Effect of forest stand type on host plant quality and direct and indirect effects on pine sawfly performance

Davide Bellone*[iD], Christer Björkman*, Axel Schmidt[†], Jonathan Gershenzon[†] and Maartje J. Klapwijk*[iD]

*Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden and [†]Department of Biochemistry, Max Planck Institute for Chemical Ecology, Jena, Germany

Abstract

1 Observed lower levels of herbivory in mixed compared with monoculture stands have been hypothesized to depend on top-down forces, through higher predation pressure by natural enemies or through bottom-up mechanisms through plant quality effects on herbivore performance.

2 In this study, we compared the performance measured as host plant induced mortality, cocoon weight, and predation mortality of the European pine sawfly *Neodiprion sertifer* (Geoffroy) (Hymenoptera, Diprionidae) in mixed and monoculture forest stands.

3 We did not observe a difference in host plant induced mortality, cocoon weight, or predation mortality between mixed and monoculture forest stands. We did find an effect of local conditions around each experimental tree on pine sawfly performance. For example, the nitrogen content of pine needles is negatively affected by the proportion of pine around the experimental tree, which in turn increases the survival of sawfly larvae.

4 The results suggest that local conditions around individual trees are more important for the performance of the European pine sawfly than stand type, *i.e.* mixed or monoculture plant stands.

5 We conclude that the ongoing trend for diversification within commercial forestry calls for more research where the effects of both bottom-up and top-down effects are studied at several spatial scales.

Keywords cocoon weight, herbivore performance, mixed forest, resin acid, secondary metabolites.

Introduction

Do herbivorous insects cause less plant damage in diverse compared with simplified habitats? The current body of literature provides different answers depending on what ecological system is considered (Letourneau *et al.*, 2011). Research in forest ecosystems shows diverging results, linking more diverse habitats to either lower (Jactel & Brockerhoff, 2007; Castagneyrol *et al.*, 2014; Setiawan *et al.*, 2014; Guyot *et al.*, 2015) or higher herbivore damage (Schuldt *et al.*, 2015; Kambach *et al.*, 2016; Verheyen *et al.*, 2016; Brezzi *et al.*, 2017; Castagneyrol *et al.*, 2018).

Two main hypotheses are underlying the research regarding the relationship between plant damage and habitat diversity (Tahvanainen & Root, 1972; Root, 1973; Barbosa *et al.*, 2009). One hypothesis postulates a higher realized top-down pressure as a result of an increased abundance of natural enemies in more diverse habitats (Staab *et al.*, 2014). The other hypothesis considers plant apparency (Sholes, 2008) and resource availability (Abdala-Roberts *et al.*, 2015) as drivers of herbivore populations and hence plant damage from specialist herbivores. One less explored mechanism is the effect of plant diversity on the quality of the host plant as resource for herbivorous insects (Mraja *et al.*, 2011; Moreira *et al.*, 2014; Kostenko *et al.*, 2017), potentially with indirect consequences for herbivore performance. The majority of studies investigating the effects of stand diversification on specialist herbivores have focused on the effect on natural enemies (Muiruri *et al.*, 2015; Leles *et al.*, 2017) or plant apparency (Jactel *et al.*, 2011; Dulaurent *et al.*, 2012). The

Correspondence: Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 75007 Uppsala, Sweden. e-mail: bellonedavide1@gmail.com

potential effects of stand diversification on host plant quality and thus on herbivorous insect performance have so far been underemphasized.

Host plant quality affects the performance of herbivorous insects through several plant traits, among which nutritional value and chemical defence (Fraenkel, 1959; Feeny, 1976; Awmack & Leather, 2002; Mithöfer & Boland, 2012). These plant traits may be affected by higher plant diversity due to increased niche differentiation of root growth (*i.e.* low competition) and segregation between species (Lang *et al.*, 2014). The segregation results in a better acquisition of soil nutrients (*e.g.* nitrogen) what in turn affects the amount of resources allocated to anti-herbivore defence (Mraja *et al.*, 2011; Lang *et al.*, 2014; Moreira *et al.*, 2014). Therefore, one could expect that plants surrounded by hetero-specifics can invest more in chemical defence traits leading to reduced herbivore performance than plants surrounded by conspecifics.

To investigate the effect of tree diversity on plant chemistry and the indirect effect on herbivore performance, we used a well-studied system, the European pine sawfly (*Neodiprion sertifer* [Geoffroy]), a common defoliator of Scots pine (*Pinus sylvestris* L.). Scots pine produces resin acids, carbon-based compounds, that function as defence against herbivores (Mumm & Hilker, 2006). The content of resin acids in pine needles varies greatly between different Scots pine genotypes (Forrest, 1980; Manninen *et al.*, 2002) and is found to be related to nitrogen levels in the soil (Björkman *et al.*, 1991; Björkman *et al.*, 1998). Increased soil nitrogen availability is positively related to resin acid concentration and the formation of resin ducts (Björkman *et al.*, 1991; Björkman *et al.*, 1998), multi-cellular tubular structures in pine needles where resin acids accumulate. High levels of resin acids are associated with increased mortality in early instar larvae (Larsson *et al.*, 1986), prolonged larval development time (Larsson *et al.*, 1986), and reduced cocoon weight (Björkman, 1997). Soil nitrogen availability is also positively related to nitrogen content in pine needles (Björkman *et al.*, 1991), potentially leading to positive effects on cocoon weight and larval development as has been shown for other insect herbivore species (Mattson, 1980). Positive effects on insect performance are often transferred to the population level, affecting population density and population fluctuations, with subsequent effects on observed damage levels (Awmack & Leather, 2002).

We set out to investigate needle chemistry of Scots pines, *i.e.* nitrogen and resin acid content, in relation to stand type, monocultures, and species mixtures. We aimed to relate sawfly performance directly to stand type and indirectly to needle chemistry. We measured performance as host plant induced mortality (bottom-up), cocoon weight (bottom-up), and the predation mortality (top-down). For our investigation, we formulated the following hypotheses: A) Pine chemistry differs between monoculture and mixed stands because of changes in competition for nutrients; B) Host plant induced mortality and cocoon weight are affected by needle chemistry and the observed differences correspond to the differences measured under A); C) Predation rates are either directly related to forest type or indirectly through forest type mediated changes in needle chemistry or tree neighbourhood.

Materials and methods

Study area and experimental design

The experiment was carried out in May and June 2014 in Sweden between the municipalities of Björklinge (60°1′54.35″N, 17°33′7.58″E) and Månkarbo (60°13′36.08″N, 17°27′52.40″E). The area is known to have regular episodes of high sawfly densities. The last high-density episode in this area was observed in 2009 (Klapwijk & Björkman, 2018), and the following years sawfly densities dropped to endemic levels. When this study was conducted the densities appeared to be increasing (Klapwijk; pers observation).

The stands within the area are characterized by semi-natural forest stands mostly dominated by Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.), and silver birch (*Betula pubescens* Ehrh.) often originated through natural regeneration after clear-cut. Other occurring tree species are rowan (*Sorbus aucuparia* L.), juniper (*Juniperus communis* L.), and oak (*Quercus robur* L.). The understory of the stands dominated by pine was characterized by the presence of mosses, lichens, heather (*Calluna vulgaris* L.), blueberry (*Vaccinium myrtillus* L.), and lingonberry (*Vaccinium vitis-idaea* L.). The understory of stands with a mixture of pine, birch, and spruce was dominated by grasses (Poaceae) and ferns (*e.g.*, *Pteridium aquilum* L. Kuhn).

We identified 12 forest stands that were judged to be between 7 and 14 years of age with pines between 2 and 3 m in height and used for our experimental purpose prior to the first pre-commercial thinning. Within each stand, we used a grid of 150 m × 90 m divided into 15 cells of 30 m × 30 m to select our experimental pines. Within each grid, we used a random number generator to randomly select 10 of the 15 grid-cells that have been previously numbered from 1 to 15. The pine at the centre of each chosen grid-cell was selected as experimental tree and considered representative for age and height of the pines of the stand. A total number of 120 experimental trees were selected. For each experimental pine, we measured tree size as the diameter at breast height (dbh) and noted whether or not aphid groups (*Cinara* spp.) were present on the branches. We made sure no other larval groups of the pine sawfly were feeding on the selected tree.

Vegetation structure and tree diversity

We recorded tree density in a radius of 4 m ($\approx$50 m^2) around each experimental pine, by counting the number of trees and noting the species. The average tree height in the stands was between 3 and 5 m, therefore we decided that woody plants higher than 1 m would be considered as trees. Any woody plant lower than 1 m was considered part of the understory. The proportion of pine around the experimental tree was calculated by dividing the number of pines by the total number of trees recorded. Our experiment was set-up in existing forest stands with high within stand heterogeneity when it comes to vegetation and tree diversity. We chose to investigate the importance of tree species diversity at the stand level ($n = 12$) and at the tree level ($n = 120$). We decided that if the stand average of number of pines around the selected experimental pines was 80% or more, the stand was classified as a monoculture. This way of dividing the selected

forest stands follows the method of characterizing monoculture stands by Toumey & Korstian (1947). This was the case for five stands, which were classified as monocultures. Seven stands were subsequently characterized as mixed stands (see Supporting information Table S1). In these stands, we observed considerable variation in pine proportion around the experimental trees, the variation the largest in the stands classified as mixed stands (Supporting information Table S1 and Fig. S1). In the analysis, we use stand type as the variable to compare among stand type (mixed and monoculture stands) and we use pine proportion as variable to assess patterns of spatial heterogeneity within the stands.

Insect herbivore study species

We used the European pine sawfly, *Neodiprion sertifer* (Geoffroy) (Hymenoptera, Diprionidae), as a study species because there is a vast knowledge about its basic biology. This pine sawfly is a specialist herbivore on pine (*Pinus* spp.) exhibiting population dynamics with irregular outbreaks that can cover thousands of hectares and last for several years (Lyytikäinen-Saarenmaa & Tomppo, 2002). Its native range is in Eurasia but the species is also common in North America, where it has been introduced (Olofsson, 1987). Females emerge from their pupae during late August—early September with their full egg load intact. The eggs from one female are laid in one batch, on needles of current-year shoots, where the eggs overwinter until they hatch in May. Oviposition preference by adult sawfly females can vary in relation to the different origin of Scots pine seeds that might reflect differences in chemical or phenological pine traits (Trewhella, Leather & Day, 2000). After hatching, the larvae feed gregariously on the needles from the previous year's shoots until the fourth (male) or fifth (female) instar.

Experimental set-up

For each experimental tree, we selected two lush branches belonging to the same whorl at breast height. We placed a small group of 25–30 second instar larvae on each branch, group size was chosen to ensure accurate counts. The larvae were collected in the selected forest stands, homogenized among groups and moved one-by-one using a small and soft brush, and directly placed on the previous year needles.

One of the two selected branches of each experimental tree was used to determine the effect of host plant quality on mortality of sawfly larvae and cocoon weight. The group on this branch was isolated with a perforated climate bag inside a mesh net sleeve cage (75 cm length × 35 cm width, made from material of Viltsäck 4, 425 cm × 145 cm, Stabilotherm AB). The cage minimized the risk for sawfly larvae to be attacked by natural enemies, hence mortality could be attributed to plant quality alone. The temperature inside the cage was measured using a logger (SL52T, Signatrol Ltd) prior to the beginning of the experiment to ensure that there was no difference from the external environment. On the second selected branch, the larvae were left exposed to predators to assess predation mortality. All predatory arthropods, *i.e.* walking arthropod predators and flying parasitoids, had free access to the larval group placed on the pine

branch. These groups were exposed on the branch for roughly three weeks and caged when the majority of the remaining larvae reached the fourth instar. The reason for caging the exposed larval groups was to avoid that the larvae left the tree to spin cocoons for diapause and pupation. Both groups were left in the field until the cocoon stage and then brought to the laboratory at the department of Ecology of SLU, Uppsala.

Using the larvae from the plant quality treatment, we calculated host plant induced mortality by dividing the number of larvae reaching cocoon stage by the initial number of larvae in the group and subtracting that from one. The female cocoons were weighed with a microbalance (Mettler Toledo MX5) approximately two to three weeks after collection and prior to adult emergence. We weighed only female cocoons as a proxy for fecundity, because a strong correlation between egg load and cocoon weight has been established (Nordkvist *et al.*, 2019). To calculate predation mortality, we used the larvae from the predation treatment by summing up the number of predated and parasitized larvae and divided that number by the initial number of larvae in the group. To correct the predation mortality for the effects of host plant quality, we subtracted the proportion of mortality obtained for host plant quality from the proportion predation mortality within the same tree. The larvae of *N. sertifer* are very sedentary, thus remain on the branch once transferred (Kaitaniemi *et al.*, 2007) and therefore disappeared larvae can be assumed dead. In order to assure that predation mortality is not overestimated, we accounted for potential host plant effects. Parasitoids are important predators of the pine sawfly. To obtain the full predation mortality, we included parasitized larvae as well. To establish parasitism, we kept the intact cocoons over winter to await emergence of parasitoids in the spring. The number of emerging parasitoids was counted and any intact cocoon remaining at this stage was dissected as the organism inside could be presumed to be dead. During dissection the fate of the larvae was classified as sawfly (larvae or adult), or parasitoid (pupae or adult). The result of the dissection was added to the numbers used for calculations of the predation mortality. Numbers of reared parasitoids were too low to allow separate analysis.

Chemical analyses

The chemical analyses focused on resin acid and nitrogen content of the needles of the experimental trees. For each experimental pine, we collected 20 needles of the previous year from the branch that hosted the sheltered groups after the sawfly larvae had spun cocoons. The collected needles reflect the food quality that the larvae experienced as the response of pine to sawfly defoliation has not been found to induce an immediate or delayed induced response (Niemelä *et al.*, 1991; Lyytikäinen, 1994; McMillin & Wagner, 1997; Lyytikäinen-Saarenmaa, 1999; Nordkvist *et al.*, 2019). The collected needles were immediately folded in aluminium foil and placed in a plastic box containing dry ice to avoid any resin acid degradation. The collected needle pairs were split, one of the two sets of needles was prepared for resin acid analysis and the other set was used for nitrogen content determination. The needles were stored at −22 °C. The needles for resin acid analysis were

ground in an oscillating mill (Retsch MM400), all the while kept frozen. The ground material was collected in small plastic tubes and stored at −22 °C before shipping to the Max Planck Institute for Chemical Ecology in Jena (Germany) for chemical analyses. For the gas chromatography–mass spectrometry (GC–MS) to analyse and quantify the concentrations of resin acids, 100 mg of ground material was extracted in 1 mL of tert-butyl methyl ether (TBME) with the internal standard dichloredehydroabietic acid (Cansyn) (0.045 mg/mL) and shaken for at least 14 h at room temperature. The ethereal extracts were washed with 0.3 mL of 0.1 m ammonium carbonate $(NH_4)_2CO_3$ (pH 8.0), transferred to a new vial, and filtered through a Pasteur pipette column filled with $NaSO_4$ and washed with 1 mL of TBME. 0.4 mL of the ethereal extracts was methylated by adding 50 μL of 0.2 m N-trimethylsulphoniumhydroxide (Macherey-Nagel) at room temperature for 2 h.

The analyses of constituent resin acids were performed using a Hewlett-Packard 6890 GC-MSD system fitted with an HP-5 column (0.25 mm × 0.25 μm × 30 m; Hewlett-Packard, Agilent Technologies, Santa Clara, California). For injections, 1 μL of the ethereal extract at 280°C was used. The instrument programme began with a starting temperature of 150°C for 3 min which was then raised at a rate of 3.5°C/min to 280°C and held for 4 min. Helium was used as carrier gas at a constant flow of 1 mL/min. Identification of resin acids was based on comparison of retention times and mass spectra with authentic standards or with mass spectra in the Wiley 275.L or National Institute of Standards and Technology 98.1 MS libraries. Resin acid concentrations in the samples were quantified relative to the internal standard (μg/mL for 1 mg). We present the results for comparisons of total and individual resin acids between monocultures and mixed stands in the Supporting information (Table S2 and Figs S2–S4). Prior to statistical analysis, we calculated the sum of the content of all identified resin acids based on their dissolved dry weights (μg/ml for 1 mg) (see Supporting information Fig. S2). The content of half of the single resin acids showed no difference between monoculture and mixed forest stands (see Supporting information Table S2, Figs S2–S4), whereas three showed a difference. We proceeded using the sum of the resin acids as a measure of total resin acid content in further analysis and used the three that were different also individually in the analysis, but only reported the ones with a significant result.

The second set of needles were used to determine nitrogen content. Prior to analysis, this material was dried (70 °C for 48 h) and subsequently ground. Needle nitrogen content (percentage of the dried weight of the sample) was determined with an elemental analyser:vario EL CNS (Elementar Analysensysteme GmbH, Elementar-Strasse 1, D-63505, Langenselbold, Germany). This analysis was performed under commission by the laboratory of 'Routine Measures and Analysis' at the Max Planck Institute of biogeochemistry in Jena, Germany.

Statistical analysis

Linear mixed models. To compare the needle chemistry in Scots pine growing in different stand types, we used linear mixed models (lme; package lme4 in R; Venables & Ripley, 2002). For the first set of models, the response variables were needle nitrogen and total resin acid content, respectively. For each response variable, we included the explanatory variables stand type (two levels: monoculture and mixed stands), size (dbh) of the experimental pine, and tree density around the experimental pine as fixed covariates in the model. Tree size (dbh) was included to control for potential effects of tree size on the response variables. Site identity was included as a random factor.

In a second set of linear mixed models, we used host plant induced mortality, predation mortality, and cocoon weight as response variables. For these response variables, stand type (two levels: monoculture and mixed stands) and presence of aphids (two levels: presence and absence) were included as fixed factors, size (dbh) of the experimental pine, the content of nitrogen, the content of total resin acids and tree density were included as fixed covariates in the model. Total resin acid and nitrogen content were included to assess the effect of needle chemistry on the response variables. Aphid presence/absence can be an indirect indication of needle chemistry and an explanation of predation mortality because ants tending the aphids are known to be predators of the European pine sawfly (Olofsson, 1992, Lindstedt *et al.*, 2006).

In all models, we restricted the analysis to two-way interactions between all variables included in the model (except tree size). Higher order interactions were excluded because of the limited biological explanatory value. Including interactions provides insight whether combinations of explanatory variables will have a non-additive effect on the response variable. Especially interactions with forest type are interesting as these would indicate that the relationship of a covariate with the response variable is dependent on forest type. Total resin acid content was log-transformed prior to analysis. We used a function that allowed different variances of the response for the levels of forest type and aphid presence (varIdent; stats package). Both the host plant induced mortality and predation mortality (proportions) were arcsine square-root transformed prior to analysis. The minimum adequate model was obtained through backwards elimination of nonsignificant variables starting with interactions (Crawley, 2012, pp. 388–448) based on significance calculated using a type II ANOVA (Anova; car package; Fox & Weisberg, 2011). This means that we removed all nonsignificant interactions from the model, we present the results for the main explanatory variables and the significant interactions. For each model, we calculated the marginal and conditional R^2 using the r.squaredGLMM-function in the MuMIn-package in *R* (Barton, 2019). We chose to use a linear mixed model over a generalized linear model to match the structural equation model presented below. The Supporting information provide the summed mean and standard deviation for each variable and the site mean and standard deviation for each variable (see Supporting information Table S1). For the differences between forest types a graphical overview is provided for each variable (see Supporting information Fig. S5). We have also provided information on the number of female cocoons and the weight per experimental tree (see Supporting information Table S3).

Piecewise structural equation model. Complementary to the linear models, we used a structural equation model (SEM) to assess how direct and indirect effects of stand type on tree density, size

(dbh) of the experimental pine, pine proportion affected nitrogen and total resin acids content, and the subsequent effects on host plant induced mortality, predation mortality and cocoon weight using PiecewiseSEM (psem; package PiecewiseSEM in R; Lefcheck, 2016). The predation mortality was not corrected for host plant quality. In the SEM, correlations between variables can be taken into account if significant, this will correct for the potential over-estimation of the predation rates. PiecewiseSEM constructs a SEM based on individual linear models. The SEM model constructed from the individual linear models contains direct significant relationship and indirect relationships. In the SEM, two variables are linked when they both have a significant relationship to shared third variables. We constructed the model of seven linear mixed models where direct relationships were modelled between stand type and proportion pine, tree density around experimental trees, and size (dbh) of the experimental pine (Fig. 1; see Supporting information Table S4). We modelled a direct relationship between proportion pine, tree density, and tree size with nitrogen and total resin acid content. Last, we modelled a direct relationship between nitrogen and total resin acid content with host plant induced mortality, predation mortality, and cocoon weight. In the model, aphid presence was included as it might influence the sawfly performance variables (host plant induced mortality, predation mortality, or cocoon weight). The goodness of fit of the model depends on how accurate the direct relationships are modelled. Based on this measure of fit, we added direct relationships that were not included in the model describe above. We included the direct relationships in the model and any significant covariance (Fig. 1). This resulted in the model presented in the results.

To build our SEM using piecewiseSEM, we used linear mixed models (lme; package—nlme) with site identity included as a random factor. In the piecewiseSEM package, the use of a binomial error structure and proportion data has not yet been implemented, therefore we arc-sine, square-root transformed the proportions prior to analysis. The total resin acid content was log-transformed prior to analysis. When necessary we included a variance function that allowed for the different levels of forest type to have different variance distributions (VarIdent; stats-package). We experienced problems with convergence and changed the method for optimization as such that multiple algorithms were applied (lmeControl(opt='optim'); stats-package).

Results

The linear mixed models

Nitrogen and total resin acid contents were not affected by forest type, tree density, tree size (dbh), or the interaction between the explanatory variables (Table 1A,B). Host plant induced mortality was negatively related to nitrogen content (Table 1C), with a steeper decline in monoculture compared to mixed stands. The variation explained by the model was 13% (marginal R^2) also when the variation explained by the random effect was taken into account (conditional R^2). Cocoon weight was related to a negative interaction between nitrogen content and total resin acid content. This interaction indicates that cocoon weights are higher when total resin acid content is high and nitrogen content low and *vice versa*. The model explains 9% of the variation and if

the variation explained by the random effect is included explains the model 16% of the total variation (Table 1D). The presence of aphids increased the predation mortality slightly (Table 1E). The model explained only 6% of the total variation, 10% if also the variation explained by the random effects is included.

The same analyses were carried out with the three individual resin acids that showed a significant relationship with forest type or pine proportion. The results are presented in the Supporting information Table S5.

The structural equation model

The only variable that appears to be different between the two stand types was pine proportion (Fig. 1B). Tree size (dbh) and density were not different between the stand types (Fig. 1B). The proportion of pine around the experimental tree was negatively related to nitrogen content in the needles (-0.127 ± 0.066). Nitrogen content was negatively related to host plant induced mortality (-0.289 ± 0.163). Host plant induced mortality and predation mortality were positively correlated ($r = 0.239$). Nitrogen content showed a positive correlation with total resin acid content ($r = 0.274$). In the presence of aphids, in the experimental tree, host plant induced mortality decrease (-0.101 ± 0.151), and predation mortality increases (0.226 ± 0.085). Aphids were more likely to be present in large trees (0.134 ± 0.078). Tree size (dbh) shows a negative correlation with tree density ($r = -0.199$). Cocoon weight was not related to any of the variables included in the model. The validity of the model was checked by testing whether or not the model contains all important direct relationships (Lefcheck, 2016). Fisher's $C = 26.863$ with P-value = 0.981 on 44° of freedom showed that the model did not significantly deviate from the assumption that all relevant direct relationships have been included in the model (see Supporting information Table S4 for the full model results). The same analysis was run but instead of total resin acids, the three individual resin acids (see Supporting information Table S2) showing a significant difference between forest types were included. Of those three resin acids, only dehydroabietic acid changed the outcome of the SEM. This resin acid was significantly lower in mixed stands and negatively related to both host plant induced mortality and cocoon weight (see Supporting information Table S6; Fig. S6).

Discussion

The aim of our study was to investigate whether stand diversity has an effect on pine needle chemistry and, subsequently, affects the performance of larvae of the European pine sawfly. We did this by comparing nitrogen and total resin acid contents of pine trees growing either in monoculture or mixed stands and related this with the performance of sawfly larvae within those stands. Our results only partially confirm the hypothesis that forest type affects host plant quality. The performance of the sawfly larvae is indirectly affected by forest type. The effects of resin acids and nitrogen appear to inhibit each other in affecting performance. Predation mortality is positively related to aphid presence in the experimental tree but not to any other variable measured. The effect of pine proportion on nitrogen content indicates that within
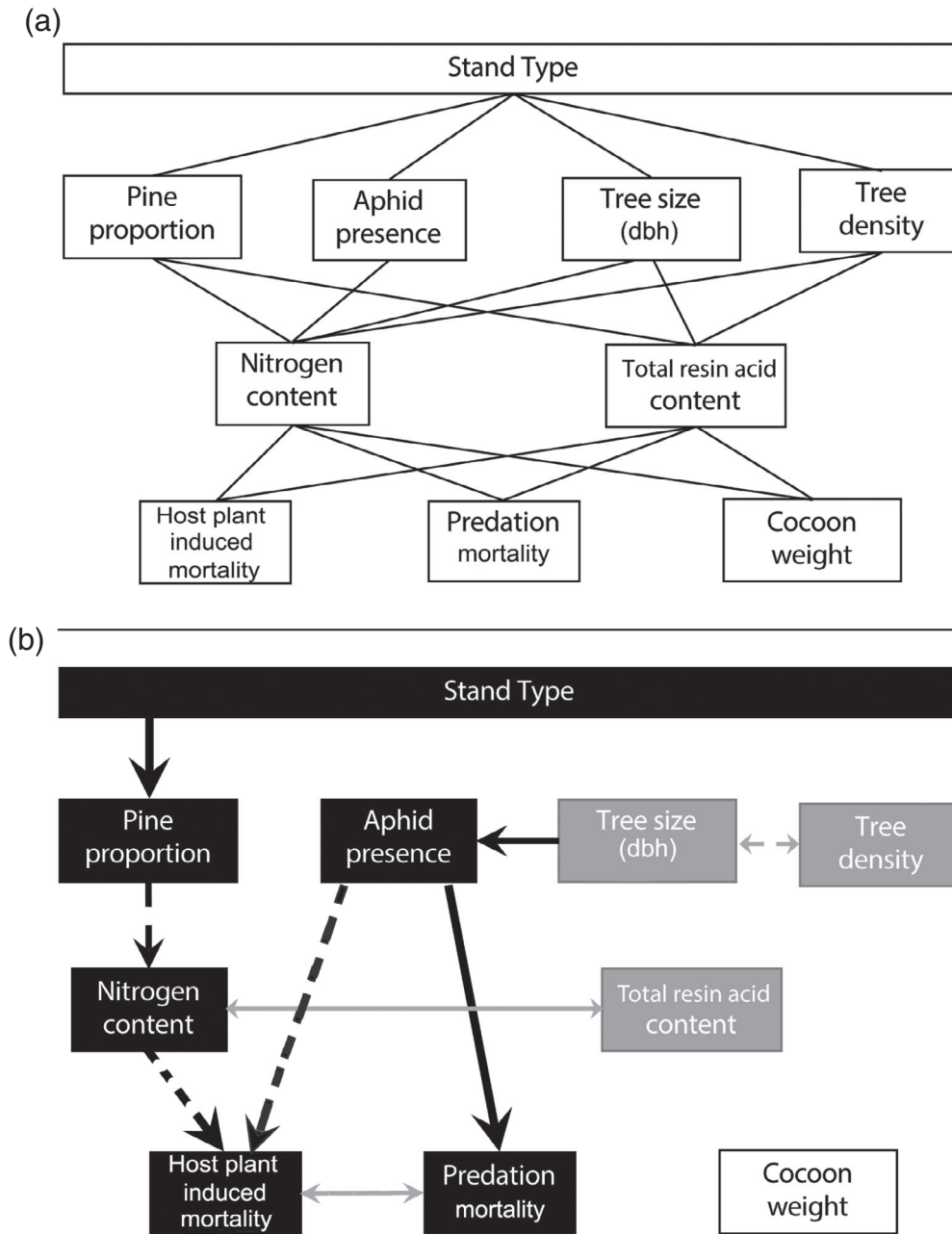
(a)

(b)

Figure 1 (a) The path model with all the tested relationships indicated. (b) The path model with the significant relationships indicated. The directed arrows indicate direct significant relationships. Grey directed arrows indicate marginally significant direct relationships. Double headed arrows indicate significant covariances. Solid arrows (single or double headed) indicate positive relationships and dashed arrows (single or double headed) represent negative relationships. The full model output can be found in the supporting material Table S4. The analysis has been performed using arcsine square-root transformed proportion for proportion survival and predation rate, and log-transformed values for resin acids, the estimates given are according the transformations.

stand variation could be more important than between stand variation (*i.e.* forest type). Based on that result we posit that at least in our system, changes in host plant quality, and subsequent effects on the herbivore performance likely depend on a wider ecological context than stand level tree species diversity alone.

Contrary to our expectation, we found no differences in nitrogen content between experimental pines when we compare the mean of monocultures or mixed stands (Table 1B). The structural equation model showed that the proportion of pine around the experimental tree (within either mixed or monoculture stands) affects the nitrogen content of needles negatively. We may, therefore, speculate that trees surrounded by hetero-specific neighbours could have better resource acquisition than trees surrounded by conspecifics as a result of reduced resource

Table 1 The results for the linear mixed effects models investigating the effect of forest characteristics on chemical composition of pine needles and insect performance

Response	Explanatory	DF	F-value	Estimate	St. error	Random effect: Site Standard deviation Intercept	Residual
(A) Resin acids (ln) (n = 118)	**(intercept)**	**1103**	**205.57**	**2.38**	**0.19**	0.20	0.34
	Dbh	1103	0.17				
	Forest type — mixed	*1,10*	*3.71*	*−0.15*	*±0.07*		
	Tree density	1103	0.05				
(B) Nitrogen (n = 118)	**(intercept)**	**1102**	**242.30**	**0.99**	**±0.06**	0.06	0.12
	Dbh	1102	0.68				
	Forest type	1,10	0.03				
	Tree density	1102	0.13				
(C) Host plant induced mortality (n = 111)	(intercept)	1,93	0.04			0.00	0.19
	Dbh	1,93	0.00			Forest type	
	Forest type — mixed	*1,10*	*3.41*	*−0.31*	*±0.17*	Mixed	Mono
	Tree density	1,93	0.04			1.00	1.06
	N-content	**1,93**	**5.15**	**−0.37**	**±0.16**		
	Resin acids (ln)	1,93	0.07			Aphid presence	
	Aphid presence — absent	*1,93*	*3.74*	*−0.06*	*±0.02*	Absent	Present
	Forest type × N-content	*1,93*	*3.62*	*−0.30*	*±0.16*	1.00	1.33
(D) Weight (mg) (n = 111)	(intercept)	1,93	0.59			1.47	4.25
	Dbh	1,93	1.28				
	Forest type	1,10	0.03				
	Tree density	1,93	2.58				
	N-content	**1,93**	**4.78**	**45.86**	**±20.97**		
	Resin acids (ln)	*1,93*	*3.54*	*14.96*	*±7.96*	Aphid presence	
	Aphid presence	1,93	0.61			Absent	Present
	N-content × resin acids	*1,93*	*3.77*	*−15.48*	*±7.98*	1.00	1.11
(E) Predation mortality (n = 75)	*(intercept)*	*1,58*	*3.65*	*0.83*	*±0.43*	0.07	0.33
	Dbh	1,58	0.16			Forest type	
	Forest type — mixed	1,10	0.02			*Mixed*	*Mono*
	Tree density	1,58	0.05			1.00	0.80
	N-content	1,58	0.01				
	Resin acids (ln)	1,58	0.47			Aphid presence	
	Aphid presence — absent	*1,58*	*3.20*	*−0.11*	*±0.06*	Absent	Present
						1.00	1.29

Note: The models are obtained using lme (package nlme in *R*). The tests are calculated using the principle of marginality. We present fixed factors and covariates and significant interactions. The estimates given are only for the significant variables and are deviations from the overall mean (intercept in the table) for factors. For certain models a variance structure was included that allowed for different variances between groups for the variable 'forest type' and 'aphid presence'. The variables printed in bold are significant at 95% (*i.e.* $P \leq 0.05$), the variables printed in italics are marginally significant at 90% (*i.e.* $0.10 \leq P \leq 0.05$).

competition (Lang *et al.*, 2014; Erfanifard & Stereńczak, 2017). The lack of effect at stand level and the observed effects at the tree-level suggest that small-scale variation in neighbourhood composition (*e.g.* pine proportion around experimental pine) could be of overriding importance in determining host plant quality.

Pine proportion tends to relate negatively to nitrogen content of the needles, and pine proportion is lower in mixed stands compared to monoculture stands. Thus, forest stand relates indirectly to host plant induced mortality (Fig. 1B), indicating that trees in mixed stands could have higher nitrogen content and thus higher plant quality related mortality because the pine proportion is often lower around individual trees (see Supporting information Fig. S1). The decreased bottom-up mortality does, hence, not provide an additional mechanism for the observed more stable insect population dynamics in diverse compared to simplified habitats (Oliver *et al.*, 2010; Haddad *et al.*, 2011). Other

bottom-up mechanisms like plant apparency (Sholes, 2008) and resource concentration (Abdala-Roberts *et al.*, 2015) might, therefore, be more important in their contribution to population regulation of pest insects in more diverse habitats.

Resin acids, as part of the constitutive defence (Mumm & Hilker, 2006), have previously been found to affect host plant induced mortality, cocoon weight, and predation mortality in the European pine sawfly (Larsson *et al.*, 1986, Björkman *et al.*, 1991; Björkman, 1997). We found a marginal difference in total needle resin acid content between pines in monoculture and mixed stands studied here. But no effect on any of our response variable was observed. Environmental factors, together with high genetic variability among Scots pine genotypes (Manninen *et al.*, 2002), could have resulted in high variability within stands. This high variation may have been masking any differences between monoculture and mixed stands. Resin acid content in Scots pine is found to depend on soil nutrient

concentration (Björkman *et al.*, 1991; Nerg *et al.*, 1994), drought stress (Turtola *et al.*, 2003; Blanch *et al.*, 2009), and sun exposure (Gref & Tenow, 1987). We did find that individual resin acids show individual responses to forest type. They have also more or less explanatory powers as shown in the Supporting information Table S2, S5, and S6. However, trying to interpret the implications of these relationship will lead to high levels of speculation and we have, therefore, only presented the results and refrained from further discussion.

Predation mortality was not found to be different between the forest types or related to any of the within stand variables or needle chemistry measures. We did find a significant effect of the presence of aphids on host plant induced mortality and predation mortality. We included aphid presence as they function as alternative prey and attract ants to trees, and, in addition, ants are known to be important predators of the pine sawfly (Lindstedt *et al.*, 2006). The natural enemy hypothesis suggests that higher diversity of plants will result in more diverse alternative prey and thus increased diversity and abundance of natural enemies (Barbosa *et al.*, 2009). But as we did not set out to investigate the link between aphid/ant presence and forest diversity and its subsequent effect on predation rates (Kaitaniemi *et al.*, 2007), this remains a subject of further investigation.

We need to point at some caveats that might affect the interpretation of our results. The susceptibility of sawfly larvae to resin acids is higher during early larval stages (Larsson *et al.*, 1986). The practical choice of using sawfly larvae at second instar could have reduced the magnitude of the effect observed for larvae survival and cocoon weight. A second caveat is the lack of standardization of whorl height among trees which could have contributed to the observed variation in total resin acid and nitrogen content (Hollinger, 1996), although our intention was to minimize this kind of variation by using approximately the branches at same whorl height in each tree. Last, our study was performed in an area notorious for epidemic sawfly density, with potential previous defoliation affecting needle chemistry (McMillin & Wagner, 1997; Trewhella, Leather & Day, 1997; Roitto *et al.*, 2008). All the three caveats are the result of choices we needed to make, prior to our experiment. We do believe that the level of replication among forest type and within the stands have led to solid results.

Although hypothesized, in our study we do not find an indication that stand diversity mediated host plant quality could be a potential explanation for the observed patterns in herbivory in previous studies (Jactel & Brockerhoff, 2007; Guyot *et al.*, 2015). On the contrary, we find that there is a potential for herbivore performance to be increased in mixed stands. Acknowledging the limitations of our study, we do believe our study sets the background for discussion and further research into the importance of the role of host plant mediated population regulation in mixed forest stands compared to monoculture forest stands (Moreira *et al.*, 2016). The link between herbivore performance and habitat diversity *via* host plant quality needs to be studied further to understand how bottom-up effects contribute to regulating herbivore populations. The need for this kind of knowledge is made all the greater by the continuing trend towards diversification of many managed systems in forestry and agriculture.

Author contributions

CB and MJK developed the ideas and study design. DB executed the experiment. AS and JG performed the chemical analysis and wrote the methodology for the chemical analysis. MJK analysed the data and designed the figures. DB wrote the first draft of the manuscript and CB and MJK contributed to further versions of the manuscript. All authors gave their consent for publication.

Data availability statement

Data available on request from the authors.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

 Appendix S1: Supporting Information.

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