# Do birds see the forest for the trees? Scale-dependent effects of tree diversity on avian predation of artificial larvae

Evalyne W. Muiruri[1], Kalle Rainio[2], Julia Koricheva[1]

[1]School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, United Kingdom

[2]Department of Biology, University of Turku, FIN-20014 Turku, Finland

Correspondence: Evalyne W. Muiruri, evalyne.muiruri.2012@live.rhul.ac.uk, +447807171932

*As part of her PhD thesis, Evalyne Muiruri proposed the idea to analyse effects of diversity on bird predation at two spatial scales and to test effects of structural heterogeneity. Here, we present the first empirical demonstration of scale-dependent effects of tree diversity on avian insectivory. Predation rates were increased with tree species richness at small but not large spatial scales and were independent of structural complexity in forest stands. Findings from this study present a timely contribution to the rapidly developing fields of biodiversity-ecosystem functioning and multi-trophic interactions.*

Declaration of authorship: JK designed the study, KR and JK conducted fieldwork, EWM performed statistical analyses and wrote the manuscript. All authors have been involved in editing the manuscript drafts.

# ABSTRACT

The enemies hypothesis states that reduced insect herbivory in mixed-species stands can be attributed to more effective top-down control by predators with increasing plant diversity. Although evidence for this mechanism exists for invertebrate predators, studies on avian predation are comparatively rare and have not explicitly tested effects of diversity at different spatial scales, even though heterogeneity at macro- and micro-scales can influence bird foraging selection. We studied bird predation in an established forest diversity experiment in SW Finland, using artificial larvae installed on birch, alder and pine trees. Effects of tree species diversity and densities on bird predation were tested at two different scales: between plots and within the neighbourhood around focal trees. At the neighbourhood scale, birds preferentially foraged on focal trees surrounded by a higher diversity of neighbours. However, predation rates did not increase with tree species richness at the plot level and were instead negatively affected by tree height variation within the plot. The highest probability of predation was observed on pine, and rates of predation increased with the density of pine regardless of scale. Strong tree-species preferences observed may be due to a combination of innate bird species preferences and opportunistic foraging on profitable-looking artificial prey. This study therefore finds partial support for the enemies hypothesis and highlights the importance of spatial scale and focal tree species in modifying trophic interactions between avian predators and insect herbivores in forest ecosystems.

# KEY WORDS

Biodiversity and ecosystem functioning, insectivorous birds, insect pests, Satakunta forest diversity experiment, tri-trophic interactions

# INTRODUCTION

Insect herbivores can have significant impacts on key ecosystem functions such as nutrient cycling, productivity and carbon sequestration (Metcalfe et al 2014). These effects may be further compounded by losses in plant diversity, and many studies have shown that insect herbivore damage and abundance is higher in less diverse plant communities (associational resistance, Kaitaniemi et al. 2007; Jactel and Brockerhoff 2007; Barbosa et al. 2009). Root (1973) was the first to suggest that natural enemies of insect herbivores may drive the observed patterns of associational resistance by being more effective as predators in diverse plant communities compared to monocultures. This prediction, termed the enemies hypothesis, was based on the observation that more species-rich habitats often support a higher diversity of prey species, provide refuges and offer additional resources such as pollen and nectar for invertebrate predators (Root 1973; Russell 1989). The enemies hypothesis has received much experimental scrutiny and support from studies in agricultural ecosystems and grasslands (Tonhasca 1993; Siemann et al 1998; Sobek et al 2009; Letourneau et al 2011; Straub et al 2014), however, fewer tests of this hypothesis have been conducted in forest ecosystems. These studies have produced mixed results with some reporting negative effects of tree diversity on predator effectiveness (Schuldt et al 2011; Zou et al 2013) and others showing stronger effects of tree species composition (Riihimäki et al 2005; Kaitaniemi et al 2007; Vehviläinen et al 2008), density (Sperber et al 2004; Schuldt et al 2008) or tree species identity (Sobek et al 2009) rather than tree species richness per se (Zhang and Adams 2011). Thus, more studies are required to better understand relationships between diversity and top-down control of insect pests in forest ecosystems.

An additional limitation of previous tests of the enemies hypothesis is that they have almost exclusively been performed for arthropod predators (Russell 1989; Andow 1991) even though insect herbivores are fed upon by both invertebrate and vertebrate predators (Letourneau et al

2009). Birds, in particular, have received little attention even though they are widely considered to be important control agents of insect pests in forest stands (Mäntylä et al 2011; Bereczki et al 2012) and can deliver a key ecosystem service (Whelan et al 2015). In addition, the diversity and abundance of avian predators has not only been shown to respond to increased structural and floristic diversity (MacArthur and MacArthur 1961; Bereczki et al 2014; Huang et al 2014), but also vary with densities of individual tree species (Wiens and Rotenberry 1981; Mason 1997). Nevertheless, very few studies have examined effects of tree diversity on avian predation in forest ecosystems (Giffard et al 2012; Poch and Simonetti 2013; Giffard et al 2013; Bereczki et al 2014) and of these studies, none have directly tested the effects of increasing tree species richness or explored the effects of tree species composition and individual tree species densities on bird predator effectiveness. Recent work by Poch and Simonetti (2013) has shown that higher bird predation occurs in structurally complex forest plantations with more developed and diverse understorey. Therefore, just as top-down control by arthropod predators was hypothesised to increase with plant diversity and associated structural complexity (Root 1973), positive effects of diversity on bird predation may be driven by increased structural complexity rather than diversity per se.

Finally, the vast majority of studies testing the enemies hypothesis have done so at a single spatial scale and thus, we still know little about the scale at which the enemies hypothesis applies (Zhang and Adams 2011). Spatial scale is believed to be an important determinant of the strength of prey-predator interactions (Langellotto and Denno 2004; Gripenberg and Roslin 2007) and effects of plant diversity on these relationships may vary with spatial scale (Bommarco and Banks 2003). The review by Bommarco and Banks (2003) found that effects of plant diversity on the effectiveness of arthropod predators was strongest in small (<16m$^2$) plots, intermediate in intermediate-sized (28-196m$^2$) but absent in large (>256m$^2$) plots; these patterns could be due to easier redistribution of predators to the more favoured mixed stands in experiments of smaller plot size. For birds, a similar pattern may arise as, even though they can travel further than arthropods in search of prey, their capacity for direct assessment of insect abundance is greater within a microhabitat compared to larger spatial scales (Strode 2009). Optimal foraging theory predicts that natural selection favours behaviours that maximise energy intake per unit time spent foraging (Stephens and Krebs 1986). Thus, even in the absence of detectable prey, birds may have evolved to use alternative indicators such as the signs of leaf damage (Heinrich and Collins 1983) or chemical cues from insect-damaged plants (Mäntylä et al 2008; Amo et al 2013) to locate insect-rich trees within small spatial scales. At larger scales, the patchy distribution of many insect herbivores may drive forage selection towards patches where the host plants of their favoured prey dominate as a strategy to minimise search time (Arvidsson and Klaesson 1986; Mason 1997). Therefore, different factors might act as drivers of bird predation depending on the spatial scale of observation. As habitat selection by birds is understood to occur in a hierarchical manner (Johnson 1980), a combination of different drivers at each spatial scale may act to maximise overall foraging efficiency, in accordance with optimal foraging theory.

The primary goal of this study was to experimentally test whether bird predation increases with tree species richness, as predicted by the enemies hypothesis. We used an established forest diversity experiment in SW Finland to examine the effects of tree species diversity, prey availability and habitat structural heterogeneity on bird foraging preferences. To assess bird predation, artificial larvae (modelled from plasticine) were installed on alder, birch and pine trees in stands of varying tree species diversity. This technique of presenting artificial prey has risen in popularity in prey-predator studies as it facilitates field assessment of relative predation rates (Howe et al 2009) and the marks left by predators in plasticine are identifiable to a coarse taxonomic level (Low et al 2014). In keeping with most tests of the enemies hypothesis, we explored how bird predation rates vary with diversity at plot level and test whether these effects are mediated by changing structural complexity. Secondly, we examine avian predation responses to tree diversity at finer spatial scales, focussing on the local neighbourhood of a focal tree. Finally, we compare the importance of natural herbivore abundance and damage on experimental trees relative to the importance of neighbourhood diversity in predicting bird predation rates.

## METHODS

### *Study site and design*

The study was carried out at the Satakunta forest diversity experiment established in 1999 in south-western Finland. The experiment consists of three separate areas with 38 plots (20 x 20 m) in each area. Diversity treatments represent monocultures and 2-, 3-, and 5-species combinations of the following five tree species: Scots pine (*Pinus sylvestris*); Norway spruce (*Picea abies*); Siberian larch (*Larix sibirica*); silver birch (*Betula pendula*); and black alder (*Alnus glutinosa*). Each plot consists of 13 rows with 13 trees planted at 1.5m intervals (total 169 trees) and the position of different tree species in mixed stands was randomised. Replanting of species was carried out in 2000 for all plots and, in 2001 for plots where mortality exceeded 10%. Other than the manual removal of naturally regenerating woody vegetation in spring 2010, no management interventions have been used in the Satakunta experiment since planting.

In the present study, we used two out of the three experimental areas (area 1, 61°42’N, 21°58’E and area 3, 61°40’N, 21°42’E) and focussed on three focal tree species: pine, birch and alder. These species were chosen as they host caterpillar larvae (e.g. *Epirrita autumnata* Borkhausen. on birch and alder and, *Neodiprion sertifer* Geoff. on pine) that could easily be modelled from plasticine. The other species present in the study areas are attacked mostly by small sucking insects (aphids or adelgids) which might be considered less profitable prey (Naef-Daenzer et al 2000) and therefore receive less bird predation compared to caterpillars. We therefore selected trees for this experiment from the seven treatments containing pine, birch or alder: three monocultures (pine, birch and alder), two 2-species mixtures (pine + birch, birch + alder), one 3-species mixture (pine + birch + alder) and the 5-species mixture (pine + birch + alder + spruce + larch). There were two replicates of each treatment per area but no pine-alder combination was present in the original experimental design so only two out of the three possible 2-species mixtures were available for this study. For each plot, six trees were selected within the interior, avoiding selection of adjacent trees and substituting tree species in mixtures such that six trees were sampled in monocultures, three trees per species were sampled in 2-species mixtures, and two trees per species were sampled in 3- and 5-species mixtures. Insect herbivore abundance and damage were assessed on experimental trees in early June 2013 prior to the start of the bird predation experiment. Pine trees in the study area have been observed to have very low herbivore densities (J. Koricheva, unpublished data) and hence assessment of insect herbivores was only performed on birch and alder trees. We assessed the presence/absence of exposed chewing insects, the abundance of concealed-feeder insects (e.g. leaf miners or rollers) and the extent of leaf area damaged (%) by defoliating insects on the same focal trees used in the predation experiment (Online Resource 1).

### *Bird predation assessment and surveys*

The experiment was timed to coincide with the peak bird nesting period when insects compose the majority of the diet fed to nestlings (Naef-Daenzer et al 2000). On 8th and 9th June 2013, five artificial larvae were installed on each experimental tree (30 larvae per plot). The larvae were modelled from odourless, light green plasticine to an approximate size of 2-3cm in length and 3-4 mm in diameter (Fig. 1a). The size of the larvae was chosen based on previous studies using artificial caterpillars on the same tree species (Mäntylä et al 2008) and to represent the average size of larvae of the autumnal moth (*E. autumnata*) and the European pine sawfly (*N. sertifer*), both of which are common defoliators on alder, birch and pine trees in Finland. Artificial larvae were installed on branches which were 1.5-3m above ground, corresponding to the mid canopy for alder and pine and to the lower canopy for birch. Five larvae per tree were distributed between different branches from all sides of the canopy to avoid systematic differences in sun/shade exposure, and secured to a branch using metal wire (diameter 0.35mm). Following installation, the condition of the artificial larvae was checked five times: 3, 6, 9, 11 or 12 and 15 or 16 days after installation. Predation attempts by birds were recorded on larvae if they exhibited marks that were consistent with bird pecking damage and could not otherwise be explained (e.g. not a scratch by a nearby branch, Fig 1b, c). Although wood ants are highly abundant in the study area, we found no evidence of ants predating the artificial larvae in this experiment or when the artificial larvae were offered to wood ants near their nests. After each larva was checked, those that were damaged were either remoulded where possible or replaced.

To identify possible culprits for predation on artificial larvae, surveys of bird territories were conducted shortly after dawn on 22nd May, 7th June and 12th June 2013. The surveyor (KR) walked a path which ensured good coverage of the experimental areas and recorded breeding bird species on the basis of sightings, singing or other acoustic encounters. As the home range size of birds in the experiment exceeded a single plot, only the overall diversity and abundance of individual bird species was assessed in each study area. To determine which species were predating on artificial larvae, we installed camera traps around three pine trees in one pine monoculture in June 2014 as this was the plot where the highest predation rates were observed the previous summer. About 30 artificial caterpillars per tree were installed and camera traps were in operation for one month.

### *Tree height variation*

In order to examine the role of structural complexity on bird predation, we used tree height measurements from 2011 where ten randomly chosen trees of each species were assessed in each experimental plot (Muiruri et al 2015). For each plot, we calculated a mean and standard deviation of tree heights, using data for all species combined in mixtures. The coefficient of variation (referred to as Tree Height Variation from here on) was then calculated by dividing the standard deviation by the mean tree height per plot. Plots with higher tree height variation are considered to be more structurally complex with greater heterogeneity in vertical canopy structure.

### *Statistical analysis*

To investigate the effects of tree diversity on bird predation, we used four continuous variables as predictors of bird damage to artificial larvae in each plot: (1) tree species richness, (2) proportion of pine, (3) birch and (4) alder trees out of the total number of live trees in a plot (hereafter referred to as pine, birch or alder density, respectively). In addition, for plot level analysis only, we used a fifth variable – tree height variation – as a predictor of bird predation. Although tree species compositions were similar at plot and neighbourhood scales, randomised species arrangements at planting and tree mortality resulted in some focal trees with different proportions or fewer heterospecific neighbours than expected in the 2-, 3- or 5-species mixtures or, no neighbours at all. Thus, as damage to larvae was recorded on individual trees, we also gathered information on the neighbourhood of each experimental tree, recording variables 1-4 from the eight trees surrounding the focal tree.

We used generalised linear mixed-effects models (GLMM) to account for the nested design and to allow specification of an error family. In order to assess bird predation, we modelled the probability of predation of artificial larvae as a bounded binary response variable (larvae damaged/not damaged) with a binomial error structure, specifying a random error structure with individual trees nested within plot (plot/tree). Due to the regularity of the experimental design at Satakunta the variables (1-4) describing tree diversity at the plot and neighbourhood scales were not independent, therefore, no more than one of the four diversity variables could be included in models at any one time. However, initial models were run to determine whether effects of all diversity variables (from either plot or neighbourhood level) on bird predation were dependent on the study area used or the time of observation (area x time x variable [1-4]). As neither area nor time significantly interacted with any diversity variable at either spatial scale, we performed all subsequent analysis on predation across all sampling points, retaining area as a fixed factor in subsequent models (not in interaction with other variables) to account for natural variation in bird activity between the two study areas.

For analysis at plot level, we first calculated the mean number of larvae damaged per plot and ran generalized linear-models (GLM) with the binomial response variable (mean number of larvae damaged per plot, number of larvae installed in each plot) against area and each variable (1-4) or tree height variation separately (ie. area + variable[1-4] or area + tree height variation). A similar approach was used at the neighbourhood scale, this time running models for neighbourhood-level predictor variables (1-4) or tree species identity. Binomial GLMMs were run for the response variable (number of damaged larvae per tree, number of larvae installed per tree) against each individual predictor variable using plot as a random factor. Tree species composition effects were assessed for mixtures at each species richness level separately but as no significant differences were detected at either plot or neighbourhood level, we focus our discussion on variables 1-4.

In order to determine which variables (at plot or neighbourhood level) best predicted bird predation, we ranked univariate models on the basis of their AICc values (second-order Akaike's Information Criterion) and used Akaike weights as an indicator of the weight of evidence in support of a given model, compared to other candidate models (Anderson et al 2001; Burnham and Anderson 2004). Models with lower AICc values were therefore considered to be better than other candidate models but could only be termed the single best model if the Akaike weight exceeded 0.9 (Anderson et al 2001). Where Akaike weights did not exceed this value, differences in the AICc were used as an indicator of the relative likelihood of the model. Candidate models differing least from the best model ($\Delta$AICc$\leq$2) are considered to be well supported but those differing most ($\Delta$AICc$\geq$10) can be omitted (Burnham and Anderson 2004). In addition to model comparison, we also calculated $R^2$ values to estimate the variance explained by fixed factors only ($R^2_m$) or, both fixed factors and random factors together ($R^2_c$) (Nakagawa and Schielzeth 2013).

Different bird species might exhibit foraging preferences for individual tree species or the insect prey they host (Holmes and Robinson 1981; Gabbe et al 2002). Therefore, we ran similar analysis for each tree species separately to test the relative importance of components of neighbourhood diversity in determining bird predation rates. In particular, for birch and alder trees, we use AICc weighing to determine whether predation rates are driven more by changes in neighbourhood diversity (variables 1-4), natural insect abundance (both exposed and concealed insects) or insect herbivore damage (understood to enhance bird predation rates). Further GLM and GLMM models were used to determine the effect of plot and neighbourhood diversity variables (1-4) on tree height variation and insect herbivore damage (log transformed) respectively. Effects of diversity on the presence/absence of exposed chewing and the abundance of concealed-feeding insects on birch and alder were also examined using GLMMs with a poisson error distribution specified for count data. All statistical tests were conducted in R software version 2.15.2 (R Core Team 2012) using the lme4 package (Bates et al 2012). Model residuals were examined for homogeneity of variance and we report AICc and Akaike weights from the MuMIn package as well as Chi-squared and corresponding p-values from ANOVA using the car package (Fox and Weisberg 2011).

## RESULTS

### *Bird species present in the study area*

A total of 19 different bird species and 140 bird territories were recorded during all three bird surveys (Online Resource 2). Of all the bird species present, willow warblers (*Phylloscopus trochilus* L.) were the most abundant in both experimental areas and across all censuses, occupying 40% of all observed territories (Online Resource 2). Other common bird species in the study areas included chaffinches (*Fringilla coelebs* L., 10% of observed territories), robins (*Erithacus rubecula* L., 6% of territories), garden warblers (*Sylvia borin* Bodd. 6% of territories), and lesser whitethroats (*Sylvia curruca* L., 5% of territories). At the start of the predation experiment, both the diversity and abundance of birds were similar in the two experimental areas. Nine bird species were observed in 29 territories in area 1 and eleven species in 27 bird territories were observed in area 3.

### *Patterns of bird predation*

The number of attacks on artificial larvae increased linearly over time ($\chi^2$=48.0, df=1, p<0.001). This pattern was more pronounced in area 1 than in area 3 (time x area: $\chi^2$=34.6, df=1, p<0.001) with overall number of attacks being higher in area 1 ($\chi^2$=11.3, df=1, p<0.001). However, despite these patterns, no significant two-way or three-way interactions were detected between time, area and each of the four main diversity variables at either spatial scale (Online Resource 3). Similarly, effects of tree height variation at the plot level and tree species identity on bird predation were independent of area or time (Online Resource 3). Therefore, we conducted all subsequent analysis on the total number of larvae damaged per tree across all sampling points and excluding interaction terms with 'area' in further models.

Throughout the experiment, we observed that while artificial larvae on birch or alder usually received single beak marks (Fig. 1b), larvae on pine frequently exhibited multiple beak marks (Fig. 1c) and were occasionally detached or missing entirely from the wire installation. Video footage from trap cameras from June 2014 showed a great tit (*Parus major*) pecking repeatedly at an artificial larva on pine, suggesting that great tits, possibly together with other Parid species, may have been responsible for the heavy damage on the artificial larvae on pine.

*Plot-level analysis*

Bird predation was not significantly affected by plot tree species richness (Fig. 2a, Table 1) but decreased with tree height variation within a plot (Fig. 2a inset, Table 1). The densities of pine, birch and alder had opposite effects on bird predation (Fig. 3a, Table 1). The number of larvae damaged significantly increased with the density of pine but decreased with increasing proportions of birch or alder (Fig 3a, Table 1). Although tree height variation increased with plot species richness (F=12.6, df=1, p=0.001), it did not depend on densities of alder (F=0.9, df=1, p=0.362), birch (F=1.5, df=1, p=0.234) or pine (F=0.2, df=1, p=0.667). Model comparisons based on AICc identified the density of pine as the variable best accounting for bird predation at the plot level compared to other predictor variables and explained the most variance (Table 1). The second-ranked predictor was birch density but as ΔAICc>10, this model had essentially no support compared to the top model with pine density.

### *Neighbourhood-level analysis*

Bird predation on artificial larvae significantly increased with species richness of the neighbouring trees (Fig 2b, Table 1). Some experimental trees in alder monocultures had no neighbours as a result of tree mortality. However, even after exclusion of these trees from the analysis, tree species richness still had a significant positive effect on the total number of larvae damaged per tree ($\chi^2$=4.8, df=1. p=0.028). Similar to the plot-level analysis, the probability of predation decreased with a higher proportion of alder and birch among the neighbouring trees but increased with pine density (Fig. 3b, Table 1).

Regardless of tree species diversity, tree species identity had a significant effect on the number of larvae damaged per tree (Table 1). Of the 551 damaged larvae, 358 (65%) were on pine trees (222 from pine monocultures), 129 (23%) on birch and 64 (12%) on alder (all *post hoc* pairwise comparisons significant, p<0.001). In model comparisons, the single best explanatory variable for the number of artificial larvae damaged per tree was the species identity of the focal tree, explaining the most variance (highest $R^2_m$ value) compared to any other model (Table 1). However, responses to diversity did not differ between the three species (tree species identity x richness: $\chi^2$=0.5, df=2, p=0.769, tree species identity x pine density: $\chi^2$=2.1, df=2, p=0.356). Only the effects of birch and alder density varied between the three focal tree species. Increasing birch density in the neighbourhood had a strong negative effect on predation rates on pine trees but only weak negative effects on predation on birch and alder (tree species identity x birch density; $\chi^2$=6.3, df=2, p=0.042, Fig 3b). At the same time, predation of artificial larvae on birch trees decreased with alder density but no relationship was observed for predation on pine or alder focal trees (tree species identity x alder density; $\chi^2$=11.0, df-2, p=0.004, Fig 3b). However, this pattern might be partially attributed to the fact that we did not have any plots with a pine/alder two-species combination so proportions of alder around pine trees rarely exceeded 33% (Fig. 3b).

*Tree species-specific analysis*

Bird predation on pine trees did not vary significantly with tree species richness or the density of alder in the neighbourhood (Fig. 2b, 3b, Table 1). However, the number of damaged larvae increased with the density of pine in the neighbourhood and declined with the density of birch (Fig 3, Table 1). In model comparisons, the neighbourhood density of pine emerged as the best predictor of bird predation on larvae installed on pine, closely followed by the density of birch in the neighbourhood (ΔAICc<2, Table 1). For artificial larvae on either birch or alder trees, bird predation appeared to increase with both neighbourhood species richness and pine density and decrease with birch or alder density (Fig 2b and 3b). However, neither the diversity variables nor insect herbivore damage or the abundance of concealed feeding insects significantly predicted predation of artificial larvae on birch and alder (Table 1). Predation of artificial larvae on alder was independent of the presence/absence of exposed chewing insects but, on birch trees, predation was higher when exposed chewing insects were present (Table 1, Online Resource 4). Model comparison ranked the presence of exposed chewing insects as the most important determinant of predation on birch, followed by alder density (ΔAICc<2, Table 1). In contrast, for alder trees, even the abundance of concealed-feeding insects, which was identified as the best explanatory variable had a weak but non-significant (negative) effect on the number of larvae damaged on alder trees (Table 1, Online Resource 4).

*Natural insect herbivory on birch and alder*

In a comparison of natural herbivory between the two broadleaved species, the percentage leaf area damage was significantly higher on birch compared to alder trees ($\chi^2$=24.8, df=1, p<0.001), but the presence of exposed insects or the abundance of concealed insect herbivores did not differ between the two species (p≥0.531). Tree species richness surrounding focal trees also had no significant effect on initial insect herbivore damage (p≥0.180) or the presence of exposed chewing insects (p≥0.918) on either tree species. However, the abundance of concealed insects was reduced with increasing neighbourhood tree species richness on birch ($\chi^2$=4.5, df=1, p=0.033) but not on alder ($\chi^2$=2.5, df=1, p=0.111). Neighbourhood densities of alder, birch or pine had no effect on insect herbivore damage, the abundance of concealed insects or the presence of exposed insect herbivores (p≥0.295).

## DISCUSSION

The results of our study provide partial support for the enemies hypothesis as we found that bird predation increased with tree species richness at the neighbourhood scale. However, effects of tree species richness were scale-dependent and absent at the plot level. To our knowledge, this is the first demonstration of differential responses of avian predators to forest diversity at two different spatial scales. Use of model prey in this experiment permitted a standardised, rapid assessment of relative predation rates across the diversity gradient and between different tree species (Howe et al 2009). Although natural prey offer more complex sensory cues compared to artificial larvae, the same number of identical green and odourless artificial larvae were installed in each plot and, as such, we consider that their use could not have modified natural bird behaviour in a way that would affect conclusions with respect to effects of tree diversity, structural heterogeneity or spatial scale.

### *Effects of tree species richness at different spatial scales*

Variable effects of diversity on predation at different spatial scales have previously been observed for arthropod predators. Plant-insect-predator interactions have been found to be stronger at small spatial scales (Langellotto and Denno 2004; Gripenberg and Roslin 2007) and the positive effects of plant diversity on top-down control by arthropod predators might even disappear at larger spatial scales (Bommarco and Banks 2003). Bommarco and Banks (2003) attributed the disappearance of plant diversity effects on arthropod predators at larger spatial scale to more effective re-distribution of arthropod predators in smaller experimental plots. However, birds are far less limited by dispersal distances than arthropod predators and can easily seek out preferred forage habitats further afield. Even during the breeding season when bird foraging occurs largely near the nest site, home range sizes of birds still exceed the area of a single plot (Online Resource 2).

When the enemies hypothesis was first proposed, Root (1973) suggested that stronger top-down control in diverse habitats is mediated by increased structural complexity where more niches were available for predators to exploit. This mechanism was supported by Poch and Simonetti (2013) who showed that bird predation rates were higher in more structurally complex forest plantations that had a higher abundance and diversity of woody species in the understorey. However, we found that, despite increased structural complexity with tree species richness, bird predation decreased with increases in tree height variation (Fig. 2a, inset). Although greater structural complexity may enhance the number of niches a predator can exploit, prey might be better concealed, increasing search time. As a result, structurally complex habitats may be considered less suitable foraging locations. For example, willow warblers, the most common bird species in the study area, have been shown to establish territories more frequently in stands where trees are of a similar size (Stostad and Menéndez 2014). Therefore, structural heterogeneity may reduce rather than enhance bird predation independently of plot species richness. As predator responses to structural complexity have been shown to change in magnitude but not direction across spatial scales (Langellotto and Denno 2004), bird predation at the neighbourhood level is unlikely to increase with structural heterogeneity within the microhabitat. Thus, structural complexity can explain neither tree species richness effects at plot and neighbourhood levels nor differential responses to tree species richness between the two scales.

Instead, scale-dependence of tree species richness effects on bird predation may result from differences in prey visibility that manifest themselves only at fine spatial scales. Bird predation rates on insects have been shown to increase where plant cover is reduced (Groner and Ayal 2001). As tree species richness increases, presence of tree species differing in growth rates and foliage structure may result in less horizontal canopy space used and thus, a more open canopy (Lang et al 2011). This has previously been shown in the Satakunta experiment, with canopy cover around birch trees decreasing with tree species richness (Muiruri et al. 2015). As a result, artificial larvae may be more visible to birds when the focal trees are surrounded by heterospecifics but these effects are likely to be restricted to small spatial scale and unlikely to manifest at plot level. Improved visibility of insect prey on trees in more open forest stands may present a key advantage as palatable caterpillars may be visually more cryptic or have more cryptic behaviour compared to unpalatable insect prey, hiding amongst foliage and feeding in such a way as to minimise their apparent damage (Heinrich and Collins 1983). Thus, neighbourhood species richness effects on avian predation may be driven by differences in the light environment minimising search time and the energetic costs of foraging.

At the plot level, the capacity for direct visual assessment of prey is hampered and birds may instead rely on other indicators of a suitable foraging patch such as the presence or absence of host tree species of their favoured prey (Wiens and Rotenberry 1981; Mason 1997). As insect prey abundance can vary significantly over space and time, insectivorous birds often have to visit different parts of the environment continually to assess prey availability to the detriment of immediate foraging efficiency (Smith and Dawkins 1971). However, with the use of different cues within each spatial scale, insectivorous birds might be able to efficiently explore the landscape, concentrating their searches on selected patches for visible and easily accessible prey. This strategy would enable birds to exploit new resources as soon as they become available, minimising the time spent locating insect prey while maximising food intake for adults and nestlings in accordance with the optimal foraging theory (Stephens and Krebs 1986).

### *Effects of tree species density and identity*

Strong foraging preference of insectivorous birds for certain tree species have been well documented in forests (Holmes and Robinson 1981; Gabbe et al 2002; Strode 2009). In this experiment, we observed that predation was consistently higher on artificial larvae installed on pine than on birch and alder. Moreover, different beak marks on damaged artificial caterpillars indicated that different bird species were responsible for predation on pine and the broadleaf tree species. Individual pecks on caterpillars installed on birch and alder (Fig. 1b) were likely to be caused by small passerines such as the willow warblers, the most abundant bird species in the study area. In contrast, the multiple large beak marks found on artificial larvae on pine trees (Fig. 1c) were likely caused by the great tits, as confirmed by the camera trapping. This generalist insectivorous bird has been shown to preferentially forage on pine trees (Eeva et al 1997) and is known to be a highly innovative, opportunistic forager capable of social learning (Aplin et al 2015). Artificial larvae used in this experiment may have presented a new and attractive resource for breeding birds which often try to find the largest, most profitable prey for their nestlings (Diaz et al 1998; Naef-Daenzer et al 2000; Hino et al 2002) regardless of nutritional quality (Brodmann and Reyer 1999). Opportunistic pecking by seed-eating birds would also be consistent with damage seen on artificial larvae (Fig. 1c) as they may have stronger beaks to pry seeds out of cones (van der Meij and Bout 2004).

Tree species-specific differences in bird predation rates may also be driven by different properties of pine compared to birch or alder. For example, the low complexity of pine canopy relative to broadleaved trees may increase the accessibility and visibility of artificial prey enhancing predation of artificial larvae on pine (Šipoš and Kindlmann 2013). At the same time, a higher colour contrast between the light green of the artificial larvae and foliage may make artificial prey more conspicuous to birds on the darker pine foliage compared to birch and alder. However, as larvae were placed on branches rather than on leaves, contrasts between model prey and bark in both colour and texture might be just as important as foliage colour, if not more so. Thus, differences in predation on artificial larvae between the three focal tree species would be difficult to predict based on background matching alone.

Regardless of scale, increases in pine density (and reduced birch and alder density) consistently increased the probability of predation on artificial larvae (Fig. 2). Passerine birds often conduct concentrated searches for prey within microhabitats (Naef-Daenzer and Keller 1999) so any trees neighbouring pine may also be more susceptible to attack by virtue of their proximity and those neighbouring birch or alder, less so. However, insectivorous birds may also return repeatedly to profitable patches (Naef-Daenzer and Keller 1999) and this might explain why predation of artificial larvae increased during the experimental period. Experiments using the same technique of model prey over the same duration usually find that predation increases initially then decreases as birds learn that the artificial prey offer no nutritional reward (Mäntylä et al 2008). We hypothesise that the continuous increase in predation in this experiment was due to increased recruitment of ‘naïve’ birds from outside the study area. In particular, as birds might develop a search image for a given prey item during feeding (Tinbergen 1960), the newly-fledged birds of early broods observed outside experimental plots may be responsible for the continued increase in predation rates.

### *Effects of insect damage and natural prey abundance*

We hypothesised that focal trees with more insect herbivore damage or a higher abundance of insect prey might experience higher predation rates. However, contrary to previous work showing that birds prefer to forage on insect-damaged trees (Mäntylä et al 2008; Amo et al 2013), leaf area damage by insect herbivores had no effect on predation rates on either birch or alder. Similarly, despite evidence suggesting concealed insects are under intense bird predation (Xiong et al 2010), we also observed no effect of concealed insect herbivore damage on the probability of larval attack on birch or alder trees. This is perhaps not surprising as, although concealed-feeding insects are sedentary and therefore potentially easy targets for avian predators, the concealed insects measured in this experiment (leaf rollers, folders and miners) are quite small (<10mm) and the difficulty of localising prey within shelters also increases search and handling time for birds for little reward in return. The only indication that density-dependent predator-prey interactions occurred in this experiment was found on birch where predation was higher on trees initially infested with exposed chewing insects (Online Resource 4). However, this could not explain the effects of tree species richness on bird predation because there was no significant difference between natural herbivory on birch trees surrounded by birches or by other tree species.

### *Conclusions*

In this study we have shown that, in accordance with the enemies hypothesis, bird predation rates increase with tree species richness but only at the small spatial scale. However, contrary to Root's predictions, our findings suggest that positive relationships between tree diversity and bird predation are not due to increased structural complexity of a forest stand but rather due to improved ability for prey assessment. With the economic benefits of birds coming under scrutiny (Whelan et al 2015), our findings not only show that birds contribute a key ecosystem service but their regulation of insect pests might be dependent on species richness at fine spatial scales only. Together with the strong tree-species foraging preferences apparent in this experiment, this suggests that greater control of insect pests by insectivorous birds may be achieved by introduction of preferred tree-species and planting a mix of species together rather than patches of individual species in production forests.

## ACKNOWLEDGEMENTS

We are grateful to Fatih Kayaanan, Miika Laihonen and Elisa Männistö for help in the field and to Ilkka Jussila for installation of the camera traps. This study was financially supported by the grant from the Kone Foundation.

## REFERENCES

Amo L, Jansen JJ, van Dam NM, et al (2013) Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. Ecol Lett 16:1348–55. doi: 10.1111/ele.12177

Anderson DR, Link WA, Johnson DH, Burnham KP (2001) Suggestions for presenting the results of data analyses. J Wildl Manage 65:373–378. doi: 10.2307/3803088

Andow DA (1991) Vegetational diversity and arthropod population response. Annu Rev Entomol 36:561–586. doi: 10.1146/annurev.en.36.010191.003021

Aplin LM, Farine DR, Cockburn A, et al (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538–541. doi: 10.1038/nature13998

Arvidsson B, Klaesson P (1986) Territory size in a Willow Warbler Phylloscopus trochilus population in mountain birch forest in Swedish Lapland. Ornis Scand 17:24–30. doi: 10.2307/3676749

Barbosa P, Hines J, Kaplan I, et al (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. Annu Rev Ecol Evol Syst 40:1–20. doi: 10.1146/annurev.ecolsys.110308.120242

Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using S4 classes.

Bereczki K, Csoka G, Ódor P, et al (2012) Birds as control agents of caterpillars in oak forests. Ecosyst. Serv. do we need birds? pp 1–2

Bereczki K, Ódor P, Csóka G, et al (2014) Effects of forest heterogeneity on the efficiency of caterpillar control service provided by birds in temperate oak forests. For Ecol Manage 327:96–105. doi: 10.1016/j.foreco.2014.05.001

Bommarco R, Banks J (2003) Scale as modifier in vegetation diversity experiments: effects on herbivores and predators. Oikos 102:440–448.

Brodmann PA, Reyer HU (1999) Nestling provisioning in water pipits (Anthus spinoletta): Do parents go for specific nutrients or profitable prey? Oecologia 120:506–514. doi: 10.1007/s004420050884

Burnham KP, Anderson DR (2004) Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol Methods Res 33:261–304. doi: 10.1177/0049124104268644

Diaz M, Illeraz JC, Atienza JC (1998) Food resource matching by foraging tits Parus spp . during spring-summer in a Mediterranean mixed forest : evidence for an ideal free distribution. Ibis (Lond 1859) 140:654–660. doi: 10.1111/j.1474-919X.1998.tb04711.x

Eeva T, Lehikoinen E, Pohjalainen T (1997) Pollution-related variation in food supply and breeding success in two hole-nesting passerines. Ecology 78:1120–1131. doi: 10.1890/0012-9658(1997)078[1120:PRVIFS]2.0.CO;2

Fox J, Weisberg S (2011) An {R} Companion to Applied Regression, Second Edi. Sage Publications, Thousand Oaks, CA

Gabbe AP, Robinson SK, Brawn JD (2002) Tree-species preferences of foraging insectivorous birds: Implications for floodplain forest restoration. Conserv Biol 16:462–470. doi: 10.1046/j.1523-1739.2002.00460.x

Giffard B, Barbaro L, Jactel H, Corcket E (2013) Plant neighbours mediate bird predation effects on arthropod abundance and herbivory. Ecol Entomol 38:448–455. doi: 10.1111/een.12035

Giffard B, Corcket E, Barbaro L, Jactel H (2012) Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. Oecologia 168:415–24. doi: 10.1007/s00442-011-2089-7

Gripenberg S, Roslin T (2007) Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. Oikos 116:181–188. doi: 10.1111/j.2006.0030-1299.15266.x

Groner E, Ayal Y (2001) The interaction between bird predation and plant cover in determining habitat occupancy of darkling beetles. Oikos 93:22–31. doi: 10.1034/j.1600-0706.2001.930102.x

Heinrich B, Collins S (1983) Caterpillar leaf damage, and the game of hide-and-seek with birds. Ecology 64:592–602. doi: 10.2307/1939978

Hino T, Unno A, Nakano S (2002) Prey distribution and foraging preference for tits. Ornithol Sci 1:81–87. doi: 10.2326/osj.1.81

Holmes R, Robinson S (1981) Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35. doi: 10.1007/BF00346985

Howe A, Lövei GL, Nachman G (2009) Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomol Exp Appl 131:325–329. doi: 10.1111/j.1570-7458.2009.00860.x

Huang Q, Swatantran A, Dubayah R, Goetz SJ (2014) The influence of vegetation height heterogeneity on forest and woodland bird species richness across the United States. PLoS One 9:e103236. doi: 10.1371/journal.pone.0103236

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol Lett 10:835–48. doi: 10.1111/j.1461-0248.2007.01073.x

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kaitaniemi P, Riihimäki J, Koricheva J, Vehviläinen H (2007) Experimental evidence for associational resistance against the European pine sawfly in mixed tree stands. Silva Fenn 41:259–268.

Lang AC, Härdtle W, Bruelheide H, et al (2011) Horizontal, but not vertical canopy structure is related to stand functional diversity in a subtropical slope forest. Ecol Res 27:181–189. doi: 10.1007/s11284-011-0887-3

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139:1–10. doi: 10.1007/s00442-004-1497-3

Letourneau DK, Armbrecht I, Rivera BS, et al (2011) Does plant diversity benefit agroecosystems? A synthetic review. Ecol Appl 21:9–21. doi: 10.1890/09-2026.1

Letourneau DK, Jedlicka J a., Bothwell SG, Moreno CR (2009) Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems. Annu Rev Ecol Evol Syst 40:573–592. doi: 10.1146/annurev.ecolsys.110308.120320

Low PA, Sam K, McArthur C, et al (2014) Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. Entomol Exp Appl 152:120–126. doi: 10.1111/eea.12207

MacArthur R, MacArthur J (1961) On bird species diversity. Ecology 42:594–598.

Mäntylä E, Alessio GA, Blande JD, et al (2008) From plants to birds: higher avian predation rates in trees responding to insect herbivory. PLoS One 3:e2832. doi: 10.1371/journal.pone.0002832

Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:143–151. doi: 10.1007/s00442-010-1774-2

Mason C (1997) Association between Willow Warbler Phylloscopus trochilus territories and birch in woodlands in southeastern England. Ibis (Lond 1859) 139:411–412. doi: 10.1111/j.1474-919X.1997.tb04648.x

Metcalfe DB, Asner GP, Martin RE, et al (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. Ecol Lett 17:324–32. doi: 10.1111/ele.12233

Muiruri EW, Milligan HT, Morath S, Koricheva J (2015) Moose browsing alters tree diversity effects on birch growth and insect herbivory. Funct Ecol 29:724–735. doi: 10.1111/1365-2435.12407

Naef-Daenzer B, Keller LF (1999) The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim Ecol 68:708–718. doi: 10.1046/j.1365-2656.1999.00318.x

Naef-Daenzer L, Naef-Daenzer B, Nager RG (2000) Prey selection and foraging performance of breeding Great Tits Parus major in relation to food availability. J Avian Biol 31:206–214. doi: 10.1034/j.1600-048X.2000.310212.x

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. doi: 10.1111/j.2041-210x.2012.00261.x

Poch TJ, Simonetti JA (2013) Insectivory in *Pinus radiata* plantations with different degree of structural complexity. For Ecol Manage 304:132–136. doi: 10.1016/j.foreco.2013.04.044

Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies hypothesis in forest stands: the important role of tree species composition. Oecologia 142:90–7. doi: 10.1007/s00442-004-1696-y

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 43:95–124. doi: 10.2307/1942161

Russell E (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ Entomol 18:590–599.

Schuldt A, Both S, Bruelheide H, et al (2011) Predator diversity and abundance provide little support for the enemies hypothesis in forests of high tree diversity. PLoS One 6:e22905. doi: 10.1371/journal.pone.0022905

Schuldt A, Fahrenholz N, Brauns M, et al (2008) Communities of ground-living spiders in deciduous forests: Does tree species diversity matter? Biodivers Conserv 17:1267–1284. doi: 10.1007/s10531-008-9330-7

Siemann E, Tilman D, Haarstad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–50. doi: 10.1086/286204

Šipoš J, Kindlmann P (2013) Effect of the canopy complexity of trees on the rate of predation of insects. J Appl Entomol 137:445–451. doi: 10.1111/jen.12015

Smith JNM, Dawkins R (1971) The hunting behaviour of individual great tits in relation to spatial variations in their food density. Anim Behav 19:695–706. doi: 10.1016/S0003-3472(71)80173-2

Sobek S, Scherber C, Steffan-Dewenter I, Tscharntke T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany’s largest connected deciduous forest. Oecologia 160:279–288. doi: 10.1007/s00442-009-1304-2

Sperber CF, Nakayama K, Valverde MJ, Neves FDS (2004) Tree species richness and density affect parasitoid diversity in cacao agroforestry. Basic Appl Ecol 5:241–251. doi: 10.1016/j.baae.2004.04.001

Stephens DW, Krebs JR (1986) Foraging Theory, 1st edn. Princeton University Press, Princeton

Stostad HN, Menéndez R (2014) Woodland structure, rather than tree identity, determines the breeding habitat of Willow Warblers Phylloscopus trochilus in the northwest of England. Bird Study 61:246–254. doi: 10.1080/00063657.2014.901293

Straub CS, Simasek NP, Dohm R, et al (2014) Plant diversity increases herbivore movement and vulnerability to predation. Basic Appl Ecol 15:50–58. doi: 10.1016/j.baae.2013.12.004

Strode PK (2009) Spring tree species use by migrating Yellow-Rumped Warblers in relation to phenology and food availability. Wilson J Ornithol 121:457–468. doi: 10.1676/05-148.1

Tinbergen L (1960) The natural control of insects in pinewoods I. Factors influencing the intensity of predation by songbirds. Arch Neerl Zool 13:265–343.

Tonhasca A (1993) Effects of agroecosystem diversification on natural enemies of soybean herbivores. Entomol Exp Appl 69:83–90.

Van der Meij MAA, Bout RG (2004) Scaling of jaw muscle size and maximal bite force in finches. J Exp Biol 207:2745–2753. doi: 10.1242/jeb.01091

Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition and diversity on abundance of predatory arthropods. Oikos 117:935–943. doi: 10.1111/j.2008.0030-1299.15972.x

Whelan CJ, Şekercioğlu ÇH, Wenny DG (2015) Why birds matter: from economic ornithology to ecosystem services. J Ornithol. doi: 10.1007/s10336-015-1229-y

Wiens J, Rotenberry J (1981) Habitat Associations and Community Structure of Birds in Shrubsteppe Environments. Ecol Monogr 51:21–42. doi: 10.2307/2937305

Xiong L-H, Wu X, Lu J-J (2010) Bird Predation on Concealed Insects in a Reed-dominated Estuarine Tidal Marsh. Wetlands 30:1203–1211. doi: 10.1007/s13157-010-0104-0

Zhang Y, Adams J (2011) Top-down control of herbivores varies with ecosystem types. J Ecol 99:370–372. doi: 10.1111/j.1365-2745.2010.01770.x

Zou Y, Sang W, Bai F, Axmacher JC (2013) Relationships between Plant Diversity and the Abundance and α-Diversity of Predatory Ground Beetles (Coleoptera: Carabidae) in a Mature Asian Temperate Forest Ecosystem. PLoS One 8:e82792. doi: 10.1371/journal.pone.0082792

TABLE

Table 1. Models describing the probability of bird attack to artificial larvae. Response variables were either at plot or neighbourhood level and variables were introduced separately into models with study area as the only other fixed factor (omitted here for clarity). Models were ranked on the basis of their AICc, where ΔAICc≤2 indicate almost equivalent models, and the Akaike weights indicate the weight of evidence for a model relative to all candidate models. $R^2$ values are given for GLM models at plot level and both marginal ($R^2_m$, i.e. for fixed effects) and conditional ($R^2_c$ i.e. for both fixed and random effects) $R^2$ values are reported for GLMM models at neighbourhood-level. To explore species-specific responses, we ran all neighbourhood models of predation on each tree species separately.

| Spatial scale | Variable | $\chi^2$ | df | p | AICc | ΔAICc | Weight | $R^2_m$ ($R^2_c$) |
|---|---|---|---|---|---|---|---|---|
| Plot | Pine density | 40.0 | 1 | <0.001 | 116.1 | 0.00 | 1 | 0.19 |
| | Birch density | 21.0 | 1 | <0.001 | 133.6 | 17.51 | 0 | 0.17 |
| | Alder density | 10.5 | 1 | <0.001 | 142.2 | 26.18 | 0 | 0.14 |
| | Tree height variation | 4.3 | 1 | 0.038 | 147.6 | 31.53 | 0 | 0.11 |
| | Tree species richness | 0.0 | 1 | 0.964 | 152.0 | 35.91 | 0 | 0.09 |
| Neighbourhood | Tree species identity | 50.4 | 2 | <0.001 | 660.5 | 0.00 | 1.00 | 0.19 (0.37) |
| (All) | Pine density | 25.2 | 1 | <0.001 | 691.5 | 31.00 | 0.00 | 0.20 (0.34) |
| | Tree species richness | 6.2 | 1 | 0.013 | 707.3 | 46.81 | 0.00 | 0.14 (0.38) |
| | Birch density | 4.5 | 1 | 0.034 | 709.3 | 48.84 | 0.00 | 0.14 (0.35) |
| | Alder density | 4.0 | 1 | 0.044 | 709.6 | 49.16 | 0.00 | 0.14 (0.36) |
| (Pine only) | Pine density | 9.8 | 1 | 0.002 | 237.2 | 0.00 | 0.68 | 0.29 (0.51) |

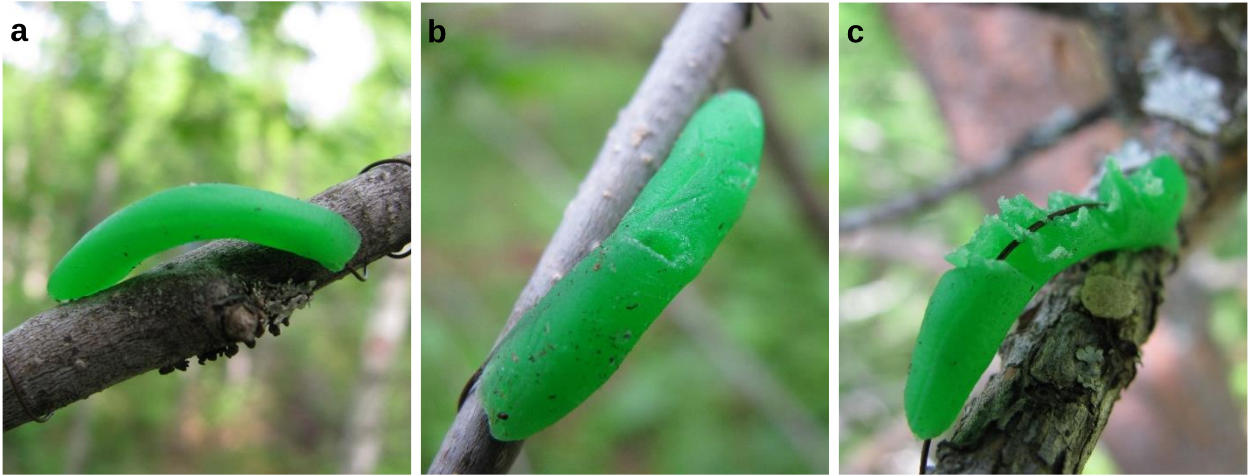
| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Birch density | 9.4 | 1 | 0.002 | 238.7 | 1.58 | 0.31 | 0.25 (0.44) |
| | Alder density | 0.0 | 1 | 0.828 | 248.0 | 10.79 | 0.00 | 0.18 (0.46) |
| | Tree species richness | 0.0 | 1 | 0.983 | 248.0 | 10.84 | 0.00 | 0.18 (0.46) |
| (Birch only) | Exposed chewing insects | 5.2 | 1 | 0.022 | 255.2 | 0.00 | 0.46 | 0.14 (0.31) |
| | Alder density | 3.6 | 1 | 0.056 | 256.3 | 0.56 | 0.27 | 0.14 (0.31) |
| | Birch density | 1.9 | 1 | 0.167 | 257.9 | 2.20 | 0.12 | 0.14 (0.39) |
| | Pine density | 0.1 | 1 | 0.742 | 260.1 | 4.34 | 0.04 | 0.12 (0.30) |
| | Tree species richness | 0.0 | 1 | 0.845 | 260.2 | 4.40 | 0.04 | 0.12 (0.29) |
| | Concealed insects | 0.0 | 1 | 0.898 | 260.2 | 4.41 | 0.04 | 0.12 (0.30) |
| | Insect herbivore damage | 0.0 | 1 | 0.825 | 260.2 | 4.43 | 0.04 | 0.12 (0.23) |
| (Alder only) | Concealed insects | 3.1 | 1 | 0.076 | 153.3 | 0.00 | 0.33 | 0.29 (0.35) |
| | Insect herbivore damage | 2.4 | 1 | 0.124 | 154.0 | 0.67 | 0.24 | 0.29 (0.35) |
| | Tree species richness | 1.1 | 1 | 0.304 | 155.2 | 1.85 | 0.13 | 0.27 (0.37) |
| | Birch density | 1.0 | 1 | 0.326 | 155.8 | 2.50 | 0.10 | 0.27 (0.31) |
| | Alder density | 0.3 | 1 | 0.578 | 156.4 | 3.07 | 0.07 | 0.28 (0.33) |
| | Pine density | 0.0 | 1 | 0.825 | 156.6 | 3.26 | 0.07 | 0.27 (0.32) |
| | Exposed chewing insects | 0.0 | 1 | 0.825 | 156.5 | 3.16 | 0.06 | 0.26 (0.31) |

FIGURES

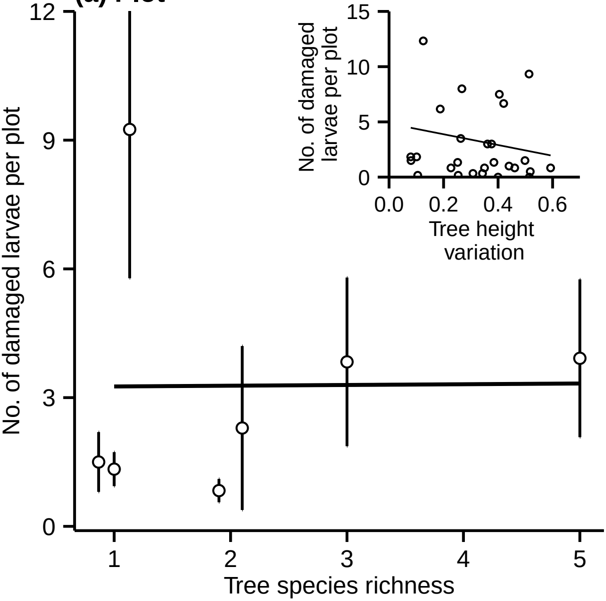
**Fig. 1** Artificial larvae secured to tree branches showing (a) no damage, (b) single beak mark and (c) multiple pecks by birds.

**Fig. 2** Bird predation responses to tree species richness (a) within a plot and (b) in the neighbourhood around a focal tree. Lines represent the best fit with a linear function and the number of larvae damaged by birds (mean ±SE) are plotted for each tree species composition in (a) and for individual tree species in (b). The effect of tree height variation on the number of larvae damaged at the plot level is shown inset. Trees with no immediate neighbours were assigned a tree species richness level of zero.

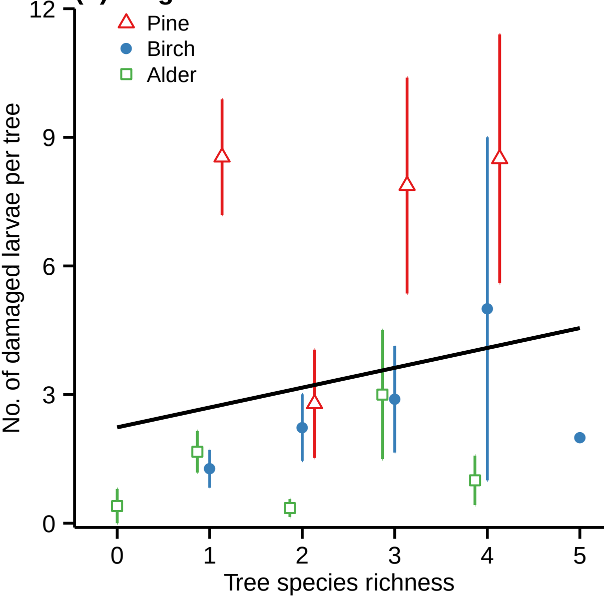
**Fig. 3** Bird predation responses to densities of pine, birch and alder either (a) within a plot or (b) in the neighbourhood around a focal tree. Solid lines represent the best fit with a linear function across all plots in (a) and for all focal trees in (b). Separate lines are also drawn in (b) for each of the three focal tree species: pine, birch and alder.

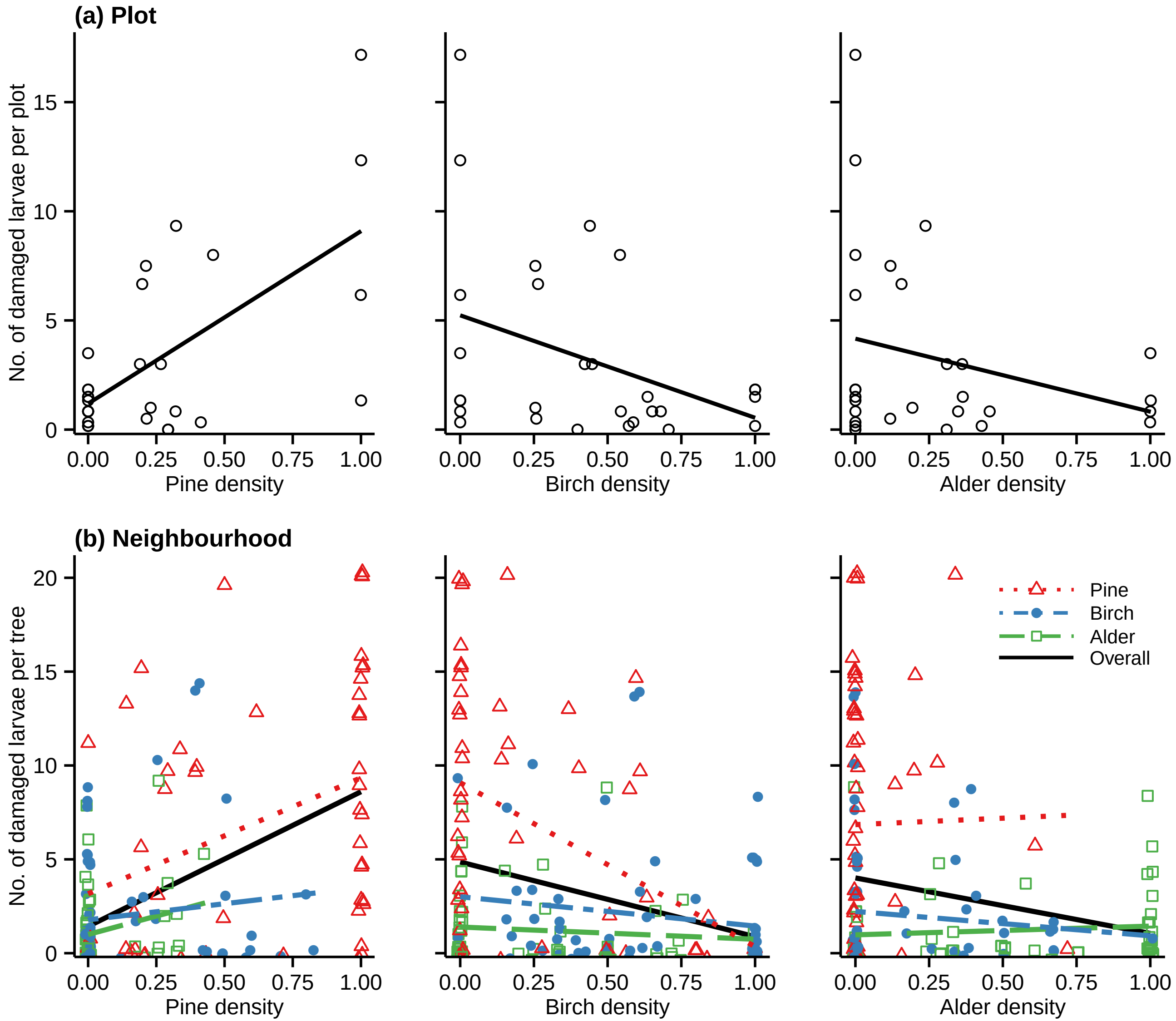

a
b
c

**(a) Plot**



**(b) Neighbourhood**




(a) Plot
No. of damaged larvae per plot
0
5
10
15
0.00
0.25
0.50
0.75
1.00
Pine density
Birch density
Alder density
(b) Neighbourhood
No. of damaged larvae per tree
0
5
10
15
20
Pine
Birch
Alder
Overall