

RESEARCH PAPER

The relationship between moose browsing, habitat structure and predation pressure on insect herbivores



Michelle Nordkvist, Maartje J. Klapwijk*, Sabine Baretts, Christer Björkman

Department of Ecology, Swedish University of Agricultural Science, SE-75007, Uppsala, Sweden

Received 8 February 2022; accepted 30 November 2022
Available online 1 December 2022

Abstract

Grazing and browsing by large ungulates can have a strong effect on habitat composition and structure. Associated effects can be reduction in the abundance of palatable tree species and alter understory properties, thereby affecting habitat complexity. Changes in habitat structure and complexity can in turn affect arthropod predation pressure, as arthropod predators are strongly influenced by habitat characteristics. This may be increasingly important in production forests, as such systems are often more vulnerable to disturbances such as pest insects. However, studies exploring this indirect link between ungulates and predation rate are sparse. We explore this link through the comparison of fenced plots excluding ungulates (for four years) with associated control plots replicated in 16 forest stands covering a large geographical area. We measured vegetation characteristics to assess the effect of exclusion on habitat structure. We used plasticine models to compare predation rates in fenced and control plots on pine trees. In addition, we sampled herbivorous insects to explore the potential relationship between predation and herbivore abundance. We could only demonstrate a weak effect of browser exclusion on habitat structure, suggesting that the time of exclusion was too short to cause a vegetation response. In terms of arthropod predation, we found that predation was positively affected by understory cover, but not related to herbivore abundance. Understory properties such as species composition and biomass has been demonstrated to be affected by ungulates in other studies. Therefore, we propose that ungulate browsing – despite weak effects of browsing exclusion in our study – can affect arthropod predation via changes in the understory, which could potentially affect pest populations. Our study is one of the first attempts to connect effects of mammalian browsing to changes in predation rates on herbivorous insects.

© 2022 The Authors. Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>)

Keywords: *Alces alces*; Herbivory; Herbivore damage; Predators; Exclosure experiment; Plasticine larvae

Introduction

Grazing and browsing by large ungulates can have strong effects on forest composition and structure (McInnes et al., 1992). The effect of disturbances such as browsing may be more important in production forests, as such systems are often

more vulnerable to disturbances such as pest insects (Jactel et al., 2017). Browsers can reduce the abundance of palatable tree species in a stand, leading to altered tree species richness, tree species composition and/or canopy cover (Kolstad et al., 2018a; Kolstad et al., 2018b). Browsers can also alter properties of the understory vegetation through, e.g., grazing. Exclusion of browsers from boreal production forests has, for instance, resulted in increased understory biomass, decreased diversity, and altered species composition (Boulanger et al., 2018; Faison

*Corresponding author.

E-mail address: maartje.klapwijk@slu.se (M.J. Klapwijk).

et al., 2016; Kolstad et al., 2018a). In addition, feeding by large mammalian browsers can have large effects on the growth and shape of individual trees (Bergqvist et al., 2001; Wallgren et al., 2014). Such and other changes to habitat characteristics caused by ungulate browsing could have cascading consequences on predators. Ground-dwelling beetle (Lilleeng et al., 2018) and spider communities (Landsman & Bowman, 2017) have been found to react to the changes in understory caused by ungulates, and tree architecture can affect predator abundance and behavior (Reynolds & Cuddington, 2012). Abundance of ants has been shown to differ on browsed vs. un-browsed trees (Nordkvist et al., 2021). In boreal forests, ants are usually more abundant in grazed areas, while web-hunting spiders are more abundant in un-grazed areas (Suominen & Danell, 2006). Spider abundance has also been shown to decrease with increasing ungulate densities (Suominen et al., 2008). Moreover, it has been demonstrated that predation by both insectivorous birds and arthropods can be affected by forest structure (Langellotto & Denno, 2004; Muiruri et al., 2016; Poch & Simonetti, 2013). However, these findings are not yet linked to browsing/grazing. Thus, mammalian browsing and grazing altering habitat structure could have indirect effects on the natural enemy pressure exerted on insect herbivores. In production forests, problems with pest damage on trees are common, and an important question is whether mammalian browsers can affect predation pressure on herbivorous insects on browsed trees.

Furthermore, browsers could affect insect herbivore communities on trees. Indirect effects of ungulate browsing on insect herbivore abundance have been shown for defoliating insects and aphids on birch; higher insect abundance and damage on trees exposed to browsing (den Herder et al., 2009), and altered habitat structure could potentially affect herbivore occurrence on trees. In turn, herbivore abundance could affect predation rates. An indication of a positive relationship was found between herbivorous insects on oak and the abundance of arthropod predators; however, plant effects could not be excluded (Forkner & Hunter, 2000). Koricheva et al., (2000) found that predator abundance is more related to plant biomass than to herbivore abundance. However, when investigating the effect of the abundance of alternative prey on predation rates on aphids in agricultural fields (Ostman, 2004) no relationship was detected. To date, research investigating the relationship between herbivore abundance and predation rate is sparse (Staab & Schuldt, 2020).

Following the argumentation above, the primary goal of this study was to explore the effect of moose browsing on forest vegetation composition and the potential cascading effects on natural enemy pressure on trees. We expected ungulate browsing to reduce habitat complexity leading to a decreased predation pressure on herbivorous insects, as increased habitat complexity has been shown to increase predation rate of herbivorous insects by birds and arthropods in *Pinus radiata* plantations (Poch & Simonetti, 2013). We measured herbivore abundance to understand whether potential patterns in predation rates were directly related to habitat complexity or indirectly through effects on herbivore

abundance. To investigate this hypothesis, we used a controlled field experiment where fenced plots excluding ungulates and associated control plots are replicated in 16 forest stands dominated by Scots pine (*Pinus sylvestris*). Using this experimental design, we formulated the following research questions: (1) Does ungulate browsing significantly alter habitat properties related to structure, e.g., understory cover and height, tree density, tree diversity and tree height? (2) Is insect abundance on pine trees affected by habitat properties? (3) Is natural enemy attack rate on pine trees affected by habitat structure measures and insect abundance? We estimated natural enemy attack rates using plasticine models placed out on pine trees. In forest ecosystems and on Scots pine we expect birds as the dominating vertebrate predators (Muiruri et al., 2016; Zvereva et al., 2020) and ants and spiders as the dominating invertebrate predators (Kaitaniemi et al., 2007; Lindstedt et al., 2006; Olofsson, 1992; Suominen et al., 2008).

Materials and methods

Experimental set-up

The forest stands for the exclusion experiment were newly regenerated stands of Scots pine (*Pinus sylvestris*). Seedlings and young trees of Scots pine can suffer high levels of moose browsing during winter and are therefore the focus of our study. At three latitudes, eight locations and sixteen different sites in Sweden a fenced area of 7×7 m was set-up in 2012 to exclude ungulate browsing (mainly moose) 32 plots, 16 Fenced and 16 Control plots, were set up (Fig. 1). A corresponding control plot of the same size was chosen near each fenced area. These plots were set-up in stands that were recently harvested after check of the establishment of either planted or natural regenerated pine seedlings. In these types of seminatural forest stands, other tree species are left for regeneration even in those stands where pine seedlings are planted. Removal of non-pine trees will start 15–20 years after establishment when a pre-commercial thinning is executed. Prior to the pre-commercial thinning the diversity of trees present in the stands and thus the experimental plots and their control is largely dependent on soil type.

Habitat characteristics

In 2016 a survey of the fenced and control plots was undertaken to measure tree and understory properties. For each plot, number of trees and diversity of trees (i.e., counts of number of species) were recorded. Furthermore, height of five haphazardly selected pines trees was measured in both fenced and control plots. Trees within 1 m from the fence were excluded to avoid edge effects. Cover of vegetation other than trees was estimated within a 5×5 m area inside the experiment plot, considering the following species: heather (*Calluna* sp.), blueberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), raspberries, blackberries,

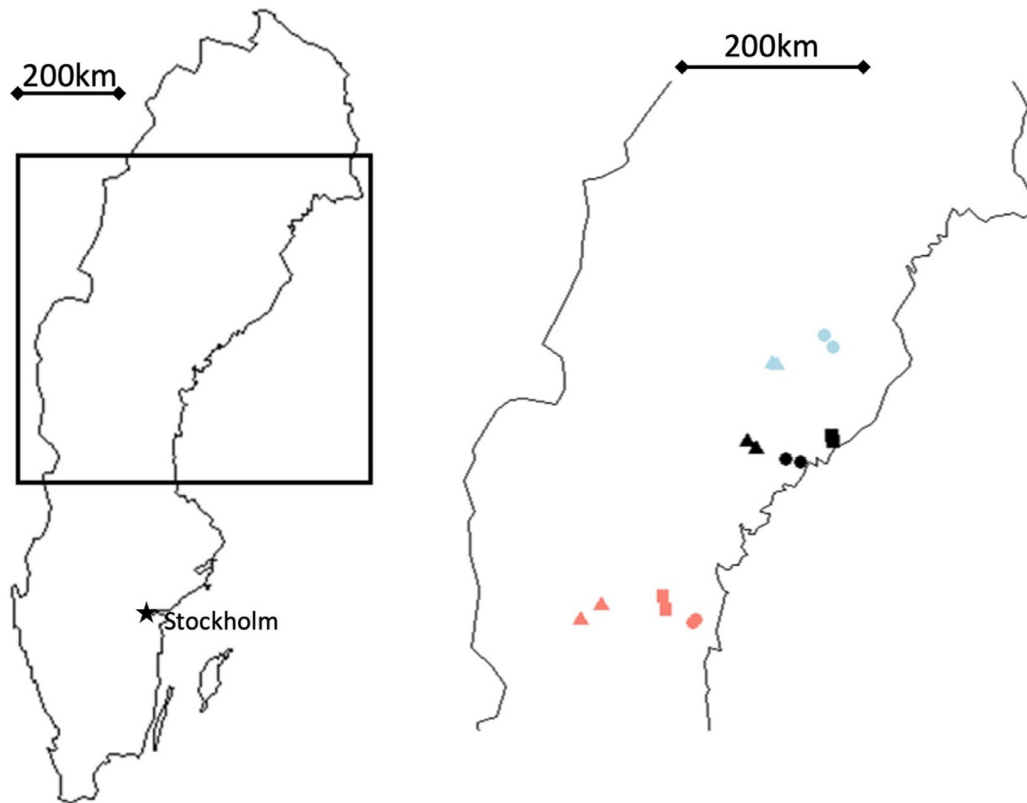


Fig. 1. Map of sample locations in Sweden, each symbol on the map represents the location of a forest stand (site) containing a control and fenced plot. The corresponding symbols are two sites at the same location. The colours of the symbols indicate the different latitudes. The map was created using R-package ‘maps: Draw Geographical Maps’ (Original S code by Richard A. Becker and Allan R. Wilks. R version by Ray Brownrigg. Enhancements by Thomas P Minka and Alex Deckmyn. (2018). maps: Draw Geographical Maps. R package version 3.3.0., <https://CRAN.R-project.org/package=maps>).

etc. (*Rubus* spp.), milkweed (*Asclepias syriaca*), other herbaceous vegetation (as a group), grasses and semi-grasses (as a group) and ferns (as a group). The average height represents the height, measured with a yardstick, below which 90% (visually assessed) of the biomass is found, to avoid individual outliers in height. The understory cover was estimated as percent cover in a 5×5 m area within fenced and control plots; it was estimated individually for each species or species group. We used the average of all observations. The tree measurements were taken in July 2016. We calculated an average tree height using the measurements. The understory measurements are part of the vegetation inventory conducted as part of the long-term monitoring of the plots (Widemo & Christofferson, SLU, Project web page, language Swedish; https://www.slu.se/globalassets/ew/org/inst/vfm/files/miljoanalys/arsrapport_2012_bilagor.pdf).

Insect abundance

Insect abundance was estimated on the five selected pine trees in each plot using the beating tray method in one time in June and one time in July 2016. We sampled branches up to 1 m from the ground on one side of the tree (or the whole side of the tree if it was shorter than 1 m). There was no minimum size of

branches sampled, but no branch was larger than the tray. The tray was held under each branch while it was beaten, and each branch was beaten 10 times. There was no method of capturing insects that left the tree during beating. Branches were beaten over the beating tray and insects in the tray were collected, stored in alcohol, and brought back to the laboratory where they were counted and sorted into orders. Samples from June and July were summed, and insect counts were pooled per plot.

Attack rate

To quantify predation pressure, we used plasticine model larvae. We aimed to make the models resemble generic insect larvae/caterpillars in size and shape. Plasticine models were roughly 2 cm long and between 0.3 and 0.5 cm in diameter, which corresponds to previous studies using plasticine models (reviewed by Lövei & Ferrante, 2017): the median length and diameter were 2.5 and 0.35 cm, respectively. We rolled the plasticine model clay (Smeedi plus, 500 gr, medium green and brown) around a copper wire. The copper wire was used to attach the model to the tree.

In each fenced and each control plot a subset of three pine trees (total 96 pine trees) were selected arbitrarily from the five trees measured. We used two colours to represent non-

specific prey. On the selected trees four plasticine models (2 brown and 2 green) were placed on branches in approximately the middle of each tree. The middle of each tree was estimated based on whorl count. Trees within 1 m from the fence were excluded. After two weeks, the models were collected and brought back to the laboratory. Prior to re-collection a picture of each plasticine model was taken. Many plasticine models had multiple attack marks; we did not distinguish between the multiple marks on the model but counted a model with signs of attack (one mark or multiple marks) as one attacked model. This was done because usually if a larval prey is attacked the prey is removed and thus not available to other predators. By doing so we believe that over-estimation of differences in predation pressure, also as predators might learn, is avoided. The attack rate used in the analysis is the number of attacked models per plot.

An important reason for using artificial prey made of plasticine was that it is easy to produce large amounts of prey items with a low degree of variation. The use of plasticine models to estimate natural enemy attack rate is an established method for comparative studies of attack rates between different habitats (Howe et al., 2009; Lövei & Ferrante, 2017; Tvardikova & Novotny, 2012). Although the absolute measure of attack rate may differ from ‘real’ attack rates, the relative difference between habitats or treatments remains the same (Lövei & Ferrante, 2017).

Statistical methods

All analyses were carried out in R version 4.1.1 (R Core Team, 2021), for separate analyses reference to the specific package will be included.

Difference in habitat variables between treatments

We used multivariate analysis of variance (manova; package stats) to assess the difference in vegetation between the two treatments. The response variables were tree diversity, tree height, tree density, understory vegetation cover and understory vegetation height. The explanatory variable in the model was treatment. We choose to include Latitude, Location and Site as fixed blocking factors to account for the spatial hierarchy in the set-up of the experiment. There were three locations at the lower latitude, three locations at the intermediate latitude and two locations at the high latitude. At each location, two sites were established, each containing one replicate (plot) of each treatment.

Parameters determining herbivorous insect abundance and attack rate

To test which habitat variables differed between treatments and affected insect abundance and attack rate we used piecewise structural equation modeling (piecewiseSEM package; Lefcheck & Freckleton, 2016). Piecewise structural equation

modeling is a useful method when dealing with more complicated networks containing multiple factors and effects as it allows for determination of all possible relationships simultaneously (Lefcheck & Freckleton, 2016). The method to compile the structural equation using piecewise SEM uses individual linear models, which are evaluated individually, allowing for a lower sample size compared to the ‘traditional’ way to model structural equation analysis. The models were evaluated locally (i.e., individually) and globally, i.e., the models were evaluated simultaneously. The more correct term for this type of analysis is ‘confirmatory path analysis’ but has been referred to Structural Equation Modeling (Lefcheck & Freckleton, 2016). Prior to constructing the structural equation models, we modeled the effect of treatment (fenced and control plots) on insect abundance and attack rate with linear and generalized linear mixed models, respectively (lme4 package; Bates et al., 2015). As there was no effect of treatment on either of those response variables, we did not include a direct link between treatment and insect abundance or attack rate in the structural equation models (Table A.5).

We used the variables tested with the MANOVA (i.e., habitat variables) as explanatory variables for insect abundance and attack rates in the structural equation model, and treatment (control or fenced) as an explanatory variable for the habitat variables. Attack rate is defined as the number of attacked models per plot and insect abundance as number of insects per plot (log-transformed). Using piecewiseSEM allowed us to build the structural equation model using linear mixed models and generalized linear mixed model (lme4 package; Bates et al., 2015). All individual models contained site nested in location nested in latitude as a grouping factor. The first SEM included the relationship between all habitat variables and treatment. In addition, it included attack rate and insect abundance in response to all habitat variables, and insect abundance was used as an additional explanatory variable for attack rate (Fig. 2). Based on the test of the directed separation, we added significant direct relationship to the model either as direct relationships or covariance structure giving us the final model. As there was a strong relationship between insect abundance and tree height, we performed a second run of structural equations models in which we scaled insect abundance for tree height. We did this for two reasons. First, because we wanted to assess if the density of insects was affected by tree height (or the other structural variables). Second, because it allows us to investigate predation in relation to structural complexity without the tree height-insect abundance relationship as a confounding factor. The procedure was otherwise identical to the one described above.

Results

Treatment differences in vegetation variables

The results of the MANOVA show a marginally significant overall difference between the fenced and the control plots (p-value 0.051, Table 1; Fig. 3) and the locations at

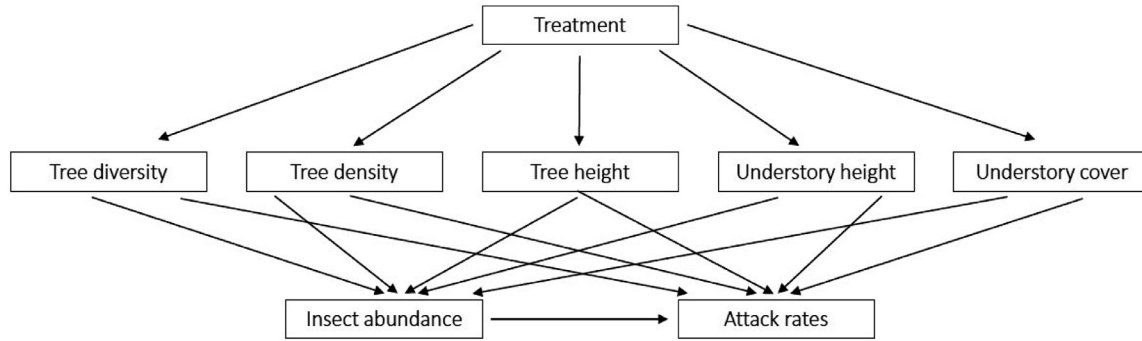


Fig. 2. The initial model with the direct relationships between treatment and habitat variables and the direct relationships between the habitat variables and attack rates and insect abundance and in addition, the direct relationship between attack rates and insect abundance.

which the experimental plots were established are strongly related to differences between the vegetation parameters. The ANOVA:s for the individual variables show that the

majority of the variables displayed differences determined by location and only tree height was significantly higher in fenced plots versus control plots (Table 2).

Table 1. Results for multivariate analysis of variance for all vegetation variables with respect to exclusion treatment (two levels – fenced and control). First the total results are provided, and the following rows are the results for the individual variables. Significant effects are marked in bold. Pillai’s trace test was used as test statistic, which is converted to F-statistics to check for significance.

MANOVA					
Total	Df	Pillai	Approx F	Num Df, Den Df	P-value
Latitude	2	1.26	4.06	10,24	0.002
Location	5	2.85	3.99	25,75	<0.001
Site	8	2.54	1.94	40,75	0.007
Treatment	1	0.59	3.17	5,11	0.051
Tree diversity	Df	Sum Sq	Mean Sq	F-value	P-value
Latitude	2	2.08	1.04	1.98	0.172
Location	5	14.79	2.96	5.63	0.004
Site	8	5.00	0.63	1.19	0.366
Treatment	1	0.13	0.13	0.24	0.632
Residuals	15	7.88	0.53		
Tree density	Df	Sum Sq	Mean Sq	F-value	P-value
Latitude	2	32.71	16.35	0.80	0.467
Location	5	214.17	42.83	2.10	0.123
Site	8	330.00	41.25	2.02	0.115
Treatment	1	0.50	0.50	0.02	0.878
Residuals	15	306.50	20.43		
Tree height	Df	Sum Sq	Mean Sq	F-value	P-value
Latitude	2	1245.3	622.7	1.44	0.268
Location	5	22124.1	4424.8	10.24	<0.001
Site	8	26477.5	3309.7	7.66	<0.001
Treatment	1	5142.8	5142.8	11.90	0.004
Residuals	15	6480.1	432.0		
Understory cover	Df	Sum Sq	Mean Sq	F-value	P-value
Latitude	2	3479.1	1739.6	26.97	<0.001
Location	5	3157.5	631.5	9.79	<0.001
Site	8	1716.8	214.6	3.33	0.021
Treatment	1	33.00	33.0	0.51	0.485
Residuals	15	967.6	64.5		
Understory height	Df	Sum Sq	Mean Sq	F-value	P-value
Latitude	2	80.1	40.0	1.25	0.312
Location	5	855.9	171.2	5.38	0.005
Site	8	155.25	19.4	0.61	0.756
Treatment	1	0.63	0.63	0.02	0.890
Residuals	15	476.9	31.8		

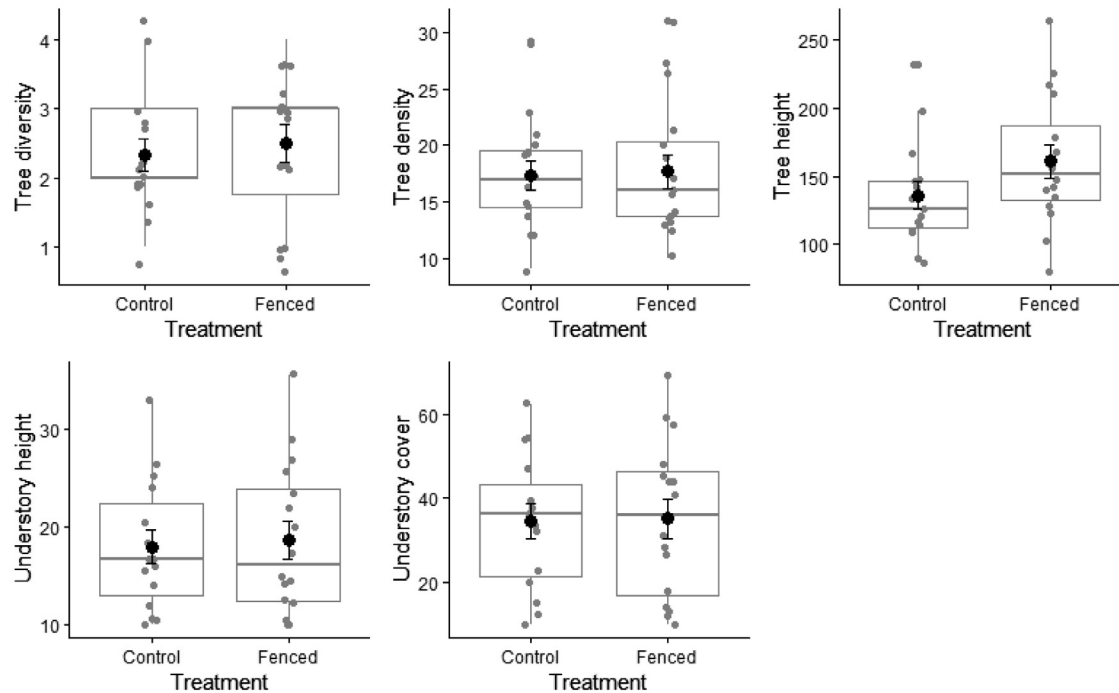


Fig. 3. Interval plots for the measured habitat variables. The grey dots are the raw data points and black dots are mean values with standard errors. The lower and upper borders of the box correspond to the first and third quartiles (the 25th and 75th percentiles). The upper whisker extends from the third quartile to the largest value no further than $1.5 \times$ Inter-Quartile Range from the third quartile. The lower whisker extends from the first quartile to the smallest value at most $1.5 \times$ IQR of the first quartile (Wickham, 2016).

Insect abundance and plasticine model attack

In total 5725 insect specimens were collected, of which 5176 belonged to the order Hemiptera (90,4%), 369 belonged to the order of Coleoptera, 66 Collembola, 55 Diptera, 37 Thysanoptera, 16 Hymenoptera. The orders Psocoptera, Neuroptera, Trichoptera were represented by one individual each. Within the order of Hemiptera, 2353 specimens were waxy pine needle aphids (*Schizolachnus* spp.), 1412 were Pine needle aphids (*Eulachnus* spp.), 914 Scots pine aphids (*Cinara pini*) and 325 belonged to the Large pine aphid (*Cinara pinea*). These genera/species dominated the collected Hemiptera sample. Within the Coleoptera the order with the largest representation were the soldier beetles (97; *Malthodes* spp.), none of the other genera were represented by more than 10 specimens.

In total 384 models were placed on pine trees in control and fenced plots, in total the models were attacked 378 times. We could determine that from the total number of marks; 43 (11%) were attributed to bird attack, 335 marks were attributed to arthropod attack (89%) using the method presented by Low et al. (2014). The bird attacks were divided over 5 plots, with 26 marks in 3 control plots and 17 marks in 1 fenced plot. Arthropod attacks were divided over 28 plots, with 194 marks in 14 control plots and 141 marks in 14 fenced plots. Overall, for the models placed out in the control and fenced plots in total 82 models were attacked at least once, 47 attacks in 15 control plots and 35 attacks in 14 fenced plots, leading to a total (both

insect and bird) attack rate of 21%. In only one control plot of all 32 fenced and control plots the attack on the plasticine models was solely caused by birds. We found that the colour of the model (brown or green) had no influence on the probability of attack. We did not distinguish between colour in subsequent analyses of treatment effects. There was no difference in number of plasticine models with marks (attack rate) (Table A.5, Fig. 4) between fenced and control plots, nor was there any difference in insect abundance between fenced and control plots (Table A.5, Fig. 4).

Parameters determining herbivorous insect abundance and attack rate

The complete results of the final structural equation models are presented in Fig. 5 and in Tables A.2 and S4. The initial models are presented in the Tables A.1 and A.3. The results presented below are the estimates (\pm SE) for the relationships included in linear model part of the structural equation model.

SEM insect abundance

The structural equation model showed treatment affected tree height, trees were taller in fenced plots compared to controls (161 ± 11.25 cm versus 136 ± 11.48 cm,

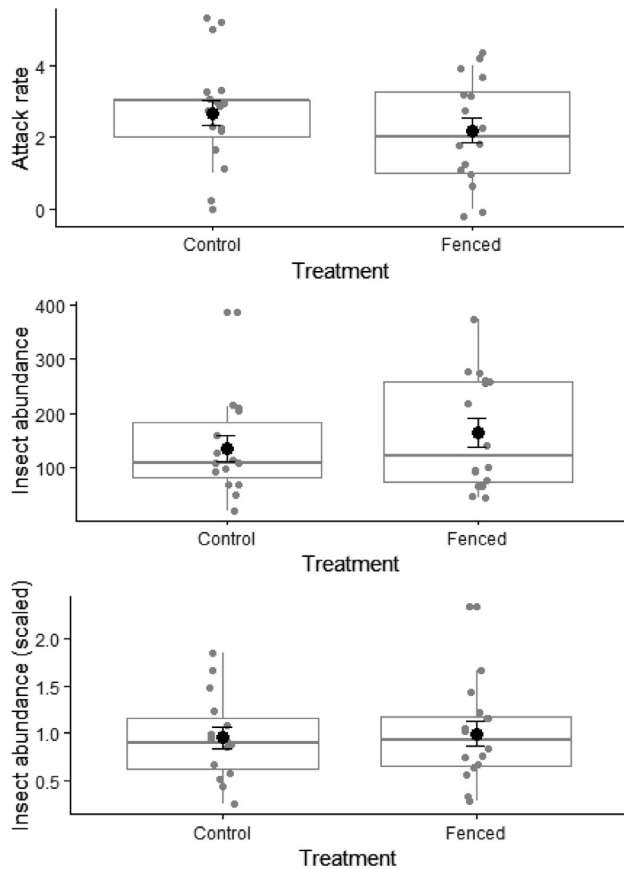


Fig. 4. Interval plots for the response variables attack rates, insect abundance and insect abundance scaled for height. The grey dots are the raw data points and black dots are mean values with standard errors. The lower and upper boarders of the box correspond to the first and third quartiles (the 25th and 75th percentiles). The upper whisker extends from the third quartile to the largest value no further than $1.5 \times$ Inter-Quartile Range from the third quartile. The lower whisker extends from the first quartile to the smallest value at most $1.5 \times$ IQR of the first quartile (Wickham, 2016).

$p < 0.01$). No other direct effect of treatment on habitat variables was found (Table A.2, Fig. 5). Insect abundance was positively affected by tree height (0.009 ± 0.002 , p -value < 0.01), and understory cover tended to show a positive effect on attack rates (marginally significant; 0.015 ± 0.008 , p -value < 0.1). The global goodness of fit shows a good fit with Fisher's $C = 14.8$ with P -value = 0.68 and on 18° of freedom.

We scaled insect abundance for tree height to ascertain that the relationship between tree height and insect abundance would not mask any other potential relationships in the model. Again, the model shows that tree height was higher in the fenced plot, no other direct relationship was found between treatment and habitat variables (Table A.4, Fig. 5). Understory cover was positively related to attack rates (0.016 ± 0.008 ; Fig. A.2). The global goodness of fit shows a good fit with Fisher's $C = 17.7$ with P -value = 0.6 and on 20° of freedom.

Discussion

We set out to investigate the effect of ungulate browsing on habitat characteristics, insect herbivore abundance and natural enemy predation pressure. Four years into the experiment, no strong effects of ungulate exclusion on any of the measured habitat variables were found, except for a positive effect of fencing on tree height. The lack of a strong effect of browser exclusion makes us unable to draw any conclusion on the effect of browsers on attack rates. However, we did find effects of habitat structure on insect abundance (positively affected by tree height) and attack rates (positively affected by understory cover), allowing us to make inferences on the link between browsers and attack rates based on previous studies on browser exclusion and habitat characteristics.

Habitat variables

Our study only found minute differences between the fenced and control plots. A possible explanation is that the exclusion experiment might have been too young to induce strong differences between the fenced and control plots. Kolstad et al. (2018a) and Speed et al. (2019) showed increased differences in both tree and understory vegetation over time after longer exposure to browsing. Another reason for the lack of a strong effect could be that the study sites were not selected based on browsing pressure, which could be different from other studies reporting a stronger effect. Boulanger et al. (2018) showed that the strength of the effect of vegetation characteristics was positively correlated to ungulate density.

Insect abundance

Herbivore insect abundance on pine trees was positively related to tree height. Higher trees provide more resources and space for species that utilize that tree species, and taller trees have been shown to hold higher abundances of herbivores (Campos et al., 2006). However, when we scaled the insect abundance for height, the model results did not change. The strong relationship between tree height and insect abundance could have masked the indirect relationship between fenced and control plots as we found differences in tree height between control and fenced plots. Thus, higher abundances found in fenced plots were mainly dictated by the difference in tree height and not related to any other habitat variables.

Attack rates

Attack rates were positively related to understory cover, which supports the hypothesis that forest vegetation structure is important in shaping the predator community and/or behavior (Langellotto & Denno, 2004) and thereby predation rates (Poch & Simonetti, 2013). Ferrante et al. (2017)

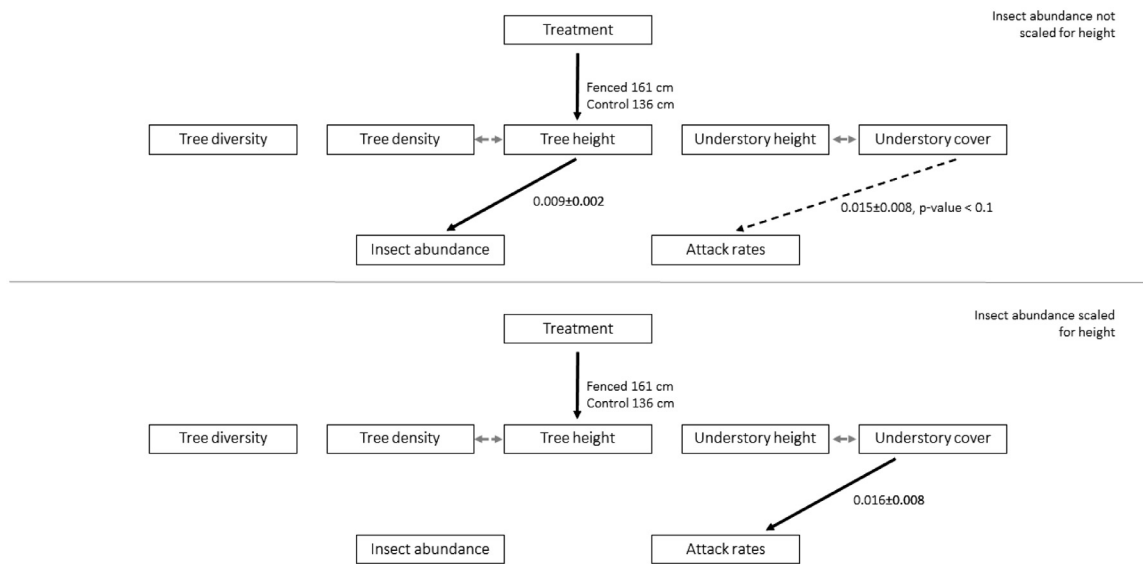


Fig. 5. The final path models describing significant relationships and covariances for insect abundance. Upper figure shows the path model with insect abundance not scaled for height, and the lower figure insect abundance scaled for height. Black arrows indicate significant relationships. Dashed black arrows indicate marginally significant relationships. The light grey dotted double-headed arrows indicate significant co-variance between variables. The full model is provided in Table S3.

found a similar pattern between understory cover and attack rates in maize fields. Understory cover has been found to be important for ground-dwelling arthropods (Magura, 2002) which are thought to be a key group attacking artificial larval models (Ferrante et al., 2014). Thus, experiments using artificial prey support the hypothesis that habitat complexity affects predators (Berezki et al., 2014; Lövei & Ferrante, 2017; Zvereva et al., 2020). Most of the attacks on the model larvae in our study were made by insects, like ants and predatory beetles, hence, improved microhabitat through the presence of understory cover (Sadler et al., 2006) could be underlying the relationship with attack rates. If we extrapolate our finding this could mean that when ungulate browsing reduces understory biomass (Kolstad et al., 2018a) and cover (Martin et al., 2010), arthropod predator attack rates could also be reduced. However, the magnitude of the effect of browsing on understory is related to browsing pressure. Future efforts to understand the direct and indirect effects of ungulate browsing on herbivorous insect abundance and predation rate would be most effective if studied over a gradient of ungulate browsing pressure.

Another driving mechanism for attack rates could be the abundance of alternative prey (Barbosa et al., 2009). More resources could sustain a more diverse and more abundant prey community and result in a more abundant and diverse predator community; both responses have been found (Staab & Schuldt, 2020). However, the unanswered question is what the relationship is between prey abundance, predator abundance and attack rates. In our study, attack rates were not related to insect abundance, we might be able to explain this through the low diversity of our alternative prey, mainly Hemipterans. We used model prey to measure attack rates.

What is unknown is whether the predator community attacking the sampled Hemiptera orders overlaps with or is equal to the community that would attack the herbivorous larvae represented by our model prey. In our samples most of the attacks were made by arthropod predators (89%, compared to 11% bird marks). Bird predation has been shown to be high in other studies using plasticine caterpillars (Muiruri et al., 2016). Low predation by birds in this study is likely related to the low age of the stands or potentially to the ‘host’ tree of the plasticine models. The type of predator attacking plasticine models could be related to the habitat the attack rates are measured in. Currently to our knowledge most studies using this method are conducted in either agricultural habitats or habitats dominated by deciduous trees.

One caveat that needs to be mentioned is that natural enemies can use plant and/or herbivore cues (such as chemical signals or movements) to locate prey, cues that are not emitted by plasticine models (Howe et al., 2009). This might bias the detection rate when predation attempts are made by mobile generalist predators versus more specialist natural enemies that will have a more targeted searching method (Birkhofer et al., 2017). In addition, this method disregards ambush predators. However, even though the measured attack rates might not represent absolute predation rates, the relative predation rates should not be affected (Lövei & Ferrante, 2017). Another limitation with the use of plasticine model larvae is reliability of distinguishing between different arthropod predators. However, one of the strengths with the method is that it allows for distinguishing between predation marks caused by bird and insect predators.

In conclusion, our study shows that attack rates are directly affected by habitat characteristics that are commonly associated with changes due to ungulate browsing (Kolstad

et al., 2018a; Martin et al., 2010). Therefore, we believe our study provides a basis to further investigate the possibility that predation pressure on trees could be negatively affected in areas with high browsing pressure, potentially creating opportunity for more insect herbivore damage. We believe further research efforts to understand these interactions would be valuable as a previous study has also found increased performance of insects on browsed trees (Nordkvist et al., 2019). Eventually, the combination of browsing-induced changes to habitat structure and host plant quality could lead to higher damage levels in forest stands where ungulate browsing pressure is high.

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.

CRedit authorship contribution statement

Michelle Nordkvist: Conceptualization, Visualization, Resources, Formal analysis, Writing – original draft. **Maartje J. Klapwijk:** Conceptualization, Visualization, Formal analysis, Writing – original draft. **Sabine Barets:** Conceptualization, Visualization, Resources, Writing – original draft. **Christer Björkman:** Conceptualization, Visualization, Writing – original draft.

Acknowledgments

This study was supported by Svenska Forskningsrådet Formas, Grant/ Award Number: 2015–55 and Future Forests, a multi-disciplinary research program supported by the Foundation for Strategic Environmental Research (MISTRA). A special thanks goes to Peter Christofferson and Holmen Skog for their continued commitment to the collaboration within the exclusion project.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2022.11.011](https://doi.org/10.1016/j.baae.2022.11.011).

References

Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A., & Szendrei, Z. (2009). Associational resistance and associational susceptibility: Having right or wrong neighbors. *Annual Review of Ecology Evolution and Systematics*, 40, 1–20.

- Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.
- Berezki, K., Ódor, P., Csóka, G., Mag, Z., & Báldi, A. (2014). Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. *Forest Ecology and Management*, 327, 96–105.
- Bergqvist, G., Bergström, R., & Edenius, L. (2001). Patterns of stem damage by Moose (*alces alces*) in young pinus sylvestris stands in Sweden. *Scandinavian Journal of Forest Research*, 16, 363–370.
- Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P. A., Klapwijk, M., Mestre, L., Roubinet, E., Schroeder, M., Stenberg, J. A., Porcel, M., Bjorkman, C., & Jonsson, M. (2017). Methods to identify the prey of invertebrate predators in terrestrial field studies. *Ecology and Evolution*, 7, 1942–1953.
- Boulanger, V., Dupouey, J. L., Archaux, F., Badeau, V., Baltzinger, C., Chevalier, R., Corcket, E., Dumas, Y., Forgeard, F., & Mårell, A. (2018). Ungulates increase forest plant species richness to the benefit of non-forest specialists. *Global Change Biology*, 24, e485–e495.
- Campos, R. I., Vasconcelos, H. L., Ribeiro, S. P., Neves, F. S., & Soares, J. P. (2006). Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography*, 29, 442–450.
- den Herder, M., Bergström, R., Niemelä, P., Danell, K., & Lindgren, M. (2009). Effects of natural winter browsing and simulated summer browsing by moose on growth and shoot biomass of birch and its associated invertebrate fauna. *Annales Zoologici Fennici*, 46, 63–74.
- Faison, E. K., DeStefano, S., Foster, D. R., Motzkin, G., & Rapp, J. M. (2016). Ungulate browsers promote herbaceous layer diversity in logged temperate forests. *Ecology and Evolution*, 6, 4591–4602.
- Ferrante, M., Cacciato, A. L., & Lövei, G. L. (2014). Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. *European Journal of Entomology*, 111(5), 649–654.
- Ferrante, M., González, E., & Lövei, G. L. (2017). Predators do not spill over from forest fragments to maize fields in a landscape mosaic in central Argentina. *Ecology and Evolution*, 7, 7699–7707.
- Forkner, R. E., & Hunter, M. D. (2000). What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Journal of Ecology*, 81, 1588–1600.
- Howe, A., Lövei, G. L., & Nachman, G. (2009). Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomologia Experimentalis et Applicata*, 131, 325–329.
- Jactel, H., Bauhus, J., Boberg, J., Bonal, D., Castagnyrol, B., Gardiner, B., Gonzalez-Olabarria, J. R., Koricheva, J., Meurisse, N., & Brockerhoff, E. G. (2017). Tree diversity drives forest stand resistance to natural disturbances. *Current Forestry Reports*, 3, 223–243.
- Kaitaniemi, P., Riihimäki, J., Koricheva, J., & Vehviläinen, H. (2007). Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. *Silva Fennica*, 41, 259–268.
- Kolstad, A. L., Austrheim, G., Solberg, E. J., De Vriendt, L., & Speed, J. D. M. (2018a). Pervasive moose browsing in boreal forests alters successional trajectories by severely suppressing keystone species. *Ecosphere*, 9, e02458.

- Kolstad, A. L., Austrheim, G., Solberg, E. J., Venete, A. M. A., Woodin, S. J., & Speed, J. D. M. (2018b). Cervid exclusion alters boreal forest properties with little cascading impacts on soils. *Ecosystems*, *21*, 1027–1041.
- Koricheva, J., Mulder, C. P., Schmid, B., Joshi, J., & Huss-Danell, K. (2000). Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia*, *125*, 271–282.
- Landsman, A. P., & Bowman, J. L. (2017). Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability. *Ecosphere*, *8*(2), e01703.
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia*, *139*, 1–10.
- Lefcheck, J. S., & Freckleton, R. (2016). piecewise SEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.
- Lilleeng, M. S., Rydgren, K., Halvorsen, R., Moe, S. R., & Hegland, S. J. (2018). Red deer structure the ground-dwelling beetle community in boreal forest. *Biodiversity and Conservation*, *27*, 2507–2525.
- Lindstedt, C., Mappes, J., Päävinen, J., & Varama, M. (2006). Effects of group size and pine defence chemicals on Diprionid sawfly survival against ant predation. *Oecologia*, *150*, 519–526.
- Lövei, G. L., & Ferrante, M. (2017). A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. *Insect Science*, *24*, 528–542.
- Low, Petah A, Sam, Katerina, McArthur, Clare, Posa, Mary Rose C, & Hochuli, Dieter F (2014). Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. *Entomologia Experimentalis et Applicata*, *152*(2), 120–126.
- Magura, T. (2002). Carabids and forest edge: Spatial pattern and edge effect. *Forest Ecology and Management*, *157*, 23–37.
- Martin, J. L., Stockton, S. A., Allombert, S., & Gaston, A. J. (2010). Top-down and bottom-up consequences of unchecked ungulate browsing on plant and animal diversity in temperate forests: Lessons from a deer introduction. *Biological Invasions*, *12*, 353–371.
- McInnes, P. F., Naiman, R. J., Pastor, J., & Cohen, Y. (1992). Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology*, *73*, 2059–2075.
- Muiruri, E. W., Rainio, K., & Koricheva, J. (2016). Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae. *Oecologia*, *180*, 619–630.
- Nordkvist, M., Bjorkman, C., & Klapwijk, M. J. (2021). Plant mediated interactions: lower sawfly survival on pines previously browsed by moose. *Frontiers in Ecology and Evolution*, *9*, 253.
- Nordkvist, M., Klapwijk, M. J., Edenius, L., Gershenzon, J., Schmidt, A., & Bjorkman, C. (2019). Trait-mediated indirect interactions: Moose browsing increases sawfly fecundity through plant-induced responses. *Ecology and Evolution*, *9*, 10615–10629.
- Olofsson, E. (1992). Predation by *Formica polyceia* Forster (Hym, formicidae) on newly emerged larvae of *Neodiprion sertifer* (Geoffroy) (Hym, Diprionidae). *Journal of Applied Entomology*, *114*, 315–319.
- Original S code by Richard A. Becker and Allan R. Wilks. R version by Ray Brownrigg. Enhancements by Thomas P Minka and Alex Deckmyn. (2022). maps: Draw Geographical Maps. <https://CRAN.R-project.org/package=maps>. R package version 3.4.1.
- Ostman, O. (2004). The relative effects of natural enemy abundance and alternative prey abundance on aphid predation rates. *Biological Control*, *30*, 281–287.
- Poch, T. J., & Simonetti, J. A. (2013). Insectivory in *Pinus radiata* plantations with different degree of structural complexity. *Forest Ecology and Management*, *304*, 132–136.
- Core Team, R. (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reynolds, P. G., & Cuddington, K. (2012). Effects of plant gross morphology on predator consumption rates. *Environmental Entomology*, *41*, 508–515.
- Sadler, J., Small, E., Fiszpan, H., Telfer, M., & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *Journal of Biogeography*, *33*, 1126–1138.
- Speed, J. D. M., Austrheim, G., Kolstad, A. L., & Solberg, E. J. (2019). Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. *Plos One*, *14*(5), e0217166.
- Staab, M., & Schuldt, A. (2020). The influence of tree diversity on natural enemies—a review of the "Enemies" hypothesis in forests. *Current Forestry Reports*, *6*, 243–259.
- Suominen, O., Danell, K., Pastor, J., Danell, K., Duncan, P., & Bergström, R. (2006). Effects of large herbivores on other fauna. *Large herbivore ecology, ecosystem dynamics and conservation* (pp. 383–412). Cambridge: Cambridge University Press.
- Suominen, O., Persson, I. L., Danell, K., Bergström, R., & Pastor, J. (2008). Impact of simulated moose densities on abundance and richness of vegetation, herbivorous and predatory arthropods along a productivity gradient. *Ecography*, *31*, 636–645.
- Tvardikova, K., & Novotny, V. (2012). Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. *Journal of Tropical Ecology*, *28*, 331–341.
- Wallgren, M., Bergquist, J., Bergström, R., & Eriksson, S. (2014). Effects of timing, duration, and intensity of simulated browsing on Scots pine growth and stem quality. *Scandinavian Journal of Forest Research*, *29*, 734–746.
- Wickman, Hadley, & Springer-Verlag New York. (2016). ggplot2: Elegant Graphics for Data Analysis. <https://ggplot2.tidyverse.org>. isbn = 978-3-319-24277-4.
- Zvereva, E. L., Paolucci, L. N., & Kozlov, M. V. (2020). Top-down factors contribute to differences in insect herbivory between saplings and mature trees in boreal and tropical forests. *Oecologia*, *193*, 167–176.