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PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats

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Abstract According to the associational resistance hypothesis, neighbouring plants are expected to influence both the insect herbivore communities and their natural enemies. However, this has rarely been tested for the effects of canopy trees on herbivory of seedlings. One possible mechanism responsible for associational resistance is the indirect impact of natural enemies on insect herbivory, such as insectivorous birds. But it remains unclear to what extent such trophic cascades are influenced by the composition of plant associations (i.e. identity of 'associated' plants). Here, we compared the effect of bird exclusion on insect leaf damage for seedlings of three broadleaved tree species in three different forest habitats. Exclusion of insectivorous birds affected insect herbivory in a species-specific manner: leaf damage increased on *Betula pendula* seedlings whereas bird exclusion had no effect for two oaks (*Quercus robur* and *Q. ilex*). Forest habitat influenced both the extent of insect herbivory and the effect of bird exclusion. Broadleaved seedlings had lower overall leaf damage within pine plantations than within broadleaved stands, consistent with the resource concentration hypothesis. The indirect effect of bird exclusion on leaf damage was only significant in pine plantations, but not in exotic and native broadleaved woodlands. Our results support the enemies hypothesis, which predicts that the effects of insectivorous birds on insect herbivory on seedlings are greater beneath non-congeneric canopy trees. Although bird species richness and abundance were greater in broadleaved woodlands, birds were unable to regulate insect herbivory on seedlings in forests of more closely related tree species.

Keywords Tritrophic interactions · Insectivorous birds · Resource concentration hypothesis · Natural enemies hypothesis · Seedling herbivory

Introduction

The relative importance of different mechanisms regulating patterns of insect herbivory in plant communities is still a matter of debate. In particular, insect herbivory is thought to depend on intrinsic plant resistance traits, as a given plant species may experience different rates of herbivory depending on the identity and concentration of neighbouring plants. This is one of the principles of the "associational resistance" theory (Barbosa et al. 2009). Two main hypotheses have been proposed to explain associational resistance: the resource concentration hypothesis and the natural enemies hypothesis (Root 1973; Russell 1989). The resource concentration hypothesis states that the likelihood of a plant being located by herbivores, i.e. its apparency (Karban 2010), is influenced by the relative abundance and the nature of neighbouring plants. In more diverse plant communities, a given host plant is proportionally less frequent and can be hidden by neighbouring non-host plants. The natural enemies hypothesis suggests that richer plant assemblages offer a greater array of

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complementary food and habitat resources that benefit natural enemies which can, in turn, control herbivores more effectively (Root 1973; Russell 1989).

It has been suggested that the resource concentration hypothesis may account for a significant part in the reduction of damage from specialised herbivores within diverse plant communities (Finch and Collier 2000; Björkman et al. 2010). In particular, the association of non-congeneric plant species with contrasting morphological or semiochemical traits can greatly reduce the ability of host-specific herbivores to locate, colonise and exploit their host plants (Jactel and Brockerhoff 2007). However, while some studies observed clearly reduced insect herbivory in more diverse forests (Jactel and Brockerhoff 2007), others found no clear evidence for this (Vehviläinen et al. 2006). Depending on the presence of host tree species in mixed forest, there can even be an opposite effect (Vehviläinen et al. 2007) that may be attributable to associational susceptibility (Barbosa et al. 2009).

Most previous studies on this subject focussed on canopy trees, but the same issues apply to seedlings and saplings which represent a critical developmental stage for forest regeneration. Interestingly, similarly varying responses of insect herbivory were observed on young trees along tree diversity gradients or underneath other adult tree species, with examples of more (White and Whitham 2000; Schuldt et al. 2010) or less damage (Maetô and Fukuyama 1997; Sobek et al. 2009). Tree seedlings can be expected to experience a higher risk of insect herbivore spillover from conspecific canopy trees (Maetô and Fukuyama 1997; Pigot and Leather 2008), according to the Janzen–Connell hypothesis (Norghauer et al. 2010).

Surprisingly few studies have investigated the role of natural enemies in controlling insect herbivory on tree seedlings along ecological gradients (Riihimäki et al. 2005; Kaitaniemi et al. 2007; Sobek et al. 2009). These provide some support for the occurrence of top-down control of forest insects by natural enemies, which may be tree species-dependent. However, these studies only focused on predatory insects. Vertebrates predators, such as birds (Bock et al. 1992), lizards (Dial and Roughgarden 1995) and bats (Kalka et al. 2008), can significantly reduce populations of herbivorous arthropods and indirectly limit damage and/or promote vegetation growth (Mooney et al. 2010; Mäntylä et al. 2011). However, the indirect effect of predators on plant biomass via a trophic cascade is highly variable due to compensation effects at the herbivore or plant levels (Pace et al. 1999).

In temperate forests, insectivorous birds are among the most important predators of herbivorous insects, especially Lepidoptera and Hymenoptera (Holmes et al. 1979; Glen 2004). Several studies have reported an increase of leaf damage when insectivorous birds were experimentally excluded using caged plants (Atlegrim 1989; Marquis and Whelan 1994; Sipura 1999; Mazía et al. 2004; Van Bael et al. 2008), whereas others reported more limited effects (Forkner and Hunter 2000; Low and Connor 2003). Insectivorous birds are considered as an element of indirect plant defences (Price et al. 1980) with many documented top-down effects on insect herbivores (Whelan et al. 2008).

The identity of the focal plant species may be important to explain both the influence of natural enemies (Vehviläinen et al. 2008), such as insectivorous birds, and the effect of host concentration on insect herbivory. Plants differ in their physical characteristics (e.g. architecture, foliage structure), which provides insectivorous birds with a wide variety of distinct foraging substrates, which, in turn, may influence trophic cascades (Marquis and Whelan 1996; Whelan 2001). Plant species also present different constitutive defences (Sipura 1999) or volatile organic compounds (Mäntylä et al. 2008) that have been demonstrated to affect both insect herbivory and insectivorous bird foraging.

In this study, we investigated the importance of bird predation and host resource concentration as mechanisms affecting insect herbivory. We designed a manipulative experiment in the Landes de Gascogne forest, the largest pine plantation forest in Europe. Previous studies in such forests have shown that deciduous trees at the understorey level or as remnants of natural forests provide key resources or habitat to several insect and bird taxa in this context of conifer plantations (Barbaro et al. 2005; Brockerhoff et al. 2008; van Halder et al. 2008). To improve the management of planted forests for the benefit of biodiversity, it is therefore important to know more about how stand composition may affect the impact of insect damage on these broadleaved species at their most susceptible developmental stages, i.e. seedlings and saplings (Vásquez et al. 2007).

We tested the effect of the identity of the plant species by comparing the level of insect herbivory on seedlings of three native broadleaved species: silver birch (*Betula pendula*), pedunculate oak (*Quercus robur*) and holm oak (*Q. ilex*). We then examined the resource concentration hypothesis, and, more specifically, the importance of taxonomic similarity between seedlings and canopy tree species, by experimentally planting seedlings of these native broadleaved trees within three forest habitats: native broadleaved, exotic broadleaved, and native conifer habitat. We hypothesised that deciduous seedlings planted within stands composed of conspecific deciduous tree species would experience higher leaf damage than when they are planted into conifer stands. To test the enemies hypothesis, we estimated the effect of removing bird predation on insect herbivory by planting seedlings within bird exclosure cages. We hypothesised that bird predation would be higher in pine stands where deciduous seedlings represent sources of alternative prey.

Materials and methods

Study site

The study was carried out in the Landes de Gascogne forest, south-western France, a region covered by ca 10,000 km^2 of planted forests of native maritime pine *Pinus pinaster*. The climate is thermo-Atlantic and soils are podzols established on several meters of sandy deposit. The study sites are located ca 40 km south of Bordeaux (44°44′N, 00°46′W) near the field research centre of the French National Institute for Agricultural Research (INRA). This area is dominated by a mosaic of maritime pine plantations of different ages with small deciduous forest remnants. These woodlands are dominated by native pedunculate oak *Quercus robur* and silver birch *Betula pendula* with scattered holm oaks *Q. ilex*. A few plantations of exotic oak species (red oak *Q. rubra* and Bartram's oak *Q. heterophylla*) also occur in the area. The understorey vegetation is relatively species-poor, due to both nutrient-poor acidic soils and intensive stand management. Dominant understorey species are common bracken (*Pteridium aquilinum*), various herbaceous species such as *Molinia cærulea* and *Pseudarrhenaterum longifolium*, dwarf and common gorse (*Ulex minor*, *U. europaeus*), heather species (*Erica scoparia*, *E. cinerea*, *Calluna vulgaris*), glossy buckthorn (*Frangula alnus*) and European honeysuckle (*Lonicera periclymenum*).

Experimental design

To test for an effect of contrasting forest habitats, we selected 20 stands comprising 6 stands of maritime pine, 6 stands of exotic oaks (*Q. rubra* or *Q. heterophylla*) and 8 native woodlands dominated by *Q. robur* and *B. pendula*. In these 20 stands, we established two experimental units to compare two treatments: control and bird exclusion. Both treatments were located in the same stand but 5–10 m from each other to avoid any potential disturbance by birds foraging in control areas. The bird exclosure was a cage measuring of 100 × 100 × 100 cm fenced off with wire netting (15 × 15 mm mesh). This treatment allowed insects to access seedlings while excluding all insectivorous birds including the smallest species recorded from the experimental plots (wren, *Troglodytes troglodytes*, and firecrest, *Regulus ignicapillus*). In the control treatment, seedlings were left uncaged so that herbivorous insects were left exposed to bird predation. A comparison of the microclimatic conditions between treatments was undertaken at the beginning of the experiment (using Hobo; Onset Computer, Bourne, USA). This showed that exclusion cages had no significant effect on soil humidity, air temperature and relative humidity (Wilcoxon matched-pairs signed-ranks tests).

In March 2007, two seedlings each of silver birch *B. pendula*, *Q. robur* and *Q. ilex* were transplanted together as an experimental unit of six seedlings. Seedlings were 1 year old and had the same south-western France origin. They were planted ca. 40 cm apart from each other and the position of each species was randomly assigned. Experimental units were protected by an exclusion cage (cage treatment) or left uncaged (control). The same paired design was replicated in the 20 experimental forest stands, for a total of 240 transplanted seedlings (2 seedlings × 3 species × 2 experimental units × 20 stands).

Herbivory measures

Nondestructive assessments of insect herbivory were performed by visual inspection of all leaves on every seedling. Damaged leaf area was estimated using transparent plastic grids of two different mesh sizes (0.25 and 1 cm^2). The smaller grid was used on leaves smaller than 6 cm^2 for greater accuracy. A percentage of leaf area removed (LAR) was calculated for each leaf and averaged per seedling. Intact leaves were recorded as 0% LAR. Within the same unit, the two seedlings of the same species were considered as pseudo-replicates and their herbivory rates were averaged. The response variable was therefore calculated as the percent LAR per species for each experimental unit. Herbivory measures were performed during two growth seasons (2007 and 2008), with assessments in May (early season) and July (mid-season) and a final assessment in September 2008.

Bird censuses

Bird communities were censused in nine of the sampled stands, providing three representative replicates of the three forest habitats. We used the point-count method with two visits during early and late breeding seasons of 2007. We recorded all birds heard and seen during the two 20-min visits and used the maximal abundance across the two visits for a given species to obtain species richness and abundance for each stand (see Barbaro et al. 2005). We classified all the species recorded according to their diet and foraging guild (Barbaro and van Halder 2009), and kept for further analyses only the insectivorous species likely to forage on the experimental seedlings (Electronic Supplemental Material Table S1).

Statistical analyses

To compare herbivory rates between seedling species and forest habitats, linear mixed-model analyses (Pinheiro and Bates 2004) were performed with the procedure *lme* (R software; R Development Core Team 2008) using LAR estimated in the control treatment at each period of assessment as response variables. We used fixed effects for seedling species, forest habitat and their interaction and a random effect for forest stand within forest habitat.

To test the effect of bird exclusion on herbivory rates according to forest habitats, we performed a second set of linear mixed-model analyses. We used fixed effects for forest habitat, bird exclusion treatment and their interaction and a random effect for forest stand within forest habitat. Analyses were performed separately on LAR values for each seedling species and each date of assessment. Repeated-measures analysis was not used to avoid confounding within-year and between-year repeated measures.

In all linear mixed-models, LAR data were arc-sine transformed to meet the assumptions of normality and homoscedasticity, which were verified by graphical analyses and Shapiro–Wilk tests on model residuals. Multiple comparisons were conducted to test for difference between seedling species or forest habitats using Tukey's HSD test.

Insectivorous bird richness and abundance were analysed by Kruskal–Wallis rank sum tests followed by Behrens–Fisher multiple comparisons to test for difference between the three forest habitats.

Ultimately, we estimated the magnitude of the effect of bird exclusion on LAR in seedlings throughout the 2 years of assessments (i.e. the difference in LAR between control and exclusion cage treatments). We tested how this magnitude varied with seedling species and forest habitat (Nakagawa and Cuthill 2007) by calculating Hedge's effect size (*d*) for each combination of seedling species × forest habitat, using stands within habitat types as replicates. All censuses were pooled following the method proposed by Borenstein et al. (2009) for repeated measurements within a study. For each combination of seedling species × forest habitat, mean LAR values were averaged across the five census dates. The averaged standard deviation was calculated as the mean standard deviations in each date weighted by the correlation coefficients between dates. The effect size was calculated as:

$$d = J[(\mathrm{X}_{\mathrm{BE}} - \mathrm{X}_{\mathrm{CTL}})/S]$$

with X_{BE} representing the mean LAR per species and forest habitat in the bird exclusion treatment, $\mathrm{X}_{\mathrm{CTL}}$ the mean LAR for the control treatment, S the pooled standard deviation and J a factor that corrects for potential bias due to small sample sizes (Hedges and Olkin 1985). An effect size was considered as significantly different from zero if its bias-corrected bootstrap confidence interval did not bracket the null value (based on 9,999 iterations). Meta-analyses were carried out using MetaWin 2.0 software (Rosenberg et al. 2000).

Results

Seedling species response to insect herbivory

The three seedling species exhibited significantly different defoliation levels (LAR) in the control treatment for all the five assessment periods over the two study years ($F = 18.64$, 45.74, 16.82, 10.26 and 21.34, respectively, $P < 0.01$). *Quercus ilex* seedlings were less damaged (7.5 ± 0.6% mean LAR ± SE) than the deciduous species, *Q. robur* (17.8 ± 1.1%) and *B. pendula* (20.2 ± 1.7%). The two deciduous species did not show any significant difference in LAR, except in July 2007 when *B. pendula* seedlings were more damaged than *Q. robur* seedlings ($|z| = 3.17$, $P = 0.005$) and in May 2008 when *Q. robur* seedlings were more damaged than *B. pendula* ($|z| = 3.78$, $P = 0.001$). Due to the strong seedling species effect on insect herbivory, further analyses on the effects of forest habitat and bird exclusion were therefore conducted separately for each species.

Effect of forest habitat on insect herbivory

Forest habitat had a significant effect on insect herbivory in the control treatment where birds were not excluded, but this effect differed between the three seedling species and the five periods of assessment. LAR in *B. pendula* seedlings was significantly lower in pine plantations than in exotic and native oak and birch woodlands only in May 2007 (Table 1; Fig. 1). For *Q. ilex* seedlings, no effect of forest habitat on herbivory was detected in 2007, but in May and September 2008 insect herbivory was significantly lower within pine plantations than within native oak and birch woodlands (Fig. 1; Table 1). Herbivory was intermediate within exotic oak woodlands. Forest habitat had a strong effect on herbivory for *Q. robur* seedlings in 2007, LAR being consistently lower within pine plantations than within native oak woodlands (Fig. 1; Table 1). Again herbivory rates were intermediate within exotic oak woodlands. These trends persisted in May and July 2008, but differences were not significant because of large between-stand variations.

Effect of forest habitat on insectivorous bird communities

Forest habitat had a significant effect on insectivorous bird richness and abundance (Kruskal–Wallis $H = 6.83$,

Table 1 Results of Tukey's HSD tests of the effects of forest habitat on leaf area removed (LAR %) by herbivorous insects for three seedling species

Date	Forest habitat	*Betula pendula*	*Quercus robur*	*Quercus ilex*
May 2007	Pine versus native	0.55	2.54*	0.15
	Pine versus exotic	1.49	1.80	1.26
	Exotic versus native	1.05	0.62	1.50
July 2007	Pine versus native	0.80	2.54*	1.86
	Pine versus exotic	0.43	2.09	1.68
	Exotic versus native	1.26	0.30	0.06
May 2008	Pine versus native	2.59**	2.11	2.44*
	Pine versus exotic	3.96***	1.92	0.41
	Exotic versus native	1.64	0.07	2.00
July 2008	Pine versus native	1.38	2.00	2.29
	Pine versus exotic	0.46	1.70	1.48
	Exotic versus native	0.82	0.17	0.71
September 2008	Pine versus native	1.65	0.34	3.23**
	Pine versus exotic	0.72	0.11	1.28
	Exotic versus native	0.83	0.22	1.87

Values show |z|-statistics for each comparison

Pine pine plantations, *Native* native deciduous woodlands, *Exotic* exotic deciduous woodlands

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

$P = 0.033$ and $H = 6.54$, $P = 0.038$, respectively). More bird species and individuals occurred in exotic and native deciduous woodlands than in pine plantations (multiple comparisons all significant, $P < 0.001$). Native deciduous woodlands had the highest mean richness ($R \pm$ SE) and abundance ($A \pm$ SE) of insectivorous birds ($R = 14.7 \pm 0.7$ and $A = 29.0 \pm 2.0$), exotic deciduous woodlands were intermediate ($R = 13.3 \pm 0.3$ and $A = 23.3 \pm 1.3$), whereas pine plantations had the lowest richness and abundance ($R = 9.7 \pm 0.3$ and $A = 19.5 \pm 0.6$).

Effect of bird exclusion on insect herbivory

For *B. pendula* seedlings, mixed-models analyses showed that herbivory rates in the bird exclusion treatment were significantly higher than in the control treatment in July 2007 and May 2008 (Table 2). Values of LAR were about 50% higher in July 2007 and twice as high in May 2008, and, although non-significantly, apparently higher in the bird exclusion treatment at the other assessment periods (Fig. 2). For none of the five periods of herbivory measure was the bird exclosure × forest habitat interaction term significant, indicating that these two effects operate independently of each other. Bird predation, therefore, contributed to reduced insect herbivory in birch seedlings. In contrast, we never observed any significant effect of bird exclusion on insect herbivory in *Q. robur* and *Q. ilex* seedlings (Table 2), except in May 2007 on *Q. robur* seedlings. The bird exclosure × forest habitat interaction term was significant due to a significant effect of forest habitat on herbivory in the control treatment (see Table 1) with no significant effect of bird exclosure.

Overall effect of forest habitat on bird insectivory

Insect herbivory on the three seedling species showed different responses to bird exclusion when data for all assessment periods were pooled (Fig. 3a). In *B. pendula* seedlings, LAR was significantly higher in bird exclusion cages than in control treatment ($d_+ = 0.55$ with bias CI = 0.34–0.69) indicating that bird predation reduced insect herbivory throughout the 2 years of measures. For the two oak species, there was no significant effect of bird exclusion on LAR ($d_+ = -0.02$ with bias CI = −0.31 to 0.51 for *Q. robur* and $d_+ = 0.16$ with bias CI = −0.24 to 0.35 for *Q. ilex*).

Forest habitat also influenced the effect of bird exclusion on insect herbivory in a similar way for the three seedling species as they shared the same gradient of response with higher bird insectivory within pine plantations than within native and exotic deciduous stands (Fig. 3b). Within pine plantations, bird exclusion had a significant effect on insect herbivory with higher damage in bird exclusion cages irrespective of the seedling species ($d_+ = 0.56$ with bias CI = 0.40–0.77). Conversely, there was no significant effect of bird exclusion in native ($d_+ = 0.24$ with bias CI = −0.05 to 0.55) or exotic deciduous woodlands ($d_+ = 0.14$ with bias CI = −0.49 to 0.33), irrespective of the seedling species (Fig. 3b).

Discussion

The resource concentration hypothesis

Our results provide new experimental evidence for the importance of resource concentration in the regulation of

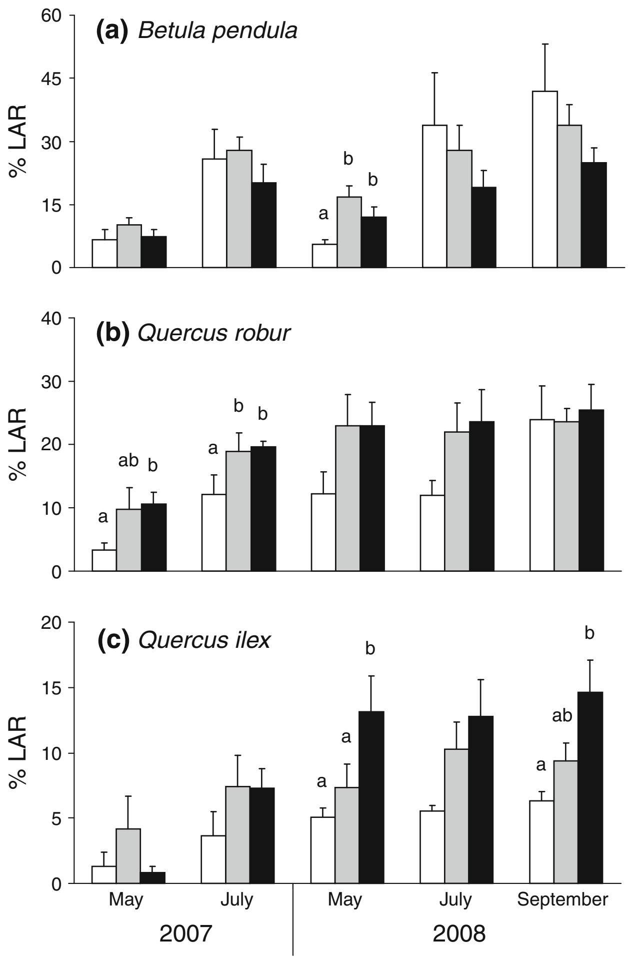

Fig. 1 Mean (+SE) percent leaf area removed (*% LAR*) by insects in control treatment on **a** *Betula pendula*, **b** *Quercus robur* and **c** *Quercus ilex* seedlings planted in pine plantations (*white bars*), exotic woodlands (*grey bars*) and native woodlands (*black bars*) at the five assessment dates. Analyses were performed separately for each seedling species and each assessment date and different *letters above bars* indicate significant differences between forest habitats (at $P < 0.05$)

insect herbivory, a mechanism of associational resistance (Root 1973). For the three broadleaved species tested, seedlings under non-broadleaved canopy trees (maritime pines) were less damaged than those planted within stands of broadleaved tree species. These results are consistent with previous observations of lower insect damage on seedlings or saplings grown in mixed stands than in pure stands of the same canopy species (Batzer et al. 1987; Keenan et al. 1995), and with decreased insect damage on beech and *Acer* saplings with higher abundance of conspecific adult trees (Maetô and Fukuyama 1997; Pigot and Leather 2008; Sobek et al. 2009). The Janzen–Connell hypothesis predicts that seedlings growing close to mother trees suffer from more damage or higher mortality than seedlings growing farther away (Lemen 1981; Norghauer et al. 2010). The resource concentration hypothesis also predicts that specialised herbivores are more likely to find a host plant in stands where this particular species is more abundant (Root 1973). Our results are consistent with both hypotheses: insect herbivory on seedlings was higher beneath a canopy of congeneric trees (i.e. on oak seedlings within native deciduous woodlands dominated by oaks) and lower when the host plant abundance decreased (i.e. on oak seedlings within pine plantations).

It is noteworthy that we observed the most significant associational resistance in *Quercus* seedlings which is a genus abundant in the canopy of deciduous woodlands. By contrast, associational susceptibility was the least in *B. pendula*, a species much less frequent in the study area. Seedlings of this rare species probably recruited mainly generalist herbivores, which could increase the risk of associational susceptibility (White and Whitham 2000). Associational susceptibility seems to be most prevalent when the herbivore species is highly polyphagous because generalist herbivores may benefit from mixed forests with multiple host tree species, whereas specialist herbivores are limited by the amount of suitable host trees (Jactel and Brockerhoff 2007). Oak seedlings were more likely to be colonised by specialised oak feeders, which could have led to increased associational resistance.

The natural enemies hypothesis

Associational resistance may also be provided by natural enemy populations which benefit from greater resources provided by plant associations and can therefore provide control of herbivores more effectively (Russell 1989; Barbosa et al. 2009). Changes in the composition of dominant canopy species assemblages or along tree diversity gradients have been shown to increase species richness and abundance of natural enemies such as predatory ants (Riihimäki et al. 2005), staphylinids (Vehviläinen et al. 2008) or birds (Greenberg et al. 1997). In tropical agroecosystems, arthropod abundance decreased when bird species richness increased (Philpott et al. 2009), and bird predation is enhanced by higher floristic diversity (Perfecto et al. 2004). Our study also provides experimental evidence of the natural enemies hypothesis since the more diversified association between seedlings and canopy species (broadleaved tree seedlings within pine stands) resulted in more intense bird predation. Surprisingly, in our experiment, pine plantations had lower insectivorous bird richness and abundance compared to deciduous woodlands, although we found a higher effect of bird predation in pine plantations than in deciduous woodlands. Some authors found no difference in indirect effect of insectivorous birds on plant damage within different forest stand types while bird abundance varied significantly between stands (Greenberg et al. 2000; Barber and Marquis 2009).

Table 2 Mixed-model analyses for the effect of bird exclusion (*BE*) and forest habitat (*FH*) on leaf area removed (LAR %) by herbivorous insects on three seedling species (*B. pendula*, *Q. robur* and *Q. ilex*)

Date	Treatment	*Betula pendula*	*Quercus robur*	*Quercus ilex*
May 2007	FH	1.25	2.83	1.04
	BE	0.45	0.23	2.80
	FH × BE	0.02	3.67*	0.99
July 2007	FH	2.43	2.06	4.11*
	BE	6.32*	2.24	0.04
	FH × BE	1.20	0.44	1.24
May 2008	FH	2.97	3.47	7.11**
	BE	8.65**	0.01	0.83
	FH × BE	0.56	0.16	0.05
July 2008	FH	1.59	1.61	5.10*
	BE	0.03	1.79	0.49
	FH × BE	0.75	0.75	0.13
September 2008	FH	8.10**	0.05	5.14*
	BE	0.02	0.04	0.79
	FH × BE	2.42	0.31	0.30

Values show *F*-statistics for each model

* $P < 0.05$

** $P < 0.01$

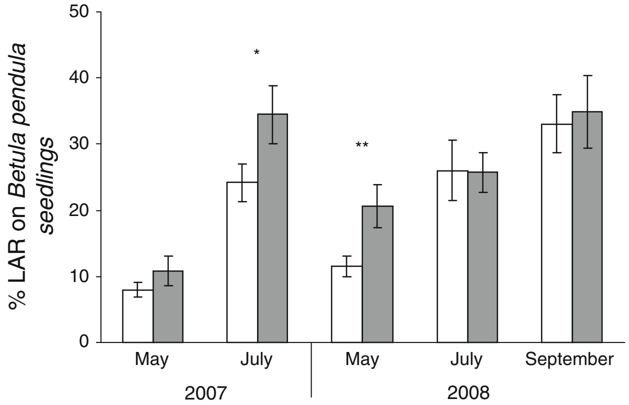

Fig. 2 Mean (±SE) percent leaf area removed (*% LAR*) by insects in control (*white bars*) and bird exclusion (*grey bars*) treatments on *Betula pendula* seedlings, irrespective of the forest habitat. *Asterisks above bars* indicate significant differences between treatments (**$P < 0.01$, *$P < 0.05$)

Conversely, González-Gómez et al. (2006) found that bird insectivory on seedlings, as measured by larval predation, was similar in exotic pine plantations and native forest fragments although bird abundance was lower in plantations. We hypothesised that broadleaved tree seedlings may have provided new feeding resources for insectivorous birds in the pine stands. Conversely, in deciduous woodlands where insect herbivores are likely to be more abundant, the effect of bird predation may have been weakened by a dilution process.

Effect of seedling identity on trophic cascades

In our study, the effects of insectivorous birds affected insect herbivory in the three seedling species differently, and irrespective of the observed effect of contrasting forest habitat. Bird exclusion led to a significant increase of insect herbivory on *B. pendula* seedlings whereas no effect was detected for the two oak species, *Q. robur* and *Q. ilex*. The identity of the plant species is therefore important as it influences the indirect effect of bird predation. Bird predation decreased insect leaf damage on many woody species such as *Vaccinium myrtillus* (Atlegrim 1989), *Quercus alba* (Marquis and Whelan 1994) or *Nothofagus pumilio* (Mazía et al. 2004). Conversely, no effect of bird predation on insect herbivory was detected on *Quercus prinus* and *Q. rubra* (Forkner and Hunter 2000) or *Salix lemonii* (Low and Connor 2003). To explain these differences, it has been proposed that bird predation effects would be negligible for plant species that show low average herbivore load. Insectivorous birds seem to prefer foraging on trees where arthropods are more abundant (Bridgeland et al. 2010) and then respond in a density-dependent way to herbivore population dynamics (Sipura 1999). Our results are consistent with this hypothesis: bird predation effect is stronger on *B. pendula* seedlings which were on average more damaged than the oak species. Antiherbivore defences may also dampen the indirect effect of predators: the effect of bird insectivory was stronger on *Salix phylicifolia* than on *S. myrsinifolia,* a willow species with higher concentrations of phenolic glycosides and hence lower insect abundance (Sipura 1999). In our study, the evergreen species *Q. ilex* was less damaged than the deciduous species. Species with long-lifespan leaves are less palatable because of important allocation to antiherbivore defences (Crawley 1989). On the contrary, pioneer species such as *B. pendula* are characterised by low investment in constitutive plant defences (Coley et al. 1985). Mäntylä et al. (2008) also showed that

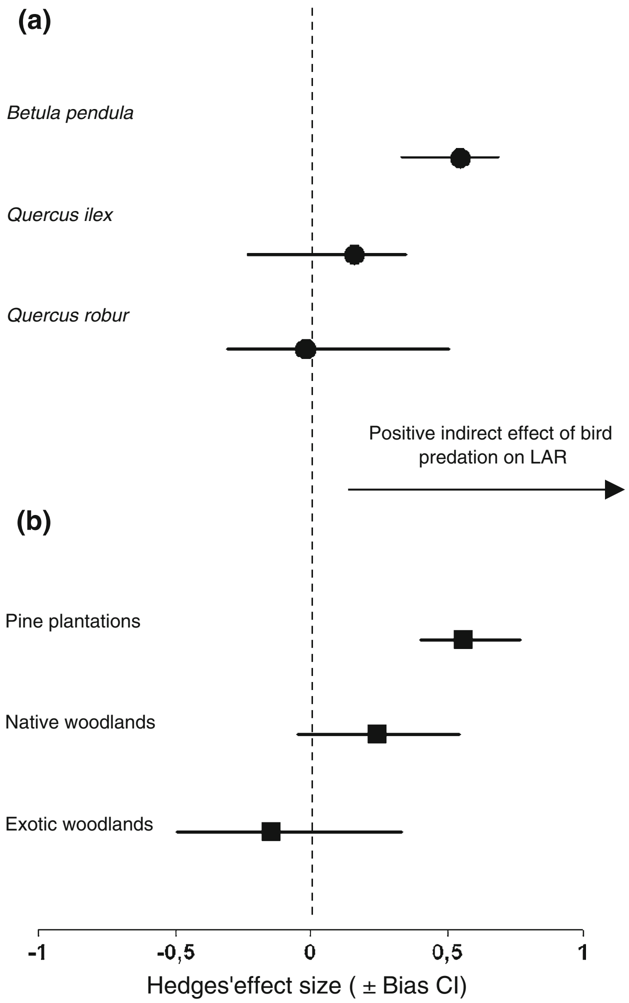

Fig. 3 Mean (±bias-corrected bootstrap confidence interval) effect size of bird exclusion on leaf area removed (*LAR*), **a** by seedling species irrespective of the forest habitat and **b** by forest habitat irrespective of the seedling species. A positive effect size indicates higher *LAR* in the bird exclusion treatment than in control (i.e. true bird predation effect) and was considered significant if the confidence interval did not bracket zero

leaves of *Betula pubescens* can release volatile organic compounds and have lower light reflectance as result of insect damage. These olfactory and visual cues are used by insectivorous birds and may explain why they prefer foraging on highly damaged plants. Lastly, birch seedlings are taller than the two oak species, with longer and less dense branches. This crown architecture may have provided insectivorous birds with easier access to insect prey since avian foraging intensity is highly dependent on foliage structure (Robinson and Holmes 1984; Marquis and Whelan 1996; Whelan 2001).

Bird exclusion clearly increased defoliation on *B. pendula* seedlings when all the herbivory assessments were pooled. However, when the five assessments were analysed separately, it appeared that bird exclusion effect showed an important temporal variation. For both years, significant bird exclusion effect was mainly observed during early- and mid-season of vegetation (July 2007 and May 2008). Again, this might be a density-dependent response since, during this period, the abundance peak of insect larvae matched with the bird breeding season when food demand for fledglings is the highest (Holmes 1990). On the other hand, *Betula pendula* leaves are known to be subjected to early leaf abscission when severely damaged (Giertych et al. 2006), which suggests a lack of accuracy in damage assessment in autumn.

Our study is one of the first providing experimental evidence of associational resistance to insect herbivory in tree seedlings. It gives support to both the natural enemies hypothesis, since bird predation was more effective in the more diverse association of seedling and canopy species (broadleaved seedlings under conifers), and the resource concentration hypothesis, since the lowest insect herbivory level was observed in seedling species planted under non-congeneric canopy species. Furthermore, our results underline the importance of considering both the identity of focal plant species and the composition of habitats as determinants of the occurrence of trophic cascades.

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