to the second period ($p = 0.062$, Table 2; Figure 6g).
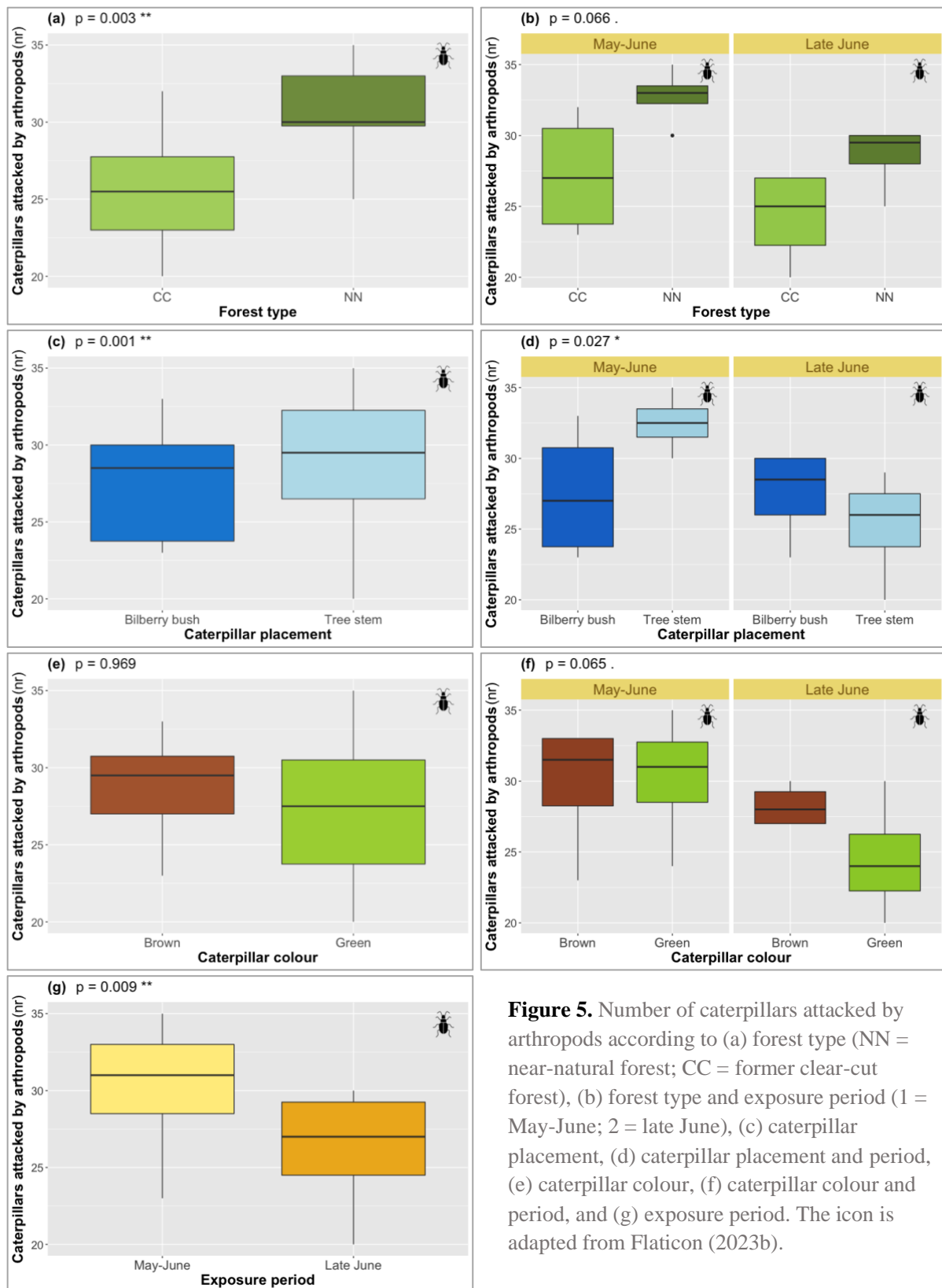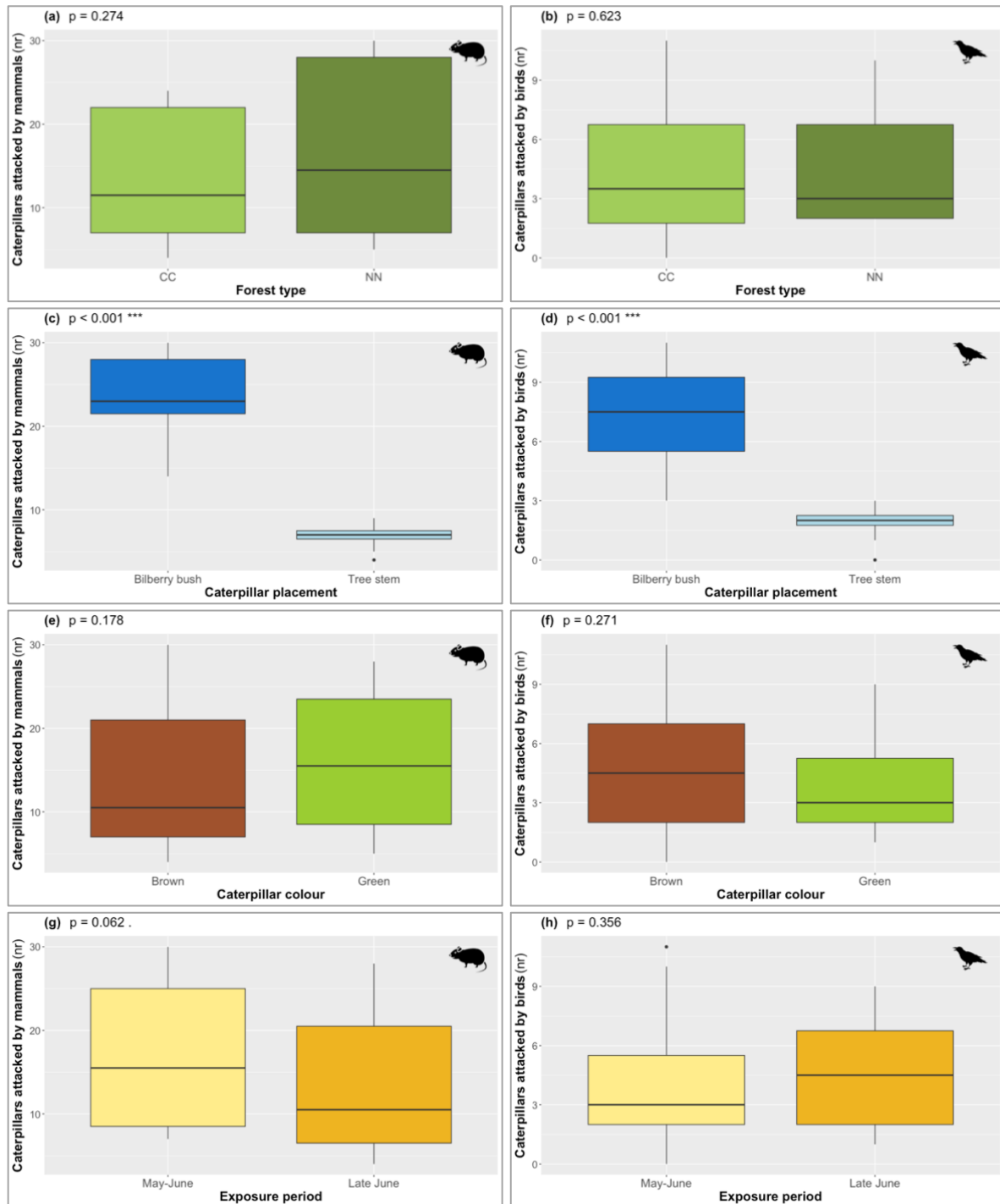

Figure 6. Number of caterpillars attacked by mammals or birds according to (a-b) forest type (NN = near-natural forest; CC = former clear-cut forest), (c-d) caterpillar placement (bilberry bush; tree stem), (e-f) caterpillar colour (brown; green), and (g-h) exposure period (first period = May-June; second period = late June). The icons are adapted from Flaticon (2023a); (2023c).

3.3 Number of arthropod attack marks per caterpillar

Although arthropods attacked more caterpillars in the near-natural forests than in former clear-cut forests (see previous subchapter), the number of arthropod attack marks per caterpillar was significantly highest in the former clear-cut forests (Table 3; Figure7a) (Supporting information in Appendix: Figure A7). Within paired sites, the forest type with highest arthropod predation rates of caterpillars did not necessarily result in the highest total numbers of arthropod attack marks on caterpillars (Figure A8).

Table 3. Generalized Linear Mixed Model (GLMM) of number of arthropod attack marks per caterpillar, fit by maximum likelihood. The table shows the estimates and standard errors for the fixed effects (site as random effect), as well as their associated p-values. Note: Only the significant two-way interaction is included in the final model (indicated with '*').

Model	Fixed effects	Estimate	Std. Error	Z value	Pr(>|z|)
Number of arthropod attack marks	(Intercept)	3. 916	0.330	11. 855	**<0.001**
	Forest type	−1.027	0.270	−3.802	**<0.001**
	Placement	0.171	0.177	0.964	0.335
	Colour	−0.980	0.270	−3.628	**<0.001**
	Anthills	0.603	0.135	4.479	**<0.001**
	Predatory beetles (nr)	0.022	0.012	1.765	0.078
	Predatory beetle species (nr)	−0.062	0.031	−1.995	**0.046**
	Forest type*colour	0.845	0.356	2.376	**0.018**

Brown caterpillars, especially in clear-cut forests, suffered significantly more arthropod attack marks per caterpillar compared to green ones (Figure 7c-d). According to the Generalized Linear Mixed Model (GLMM) analysis, neither caterpillars on tree stems nor on bilberry bushes showed significant trends towards more arthropod attack marks ($p = 0.335$, Table 3). However, the effect plot of the GLMM (Figure A7) revealed a significant trend indicating that arthropods primarily targeted caterpillars on tree stems (Figure 7b).

The presence and proximity to anthills had a significantly increasing effect on the number of arthropod attack marks per caterpillar (Figure 7g). Additionally, a higher number of predatory beetles caught in traps showed a significant trend towards a higher number of arthropod attack marks per caterpillar ($p = 0.078$, Table 3; Figure 7e). Conversely, an increasing number of predatory beetle species led to significantly fewer attack marks per caterpillar (Figure 7f).
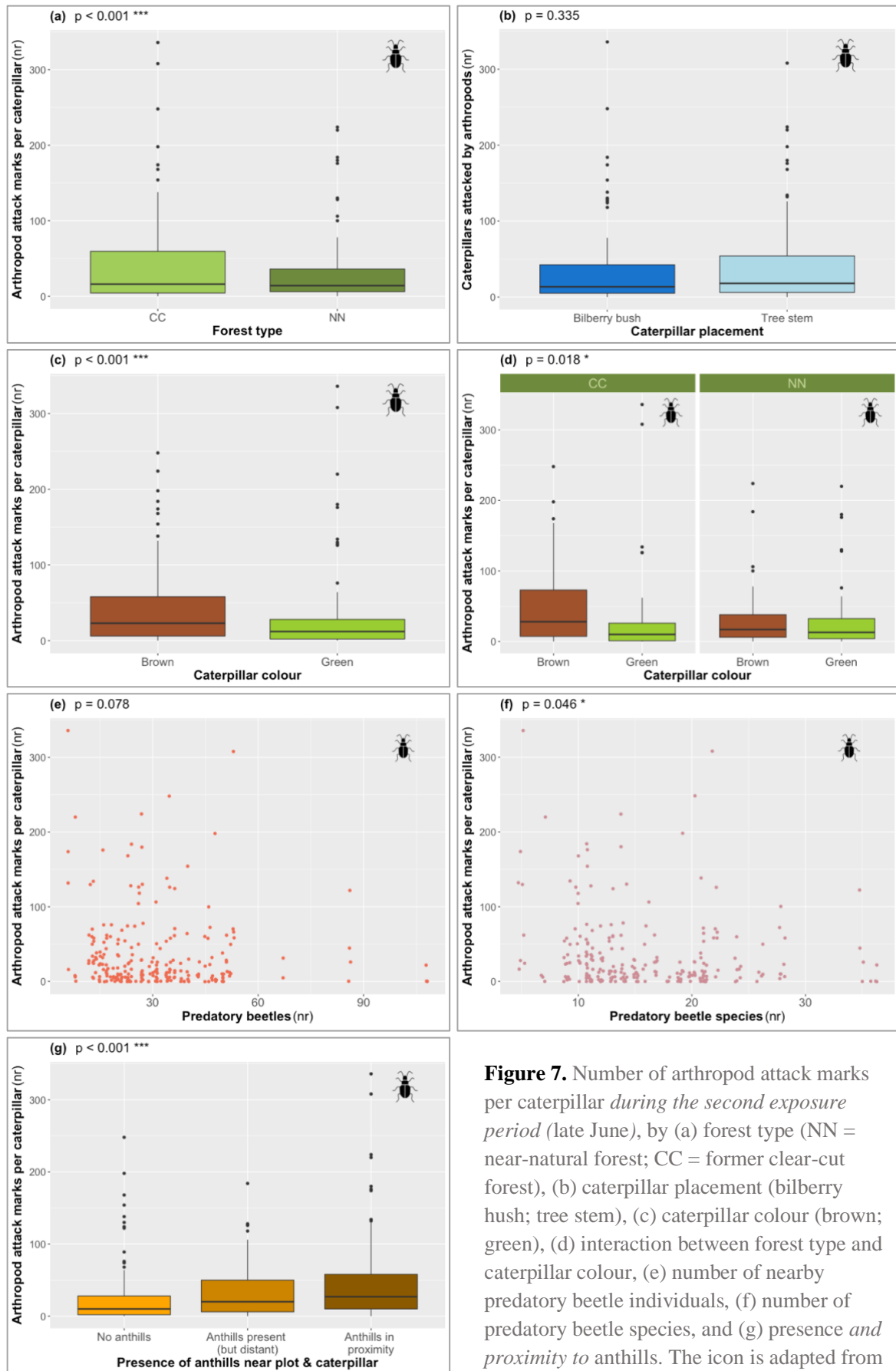
Figure 7. Number of arthropod attack marks per caterpillar *during the second exposure period (*late June*)*, by (a) forest type (NN = near-natural forest; CC = former clear-cut forest), (b) caterpillar placement (bilberry hush; tree stem), (c) caterpillar colour (brown; green), (d) interaction between forest type and caterpillar colour, (e) number of nearby predatory beetle individuals, (f) number of predatory beetle species, and (g) presence *and proximity to* anthills. The icon is adapted from Flaticon (2023b).

4 Discussion

Caterpillar predation rates differed between the two forest types for arthropods, as predicted, but not for mammals and birds exhibiting bite marks. Arthropod predation rates were significantly higher in the near-natural forests, while number of removed caterpillars was significantly higher in the former clear-cut forests. Different interactions between forest type, period, placement, and colour helped explain both the predation rates by arthropods and the removal of caterpillars in further detail.

4.1 Forest type

4.1.1 Near-natural forests have higher arthropod predation rates

Previous studies have shown that arthropods (e.g., carabids and ground beetles) are negatively affected by forest management (Chumak et al., 2015; Lange et al., 2014; Martikainen et al., 2000; Paillet et al., 2010). These findings are corresponding with my results, which showed significant differences of arthropod predation between the forest types, with significantly lower arthropod predation rates in former clear-cut forests compared to near-natural forests. The near-natural forests are expected to have higher habitat heterogeneity compared to former clear-cut ones, which indirectly promotes natural enemies by increasing the availability of alternative prey through greater resource availability (Klapwijk et al., 2016). Specific characteristics directly promoting natural enemies, like predatory arthropods, increased understory vegetation, diversity, and tree age structure. A wider range of microhabitats, like in near-natural forests, provide the predatory arthropods with increased feeding resources, habitat shelters, and hiding places (Bellone et al., 2020; Klapwijk et al., 2016; Matevski et al., 2021), and thus higher arthropod predation rates within near-natural forests, corresponding with my results.

4.1.2 Former clear-cut forests have higher numbers of arthropod attack marks per caterpillar

Despite overall higher abundances of predatory arthropods in near-natural forests compared to former clear-cut forests (Chumak et al., 2015), as evidenced in my study by higher arthropod predation rates, number of arthropod attack marks per caterpillar showed contradicting results, with significantly more attack marks per caterpillar in the clear-cut forests. These contradicting results emphasises the crucial need to consider the specific species compositions and densities of the predators when evaluating predation rates, caused by different species' different behaviour and foraging preference (Khan, F. & Joseph, S., 2021; Liu et al., 2020). Research have demonstrated instances where a single predatory species accounted for a significant proportion of all predatory individuals present (Fora et al., 2014), while others have showcased that not all predatory arthropods predate on caterpillars, as evidenced by Greenop et al. (2019). This further emphasise the consideration that certain species and individuals possibly drive higher predator activity, causing more arthropod attack marks in certain cases.

4.1.3 Forest type has no effect on mammal or bird predation rates

Mammal predation did not show any significant differences between the two forest types, and neither did bird predation when only taking account for the remaining caterpillars with bird bite marks. Birds and mammals, being highly mobile and visual species, are efficient in detecting new sources of prey, and are likely to forage in both forest types (Gossner et al., 2020). However, as this study solely examined predation rates of artificial prey and did not assess the abundances or species diversity of mammals and birds within the forests, the underlying mechanisms driving these observed patterns remain unclear. Further studies are needed to shed light whether these terrestrial predators are negatively affected by forest management intensities.

4.1.4 Former clear-cut forests have higher removal predation rates

Contrary to my predictions, and the results of arthropod predation rates, the former clear-cut forests exhibited nearly twice as many removed caterpillars compared to the near-natural forests, highlighting the significant influence of forest type on removal rates. While the exact predator group responsible for these removals cannot be determined through bite mark identification, previous research documenting complete removal of artificial caterpillars by birds (Low et al., 2014) suggests that birds are likely the primary predators in this context, but we cannot exclude other taxa, like small mammals such as squirrels. Assuming that birds are responsible for removal rates, these significant results of forest type on birds' removal predation is contradicting for caterpillars with only bird bite mark occurrences, which showcased no significant effect of forest type.

In my study, caterpillars were significantly more removed in former clear-cut forests, contradicting to expected results. These results might be explained by the reduced structural diversity of forest stands. Even-aged stands in former clear-cut forests may result in fewer refuges for prey, and thus greater vulnerability to natural enemies (Klapwijk et al., 2016), like visual-oriented birds. In contrast, near-natural forests with greater habitat heterogeneity serve as higher densities of visual obstacles for birds, potentially resulting in lower bird predation rates in near-natural forests.

These contradicting findings of whether bird predation rates are influenced by forest types or not, express a weakness in the study method with artificial caterpillars. Without camera monitoring or any other concrete evidence, we cannot with certainty conclude, only assume, whether the removed caterpillars were predated by birds or other predators. Other studies on bird predation rates between forest types did not find significant effects between managed and unmanaged forests (Gossner et al., 2020), and neither did this study, unless assuming only birds fully removed the artificial caterpillars.

The unexpected results of higher removal rates within former clear-cut forests compared to in near-natural forests suggests that additional factors may be influencing the observed patterns, possibly landscape pattern. Other possible explanations could include altered resource availability or specific foraging preferences of bird species within the former clear-cut forests. Moreover, global variations in species richness among different forest types highlight the importance of studying poorly investigated species groups in specific locations (Paillet et al., 2010). Further investigation is warranted to unravel the underlying mechanisms driving the observed differences in bird predation rates between the forest types. Understanding these dynamics will provide valuable insights into the complex interactions between forest management, forest community structure, and bird predation in ecological systems.

4.2 Caterpillar placement

4.2.1 Tree stems have higher arthropod predation rates

Caterpillar placement significantly affected arthropod predation rates, with overall more attacked caterpillars on tree stems than on bilberry bushes, especially the first period. To better explain this predation preference of caterpillar placement, one can look further into the vertical distribution of arthropods in forests (Ulyshen, 2011). Many arthropods can be found in microhabitats on tree stems and branches (Plewa et al., 2017), and predatory arthropods can even be attracted by volatile compounds released by damaged trees. This attracting of natural enemies is a way for the tree to indirectly get rid of pests, while the predators get a delicious meal with high prey densities (Mumm & Hilker, 2006). High prey abundances within microhabitats on trees cause many predatory arthropods to search for prey between the canopy and stem, where prey density and species richness is high (Plewa et al., 2017), causing high arthropod predation of caterpillars on tree stems as presented in my study.

Another explanatory variable can be the increased visual exposure on stems compared to when hidden within the microhabitats in the vegetation (Matevski et al., 2021). For example, caterpillars placed on trees containing reduced numbers of branches, are at higher risks of being attacked by predators due to fewer refuges (Sipos & Kindlmann, 2013). No conscious attempt was made to try and hide the caterpillars within the vegetation, probably causing caterpillars on stems versus bushes being more visually exposed to predators. Within the forest floor vegetation, predators likely had to search longer for the caterpillars, causing highest predation rates on easily spotted caterpillars on tree stems. My results of higher arthropod predation rates are inconsistent with some other studies showing higher predation rates on the ground (Wetherbee et al., 2020). This express the further need for research on complex interactions like predator-prey. Take spatial structure into account when analysing predation rates on caterpillars.

The arthropod predation on tree stems was highest during the first period (May-June). This corresponds with the knowledge of predator-prey ratios distinct seasonal patterns on trees. Prey species richness and abundances have been reported to peak in May (Southwood et al., 2004; Southwood et al., 2005), and predatory and herbivore beetles have been observed to peak in May–June (Stork & Hammond, 2013).

4.2.2 Bilberry bushes have higher mammal and bird predation rates

Caterpillar placement was the only variable statistically significant for all predator groups. Mammal predation rates of caterpillars was significantly higher on bilberry bushes than on tree stems. These results are consistent with the common knowledge of many small mammals, like rodents, being ground-dwelling species (Bogdziewicz & Zwolak, 2014; Ulyshen, 2011). As expected, caterpillars placed closer to the ground, on bilberry bushes, therefore showed higher mammal predation rates compared to caterpillars positioned on tree stems.

Caterpillars with bird bite marks also suffered higher predation rates on bilberry bushes compared to on tree stems. Many insectivorous birds use a foraging strategy of carefully inspecting surfaces within microhabitats, called gleaning, rather than hovering (Holmes & Robinson, 1981; Kwok, 2009). With this foraging strategy, will birds be able to locate the artificial caterpillars within the bilberry bushes in the understory vegetation, and predate more on them. Studies have also proven that bird predation

rates is highest in the understory up to 2 meters above the forest floor, and decreasing with height (Aikens et al., 2013). These findings help support the results in present study, with higher bird predation rates closer to the ground.

4.2.3 Tree stems have higher removal predation rates

Caterpillars placed on tree stems suffered significantly higher removal rates than caterpillars on bilberry bushes, contradicting to my previous findings of more caterpillars with bird bite marks placed on bilberry bushes. Still assuming birds are the primary predators of completely removed caterpillars (Low et al., 2014), the higher removal rates on tree stems implies that the responsible bird species employ different foraging strategies compared to those leaving only bite marks. Studies on foraging ecology of insectivorous bird species have showcased variations in their utilization of vertical strata and microhabitats, further indicating differences in foraging preferences between species (Kwok, 2009).

Another possible cause for the birds' abilities to more easily fully remove caterpillars placed on tree stems compared to on bilberry bushes, is the fact that these caterpillars are visually more exposed, making them easier targets. Bilberry bushes facilitates microhabitats with refuges from predators (Aikens et al., 2013). The exposed nature of caterpillars on tree stems gives the predators the possibility to easier capture the entire plasticine, with only the wire remaining. Interestingly, were higher removal rates on tree stems versus on bilberry bushes significant within the near-natural forests, but not within clear-cut forests. This can further possibly be explained by the higher vegetational diversity within near-natural forests, rendering better shelters and hiding places from predators compared to on tree stems (Klapwijk et al., 2016). These contradictory findings regarding bird predation rates according to removal rates versus beak marks on caterpillars, underscore the importance of conducting additional research on bird species' foraging strategies on caterpillars within different vertical stratification of forests.

4.3 Caterpillar colour

4.3.1 Contrasting colours give higher removal predation and higher numbers of arthropod attack marks per caterpillar

Caterpillar colour did not significantly affect mammal or bird predation rates, corresponding with previous studies (Seifert et al., 2015), and neither did it for arthropod predation rates, corresponding with previous studies (Aslam et al., 2020; Pan et al., 2021). Removal rates showed a slight trend towards more removed green rather than brown caterpillars, especially on tree stems, while arthropods showed a different trend towards fewer green compared to brown caterpillars during the second period. During this period, numbers of arthropod attack marks per caterpillar was also recorded, corresponding with a significant preference for brown rather than green caterpillars. Both these results can possibly be explained by the background substrate (Roeder et al., 2023; Wetherbee et al., 2020).

Green caterpillars on bilberry bushes, and brown caterpillars on tree stems, both works as camouflaging colours, thus rendering brown caterpillars on bilberry bushes and green ones on tree stems as contrasting and easier to detect. For arthropod predation rates for instance, as the season progresses, green caterpillars blended more effectively with the surrounding forest vegetation, affording them greater protection and reduced visibility. Consequently, brown caterpillars with

contrasting colour compared to the vegetation experience higher rates of arthropod predation and a greater number of attack marks per caterpillar. These camouflaging versus contrasting results can also explain the removal rates of caterpillars (Bateman et al., 2017; Hernandez-Agueroa et al., 2020). This visual impact is further supported by the findings of Khan, F. and Joseph, S. (2021), who specifically identified a colour effect on arthropod predation during daytime versus night, underscoring the importance of prey visibility in daylight conditions. These findings suggest that colour plays a crucial role in the survival of caterpillars in the wild, as it affects their vulnerability to predation. The effectiveness of colour can also vary depending on factors such as the geographical location, time of year, and the placement of the caterpillar.

4.4 Anthills and predatory beetles

4.4.1 Proximity to anthills cause higher numbers of arthropod attack marks per caterpillar

Forest stands without anthills received lower numbers of attack marks per caterpillar compared to stands with anthills. Additionally, when an anthill was in proximity to the specific caterpillar, the number of marks per caterpillars was even higher. Anthills have been recorded as the dominant predator of caterpillars in several studies (Hernandez-Flores et al., 2021; Khan, F. & Joseph, S., 2021; Liu et al., 2020). Ant assemblage composition, compared to total abundance and species richness, have been shown to better explain variations in predation rate of artificial caterpillars, showcased in a study where 85% of the present ant species were caterpillar predators (Liu et al., 2020). With this additional knowledge, my results could further have explained relationships between predatory arthropod species and caterpillars with calculations of ant assemblages with Shannon's evenness.

Previous studies have also documented that the presence of ant colonies increased densities of both generalist predators and herbivores (Sanders & van Veen, 2011). Ants are known to have mutalistic interactions with sap-feeding herbivores (e.g., aphids) (Clark et al., 2016), causing us to believe that forest stands with anthills contained higher prey densities, and thus higher predator densities. These results align with my study, by proving that higher densities of ants, through the presence of anthills, promote higher numbers of attack marks on caterpillars. My findings highlight the importance of certain predatory species or groups within trophic interactions.

4.4.2 Increasing numbers of predatory beetle species and individuals cause contradicting numbers of arthropod attack marks per caterpillar

With higher abundances of predatory beetles caught nearby, each caterpillar suffered correspondingly higher numbers of arthropod attack marks, supported by other studies showing increased attack rates with higher densities of predators (Greenop et al., 2019).

Contrary to the effect of number of predatory beetle individuals, increasing abundances of predatory beetle species caused fewer arthropod attack marks per caterpillar. This reducing rather than increasing effect can be due to the actual composition of species. In some cases, there might be several species, but not necessarily many individuals, while in other cases, most of the present individuals are of the same species (Fora et al., 2014). The identity of said species is also important for the attack rates (Greenop et al., 2019). For example, predatory carabids are presumed to significantly regulate the ecological network of invertebrates through predation (Ruzickova & Elek, 2021), but this is not be the case for all predatory species and families. Greenop et al. (2019) found that the foliar-active ladybird

(*Harmonia axyridis* (Coleoptera: Coccinellidae)) only predated on live aphids, and not the caterpillar-mimicking prey. Another study found that higher densities of ants, rather than carabids, attacked artificial caterpillars (Khan, F. & Joseph, S., 2021). These results emphasise that although there might be many individuals in a forest stand, it is important to consider the species identity of the predators. Additionally, although there are many species, they might not predate on the same prey, highlighting important trophic interactions within forests.

4.5 Limitations and recommendations for future research

In addition to the factors discussed previously, there are several other considerations to keep in mind when using the artificial prey method. One important factor is the marks left on the prey by predators. Low et al. (2014) recommend using multiple individuals to identify bite marks on prey, as this can improve the accuracy of predator identification. In this study, having several people identify bite marks on the artificial caterpillars may have strengthened the results.

Another important factor is scent. Chemical cues from prey can play an important role in predator-prey interactions, as shown in a study by Ferrante et al. (2017) that tested the impact of chemical cues from dead cabbage moth larvae on predation rates by carabid predators. The use of artificial prey may be biased towards visual-oriented predators, but the addition of scent cues may help to make the prey more realistic and attract predators that rely on chemical cues.

Camera monitoring can also be useful for identifying predator species on artificial prey, as demonstrated in a study by Khan, F. Z. A. and Joseph, S. V. (2021). However, it is important to note that not all attack marks may be caused by predators using their mouthparts, as arthropods may also use their legs to manipulate their prey.

Furthermore, there is a need to develop alternative methods for identifying predators of artificial caterpillars in cases where they are completely removed from the field, leaving no discernible attack marks. These efforts will contribute to a more comprehensive understanding of predator-prey dynamics and improve our ability to accurately assess the role of birds or potential other predators in caterpillar predation.

5 Conclusions

The artificial caterpillar method is a simple way to measure predation rates between different forest types, although it has some limitations. Arthropod predation rates differ between forest types, with more occurrences of predation of caterpillars in near-natural forests, but higher numbers of attack marks per caterpillar in former clear-cut forests. Higher arthropod predation rates within near-natural forests are possibly caused by increased numbers of microhabitats, both on the older and structurally tree stems, and within the forest floor. Increased numbers of microhabitats both promote higher prey and natural enemy abundances, providing shelters and hiding places. Such structures promote habitat heterogeneity, which additionally cause caterpillars on bilberry bushes rather than on tree stems to be predated on. Camouflaging caterpillar colours can help prey escape certain death by predators, especially green caterpillars that also hide within the vegetation on the forest floor, highlighting the importance of several interactions in forest ecosystems.

Mammal and bird predation was not affected by forest type, showcasing their ability to better adapt within different forest management regimes. Dominant species, like ants, promote higher numbers of attack marks on caterpillars. Additionally, when looking at either abundances of predatory beetles or number of predatory beetle species, the number of bite marks per caterpillar are contradicting. Higher numbers of predatory beetles present increased number of attack marks, as expected, but it is important to look further into the species compositions, showcased with reduced numbers of attack marks with more predatory beetle species. All these results highlight the importance of taking account for several variables when looking at predator-prey interaction in forest ecosystems, and thus maybe promoting potential strategies for conservation and management of different forest species.

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Appendix

Table A1. Coordinates (latitude, longitude, and metres above sea level) of the main plots in the forest stands (NN = near-natural forest; CC = former clear-cut forest).

Abbreviation	Site	Forest type	Latitude	Longitude	m.a.s.l
HAL	Halden	NN	59.079766	11.546541	213
		CC	59.079808	11.55948	205
BLA	Blåfjell	NN	59.783114	10.381255	289
		CC	59.788026	10.386507	322
STO	Storås	NN	60.259161	9.700641	488
		CC	60.261514	9.709084	423
SKO	Skotjernfjell	NN	60.24224	10.795997	602
		CC	60.241347	10.808372	577
GUL	Gullenhaugen	NN	60.352613	10.796628	667
		CC	60.369963	10.787187	590
TRE	Tretjerna	NN	60.583648	10.226522	418
		CC	60.577289	10.228499	516
OYT	Øytjern	NN	60.838906	10.38122	644
		CC	60.843198	10.408981	662
HEM	Hemberget	NN	60.915115	12.206472	579
		CC	60.921114	12.188859	580
BRA	Braskreidfoss	NN	60.739768	11.928444	425
		CC	60.747583	11.926343	367
SAR	Särkilampi	NN	60.187711	12.508022	359
		CC	60.200019	12.529663	372

Table A2. Number of removed caterpillars (% (nr)) according to each forest type (NN = near-natural forest; CC = former clear-cut forest), for different variables of the artificial caterpillar: placement, colour, and exposure period (1 = May-June; 2 = late June).

Predator	Placement	Colour	Period	Forest type		
				NN	**CC**	**Total**
Unknown (removed)	Bilberry bush	Brown	1	10.0 (4)	20.0 (8)	**15.0** (12)
			2	15.4 (6)	25.0 (10)	**20.3** (16)
		Green	1	7.5 (3)	17.5 (7)	**12.5** (10)
			2	5.1 (2)	23.1 (9)	**14.1** (11)
	Tree stem	Brown	1	12.5 (5)	12.5 (5)	**12.5** (10)
			2	15.4 (6)	30.0 (12)	**22.8** (18)
		Green	1	12.5 (5)	10.0 (4)	**11.3** (9)
			2	23.1 (9)	33.3 (13)	**28.2** (22)
	Bilberry bush	Brown		12.7 (10)	22.5 (18)	**17.6** (28)
		Green		6.3 (5)	20.3 (16)	**13.3** (21)
	Tree stem	Brown		13.9 (11)	21.3 (17)	**17.6** (28)
		Green		17.7 (14)	21.5 (17)	**19.6** (31)
	Bilberry bush		1	8.8 (7)	18.8 (15)	**13.8** (22)
			2	10.3 (8)	24.1 (19)	**17.2** (27)
	Tree stem		1	12.5 (10)	11.3 (9)	**11.9** (19)
			2	19.2 (15)	31.7 (25)	**25.5** (40)
	Bilberry bush			9.5 (15)	21.4 (34)	**15.5** (49)
	Tree stem			15.8 (25)	21.4 (34)	**18.6** (59)
		Brown		13.3 (21)	21.9 (35)	**17.6** (56)
		Green		12.0 (19)	20.9 (33)	**16.5** (52)
			1	10.6 (17)	15.0 (24)	**12.8** (41)
			2	14.7 (23)	27.8 (44)	**21.3** (67)
Total				**12.7** (40)	**21.4** (68)	**17.0** (108)

Table A3. Number of caterpillars attacked by arthropods (% (nr)) from the remaining caterpillars according to each exposure period, with different variables and interactions for the artificial caterpillars: forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement and colour.

Predator	Forest type	Placement	Colour	Exposure period		
				May-June	**Late June**	**Total**
Arthropod	NN	Bilberry bush	Brown	91.7 (33)	90.9 (30)	**91.3** (63)
			Green	81.1 (30)	81.1 (30)	**81.1** (60)
		Tree stem	Brown	94.3 (33)	87.9 (29)	**91.2** (62)
			Green	100.0 (35)	83.3 (25)	**92.3** (60)
	CC	Bilberry bush	Brown	71.9 (23)	90.0 (27)	**80.6** (50)
			Green	72.7 (24)	76.7 (23)	**74.6** (47)
		Tree stem	Brown	85.7 (30)	96.4 (27)	**90.5** (57)
			Green	88.9 (32)	76.9 (20)	**83.9** (52)
	NN	Bilberry bush		86.3 (63)	85.7 (60)	**86.0** (123)
		Tree stem		97.1 (68)	85.7 (54)	**91.7** (122)
	CC	Bilberry bush		72.3 (47)	83.3 (50)	**77.6** (97)
		Tree stem		87.3 (62)	87.0 (47)	**87.2** (109)
	NN		Brown	93.0 (66)	89.4 (59)	**91.2** (125)
			Green	90.3 (65)	82.1 (55)	**86.3** (120)
	CC		Brown	79.1 (53)	93.1 (54)	**85.6** (107)
			Green	81.2 (56)	76.8 (43)	**79.2** (99)
		Bilberry bush	Brown	82.4 (56)	90.5 (57)	**86.3** (113)
			Green	77.1 (54)	79.1 (53)	**78.1** (107)
		Tree stem	Brown	90.0 (63)	91.8 (56)	**90.8** (119)
			Green	94.4 (67)	80.4 (45)	**88.2** (112)
	NN			91.6 (131)	85.7 (114)	**88.8** (245)
	CC			80.1 (109)	85.1 (97)	**82.4** (206)
		Bilberry bush		81.0 (119)	84.6 (110)	**82.1** (220)
		Tree stem		92.2 (130)	86.3 (101)	**89.5** (231)
			Brown	86.2 (119)	91.1 (113)	**88.5** (232)
			Green	85.8 (121)	79.7 (98)	**83.0** (219)
Total				**86.0** (240)	**85.4** (211)	**85.7** (451)

Table A4. Number of caterpillars attacked by mammals (% (nr)) from the remaining caterpillars according to each exposure period, with different variables and interactions for the artificial caterpillars: forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement, and caterpillar colour.

Predator	Forest type	Placement	Colour	Exposure period		
				May-June	**Late June**	**Total**
Mammal	NN	Bilberry bush	Brown	83.3 (30)	60.6 (20)	**72.5** (50)
			Green	75.7 (28)	75.7 (28)	**75.7** (56)
		Tree stem	Brown	20.0 (7)	21.2 (7)	**20.6** (14)
			Green	25.7 (9)	16.7 (5)	**21.5** (14)
	CC	Bilberry bush	Brown	75.0 (24)	46.7 (14)	**61.3** (38)
			Green	66.7 (22)	73.3 (22)	**69.8** (44)
		Tree stem	Brown	20.0 (7)	14.3 (4)	**17.5** (11)
			Green	25.0 (9)	26.9 (7)	**25.8** (16)
	NN	Bilberry bush		79.5 (58)	68.6 (48)	**74.1** (106)
		Tree stem		22.9 (16)	19.0 (12)	**21.1** (28)
	CC	Bilberry bush		70.8 (46)	60.0 (36)	**65.6** (82)
		Tree stem		22.5 (16)	20.4 (11)	**21.6** (27)
	NN		Brown	52.1 (37)	40.9 (27)	**46.7** (64)
			Green	51.4 (37)	49.3 (33)	**50.4** (70)
	CC		Brown	46.3 (31)	31.0 (18)	**39.2** (49)
			Green	44.9 (31)	51.8 (29)	**48.0** (60)
		Bilberry bush	Brown	79.4 (54)	54.0 (34)	**67.2** (88)
			Green	71.4 (50)	74.6 (50)	**73.0** (100)
		Tree stem	Brown	20.0 (14)	18.0 (11)	**19.1** (25)
			Green	25.4 (18)	21.4 (12)	**23.6** (30)
	NN			51.7 (74)	45.1 (60)	**48.6** (134)
	CC			45.6 (62)	41.2 (47)	**43.6** (109)
		Bilberry bush		75.4 (104)	64.6 (84)	**70.1** (188)
		Tree stem		22.7 (32)	19.7 (23)	**21.3** (55)
			Brown	49.3 (68)	36.3 (45)	**43.1** (113)
			Green	48.2 (68)	50.4 (62)	**49.2** (130)
Total				**48.7** (136)	**43.3** (107)	**46.2** (243)

Table A5. Number of caterpillars attacked by birds (% (nr)) from the remaining caterpillars according to each exposure period, with different variables and interactions for the artificial caterpillars: forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement, and caterpillar colour.

| Predator	Forest type	Placement	Colour	Exposure period		
				May-June	**Late June**	**Total**
Bird	NN	Bilberry bush	Brown	27.8 (10)	18.2 (6)	**23.2** (16)
			Green	8.1 (3)	24.3 (9)	**16.2** (12)
		Tree stem	Brown	5.7 (2)	9.1 (3)	**7.4** (5)
			Green	5.7 (2)	6.7 (2)	**6.2** (4)
	CC	Bilberry bush	Brown	34.4 (11)	20.0 (6)	**27.4** (17)
			Green	12.1 (4)	30.0 (9)	**20.6** (13)
		Tree stem	Brown	0.0 (0)	7.1 (2)	**3.2** (2)
			Green	8.3 (3)	3.8 (1)	**6.5** (4)
	NN	Bilberry bush		17.8 (13)	21.4 (15)	**19.6** (28)
		Tree stem		5.7 (4)	7.9 (5)	**6.8** (9)
	CC	Bilberry bush		23.1 (15)	25.0 (15)	**24.0** (30)
		Tree stem		4.2 (3)	5.6 (3)	**4.8** (6)
	NN		Brown	16.9 (12)	13.6 (9)	**15.3** (21)
			Green	6.9 (5)	16.4 (11)	**11.5** (16)
	CC		Brown	16.4 (11)	13.8 (8)	**15.2** (19)
			Green	10.1 (7)	17.9 (10)	**13.6** (17)
		Bilberry bush	Brown	30.9 (21)	19.0 (12)	**25.2** (33)
			Green	10.0 (7)	26.9 (18)	**18.2** (25)
		Tree stem	Brown	2.9 (2)	8.2 (5)	**5.3** (7)
			Green	7.0 (5)	5.4 (3)	**6.3** (8)
	NN			11.9 (17)	15.0 (20)	**13.4** (37)
	CC			13.2 (18)	15.8 (18)	**14.4** (36)
		Bilberry bush		20.3 (28)	23.1 (30)	**21.6** (58)
		Tree stem		5.0 (7)	6.8 (8)	**5.8** (15)
			Brown	16.7 (23)	13.7 (17)	**15.3** (40)
			Green	8.5 (12)	17.1 (21)	**12.5** (33)
Total				**12.5** (35)	**15.4** (38)	**13.9** (73)
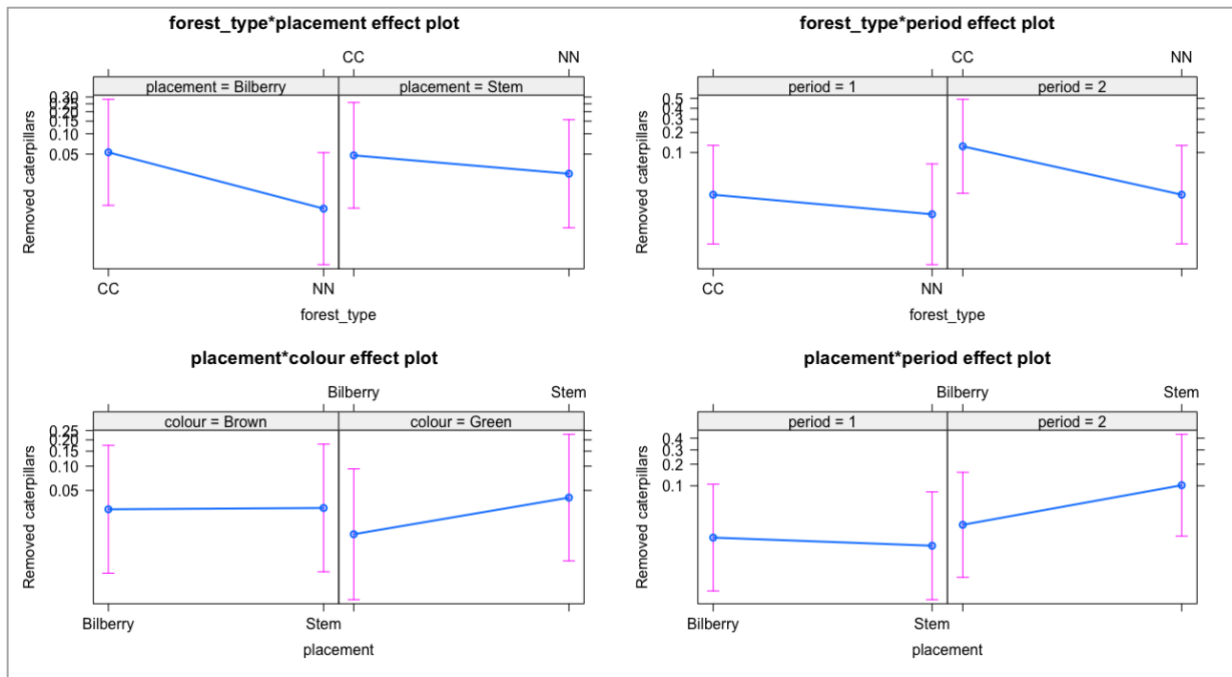
Figure A1. Effect plots of the Generalized Linear Mixed Model (GLMM) of removed caterpillars, including interactions between forest type (NN = near-natural forest; CC = former clear-cut forest) and caterpillar placement, forest type and exposure period (1 = May-June; 2 = late June), caterpillar placement and colour, and caterpillar placement and exposure period.
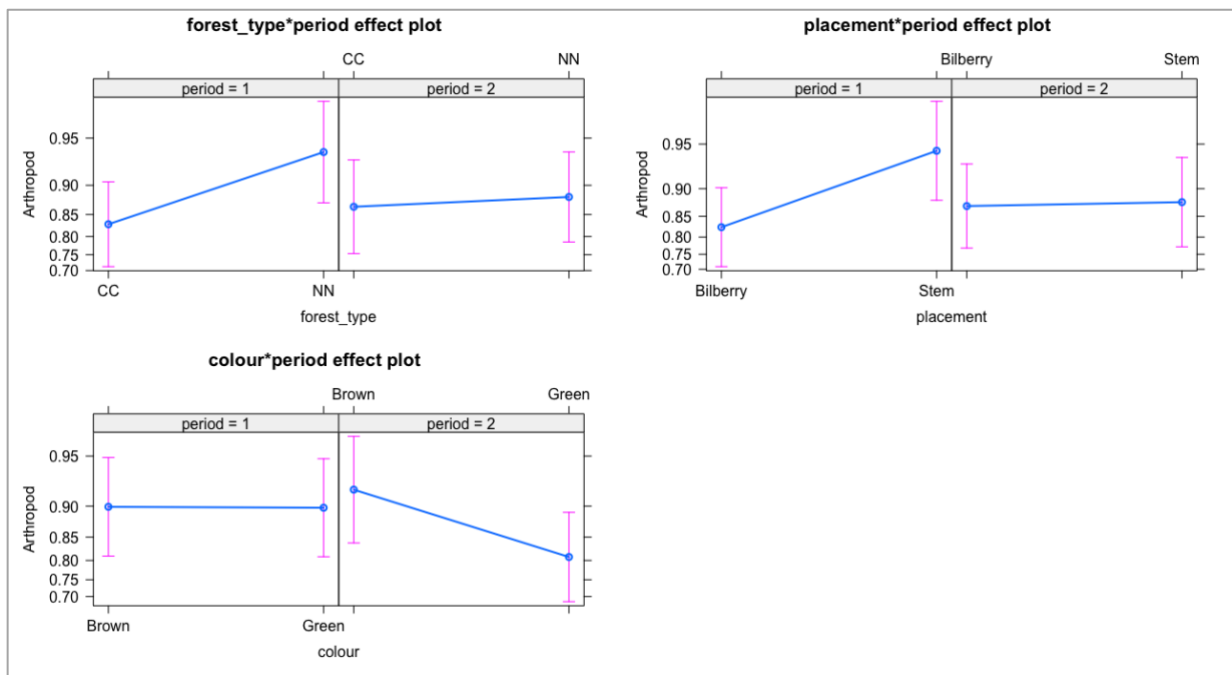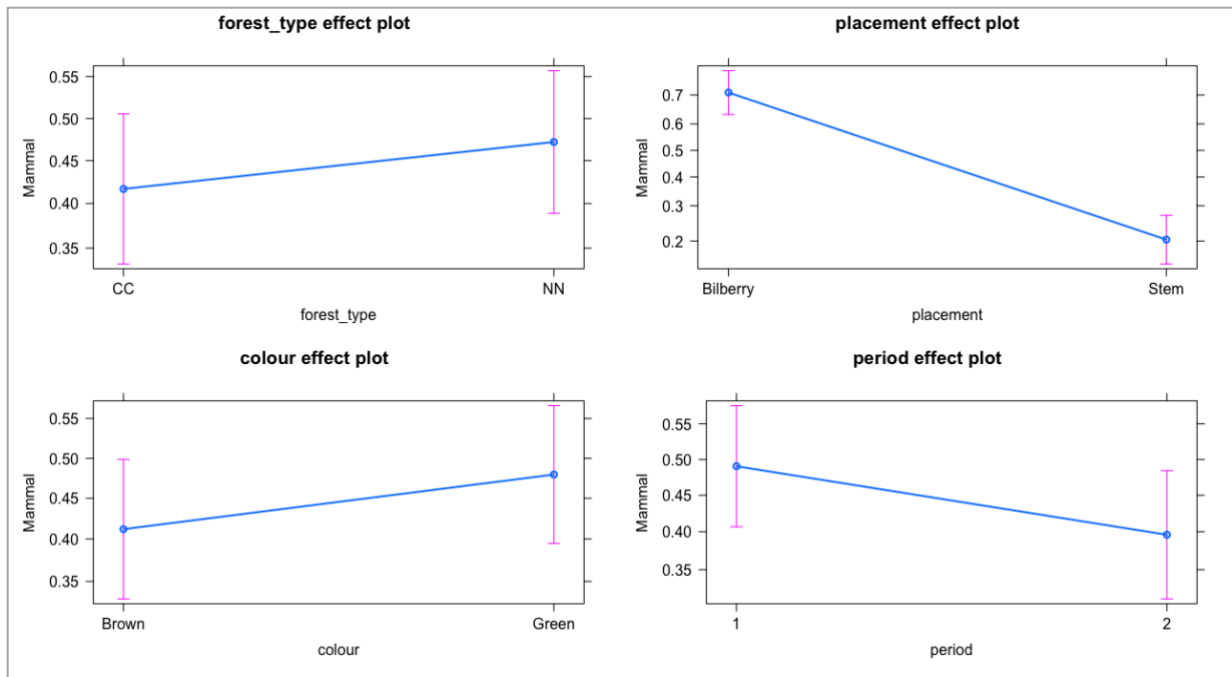

Figure A2. Effect plots of the Generalized Linear Mixed Model (GLMM) of artificial caterpillars attacked by arthropods, including interactions between forest type (NN = near-natural forest; CC = former clear-cut forest) and exposure period (1 = May-June; 2 = late June), caterpillar placement and exposure period, and caterpillar colour and exposure period.

Figure A3. Effect plots of the Generalized Linear Mixed Model (GLMM) of caterpillars attacked by mammals, including forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement, caterpillar colour, and exposure period (1 = May-June; 2 = late June).
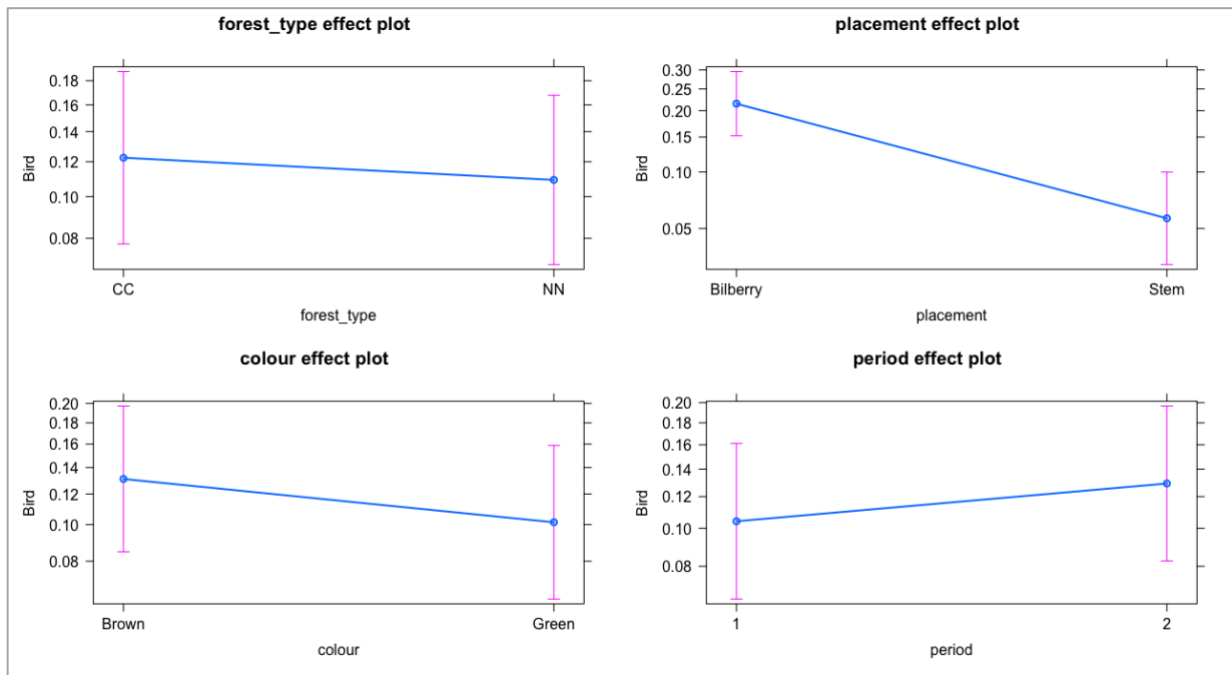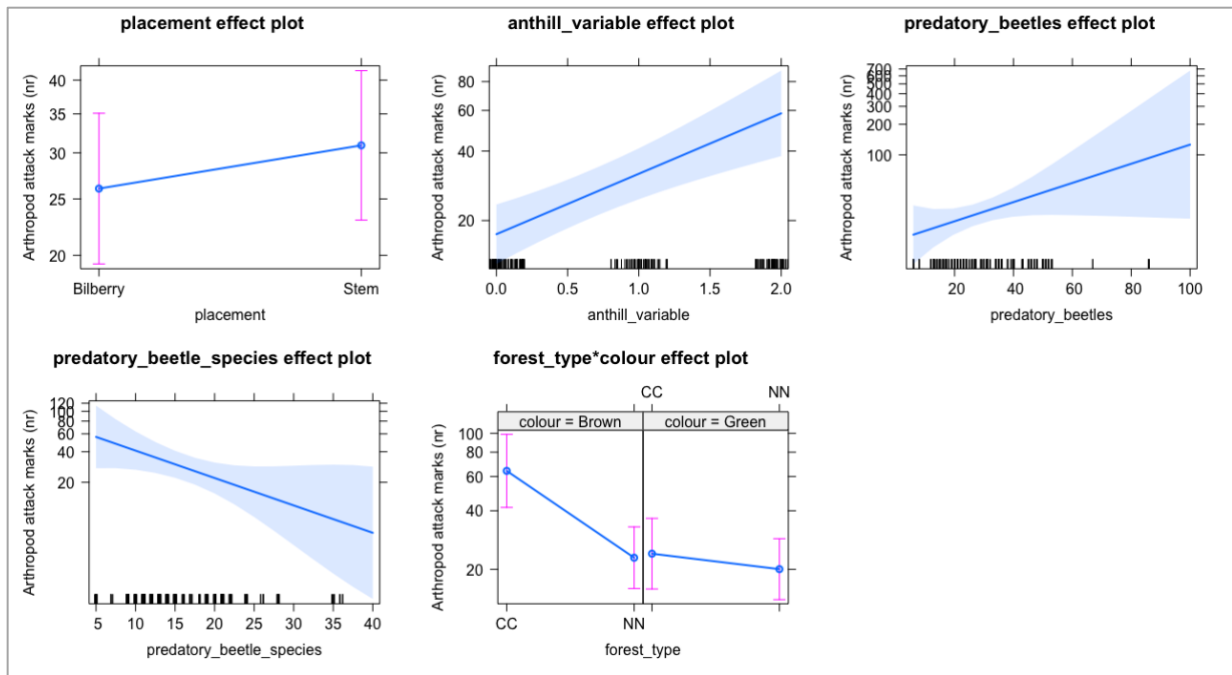

Figure A4. Effect plots of the Generalized Linear Mixed Model (GLMM) of caterpillars attacked by birds, including forest type (NN = near-natural forest; CC = former clear-cut forest), caterpillar placement, caterpillar colour, and exposure period (1 = May-June; 2 = late June).

Figure A7. Effect plots of the Generalized Linear Mixed Model (GLMM) of number of arthropod attack marks per caterpillar, including caterpillar placement, presence and proximity to anthills, number of predatory beetles, and number of predatory beetle species, and interactions between forest type (NN = near-natural forest; CC = former clear-cut forest) and caterpillar colour.
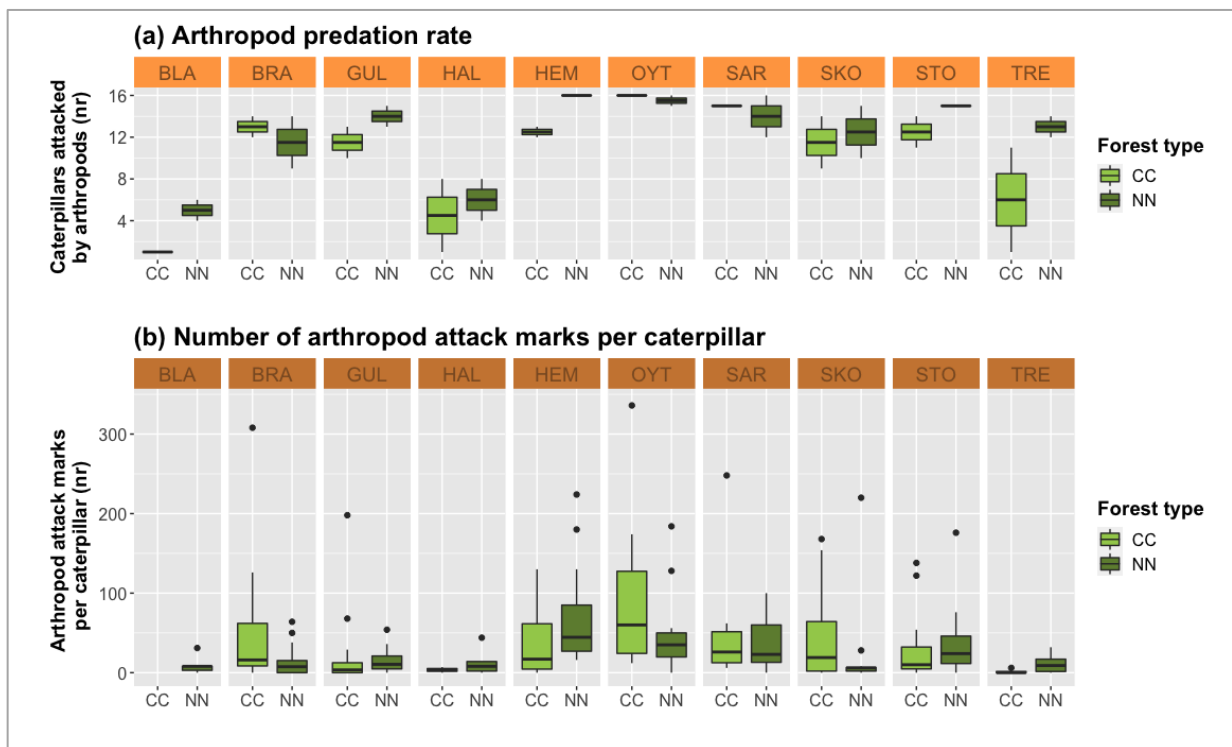

Figure A8. Arthropod predation rates of caterpillars within sites and forest types (NN = near-natural forest; CC = former clear-cut forest), comparing (a) Number of caterpillars attacked by arthropods, and (b) number of arthropod attack marks per caterpillar.