

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

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4 Evalyne W. Muiruri¹, Kalle Rainio², Julia Koricheva¹

5
6 ¹School of Biological Sciences, Royal Holloway University of London, Egham, Surrey,
7 TW20 0EX, United Kingdom

8 ²Department of Biology, University of Turku, FIN-20014 Turku, Finland

9
10 Correspondence: Evalyne W. Muiruri, evalyne.muiruri.2012@live.rhul.ac.uk,

11 +447807171932

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

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

25 ABSTRACT

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

44

45 KEY WORDS

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

48

49 INTRODUCTION

50 Insect herbivores can have significant impacts on key ecosystem functions such as nutrient
51 cycling, productivity and carbon sequestration (Metcalf et al 2014). These effects may be
52 further compounded by losses in plant diversity, and many studies have shown that insect
53 herbivore damage and abundance is higher in less diverse plant communities (associational
54 resistance, Kaitaniemi et al. 2007; Jactel and Brockerhoff 2007; Barbosa et al. 2009). Root
55 (1973) was the first to suggest that natural enemies of insect herbivores may drive the observed
56 patterns of associational resistance by being more effective as predators in diverse plant
57 communities compared to monocultures. This prediction, termed the enemies hypothesis, was
58 based on the observation that more species-rich habitats often support a higher diversity of prey
59 species, provide refuges and offer additional resources such as pollen and nectar for
60 invertebrate predators (Root 1973; Russell 1989). The enemies hypothesis has received much
61 experimental scrutiny and support from studies in agricultural ecosystems and grasslands
62 (Tonhasca 1993; Siemann et al 1998; Sobek et al 2009; Letourneau et al 2011; Straub et al
63 2014), however, fewer tests of this hypothesis have been conducted in forest ecosystems. These
64 studies have produced mixed results with some reporting negative effects of tree diversity on
65 predator effectiveness (Schuldt et al 2011; Zou et al 2013) and others showing stronger effects
66 of tree species composition (Riihimäki et al 2005; Kaitaniemi et al 2007; Vehviläinen et al
67 2008), density (Sperber et al 2004; Schuldt et al 2008) or tree species identity (Sobek et al
68 2009) rather than tree species richness per se (Zhang and Adams 2011). Thus, more studies are
69 required to better understand relationships between diversity and top-down control of insect
70 pests in forest ecosystems.

71

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

75 2009). Birds, in particular, have received little attention even though they are widely considered
76 to be important control agents of insect pests in forest stands (Mäntylä et al 2011; Bereczki et
77 al 2012) and can deliver a key ecosystem service (Whelan et al 2015). In addition, the diversity
78 and abundance of avian predators has not only been shown to respond to increased structural
79 and floristic diversity (MacArthur and MacArthur 1961; Bereczki et al 2014; Huang et al 2014),
80 but also vary with densities of individual tree species (Wiens and Rotenberry 1981; Mason
81 1997). Nevertheless, very few studies have examined effects of tree diversity on avian
82 predation in forest ecosystems (Giffard et al 2012; Poch and Simonetti 2013; Giffard et al 2013;
83 Bereczki et al 2014) and of these studies, none have directly tested the effects of increasing
84 tree species richness or explored the effects of tree species composition and individual tree
85 species densities on bird predator effectiveness. Recent work by Poch and Simonetti (2013)
86 has shown that higher bird predation occurs in structurally complex forest plantations with
87 more developed and diverse understorey. Therefore, just as top-down control by arthropod
88 predators was hypothesised to increase with plant diversity and associated structural
89 complexity (Root 1973), positive effects of diversity on bird predation may be driven by
90 increased structural complexity rather than diversity per se.

91

92 Finally, the vast majority of studies testing the enemies hypothesis have done so at a single
93 spatial scale and thus, we still know little about the scale at which the enemies hypothesis
94 applies (Zhang and Adams 2011). Spatial scale is believed to be an important determinant of
95 the strength of prey-predator interactions (Langellotto and Denno 2004; Gripenberg and Roslin
96 2007) and effects of plant diversity on these relationships may vary with spatial scale
97 (Bommarco and Banks 2003). The review by Bommarco and Banks (2003) found that effects
98 of plant diversity on the effectiveness of arthropod predators was strongest in small ($<16\text{m}^2$)
99 plots, intermediate in intermediate-sized ($28\text{-}196\text{m}^2$) but absent in large ($>256\text{m}^2$) plots; these

100 patterns could be due to easier redistribution of predators to the more favoured mixed stands in
101 experiments of smaller plot size. For birds, a similar pattern may arise as, even though they can
102 travel further than arthropods in search of prey, their capacity for direct assessment of insect
103 abundance is greater within a microhabitat compared to larger spatial scales (Strode 2009).
104 Optimal foraging theory predicts that natural selection favours behaviours that maximise
105 energy intake per unit time spent foraging (Stephens and Krebs 1986). Thus, even in the
106 absence of detectable prey, birds may have evolved to use alternative indicators such as the
107 signs of leaf damage (Heinrich and Collins 1983) or chemical cues from insect-damaged plants
108 (Mäntylä et al 2008; Amo et al 2013) to locate insect-rich trees within small spatial scales. At
109 larger scales, the patchy distribution of many insect herbivores may drive forage selection
110 towards patches where the host plants of their favoured prey dominate as a strategy to minimise
111 search time (Arvidsson and Klaesson 1986; Mason 1997). Therefore, different factors might
112 act as drivers of bird predation depending on the spatial scale of observation. As habitat
113 selection by birds is understood to occur in a hierarchical manner (Johnson 1980), a
114 combination of different drivers at each spatial scale may act to maximise overall foraging
115 efficiency, in accordance with optimal foraging theory.

116

117 The primary goal of this study was to experimentally test whether bird predation increases with
118 tree species richness, as predicted by the enemies hypothesis. We used an established forest
119 diversity experiment in SW Finland to examine the effects of tree species diversity, prey
120 availability and habitat structural heterogeneity on bird foraging preferences. To assess bird
121 predation, artificial larvae (modelled from plasticine) were installed on alder, birch and pine
122 trees in stands of varying tree species diversity. This technique of presenting artificial prey has
123 risen in popularity in prey-predator studies as it facilitates field assessment of relative predation
124 rates (Howe et al 2009) and the marks left by predators in plasticine are identifiable to a coarse

125 taxonomic level (Low et al 2014). In keeping with most tests of the enemies hypothesis, we
126 explored how bird predation rates vary with diversity at plot level and test whether these effects
127 are mediated by changing structural complexity. Secondly, we examine avian predation
128 responses to tree diversity at finer spatial scales, focussing on the local neighbourhood of a
129 focal tree. Finally, we compare the importance of natural herbivore abundance and damage on
130 experimental trees relative to the importance of neighbourhood diversity in predicting bird
131 predation rates.

132

133 METHODS

134 *Study site and design*

135 The study was carried out at the Satakunta forest diversity experiment established in 1999 in
136 south-western Finland. The experiment consists of three separate areas with 38 plots (20 x 20
137 m) in each area. Diversity treatments represent monocultures and 2-, 3-, and 5-species
138 combinations of the following five tree species: Scots pine (*Pinus sylvestris*); Norway spruce
139 (*Picea abies*); Siberian larch (*Larix sibirica*); silver birch (*Betula pendula*); and black alder
140 (*Alnus glutinosa*). Each plot consists of 13 rows with 13 trees planted at 1.5m intervals (total
141 169 trees) and the position of different tree species in mixed stands was randomised. Replanting
142 of species was carried out in 2000 for all plots and, in 2001 for plots where mortality exceeded
143 10%. Other than the manual removal of naturally regenerating woody vegetation in spring
144 2010, no management interventions have been used in the Satakunta experiment since planting.

145

146 In the present study, we used two out of the three experimental areas (area 1, 61°42'N, 21°58'E
147 and area 3, 61°40'N, 21°42'E) and focussed on three focal tree species: pine, birch and alder.
148 These species were chosen as they host caterpillar larvae (e.g. *Epirrita autumnata* Borkhausen.
149 on birch and alder and, *Neodiprion sertifer* Geoff. on pine) that could easily be modelled from

150 plasticine. The other species present in the study areas are attacked mostly by small sucking
151 insects (aphids or adelgids) which might be considered less profitable prey (Naef-Daenzer et
152 al 2000) and therefore receive less bird predation compared to caterpillars. We therefore
153 selected trees for this experiment from the seven treatments containing pine, birch or alder:
154 three monocultures (pine, birch and alder), two 2-species mixtures (pine + birch, birch + alder),
155 one 3-species mixture (pine + birch + alder) and the 5-species mixture (pine + birch + alder +
156 spruce + larch). There were two replicates of each treatment per area but no pine-alder
157 combination was present in the original experimental design so only two out of the three
158 possible 2-species mixtures were available for this study. For each plot, six trees were selected
159 within the interior, avoiding selection of adjacent trees and substituting tree species in mixtures
160 such that six trees were sampled in monocultures, three trees per species were sampled in 2-
161 species mixtures, and two trees per species were sampled in 3- and 5-species mixtures. Insect
162 herbivore abundance and damage were assessed on experimental trees in early June 2013 prior
163 to the start of the bird predation experiment. Pine trees in the study area have been observed to
164 have very low herbivore densities (J. Koricheva, unpublished data) and hence assessment of
165 insect herbivores was only performed on birch and alder trees. We assessed the
166 presence/absence of exposed chewing insects, the abundance of concealed-feeder insects (e.g.
167 leaf miners or rollers) and the extent of leaf area damaged (%) by defoliating insects on the
168 same focal trees used in the predation experiment (Online Resource 1).

169

170 *Bird predation assessment and surveys*

171 The experiment was timed to coincide with the peak bird nesting period when insects compose
172 the majority of the diet fed to nestlings (Naef-Daenzer et al 2000). On 8th and 9th June 2013,
173 five artificial larvae were installed on each experimental tree (30 larvae per plot). The larvae
174 were modelled from odourless, light green plasticine to an approximate size of 2-3cm in length

175 and 3-4 mm in diameter (Fig. 1a). The size of the larvae was chosen based on previous studies
176 using artificial caterpillars on the same tree species (Mäntylä et al 2008) and to represent the
177 average size of larvae of the autumnal moth (*E. autumnata*) and the European pine sawfly (*N.*
178 *sertifer*), both of which are common defoliators on alder, birch and pine trees in Finland.
179 Artificial larvae were installed on branches which were 1.5-3m above ground, corresponding
180 to the mid canopy for alder and pine and to the lower canopy for birch. Five larvae per tree
181 were distributed between different branches from all sides of the canopy to avoid systematic
182 differences in sun/shade exposure, and secured to a branch using metal wire (diameter
183 0.35mm). Following installation, the condition of the artificial larvae was checked five times:
184 3, 6, 9, 11 or 12 and 15 or 16 days after installation. Predation attempts by birds were recorded
185 on larvae if they exhibited marks that were consistent with bird pecking damage and could not
186 otherwise be explained (e.g. not a scratch by a nearby branch, Fig 1b, c). Although wood ants
187 are highly abundant in the study area, we found no evidence of ants predated the artificial
188 larvae in this experiment or when the artificial larvae were offered to wood ants near their nests.
189 After each larva was checked, those that were damaged were either remoulded where possible
190 or replaced.

191

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

200 the previous summer. About 30 artificial caterpillars per tree were installed and camera traps
201 were in operation for one month.

202

203 *Tree height variation*

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

212

213 *Statistical analysis*

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

225

226 We used generalised linear mixed-effects models (GLMM) to account for the nested design
227 and to allow specification of an error family. In order to assess bird predation, we modelled the
228 probability of predation of artificial larvae as a bounded binary response variable (larvae
229 damaged/not damaged) with a binomial error structure, specifying a random error structure
230 with individual trees nested within plot (plot/tree). Due to the regularity of the experimental
231 design at Satakunta the variables (1-4) describing tree diversity at the plot and neighbourhood
232 scales were not independent, therefore, no more than one of the four diversity variables could
233 be included in models at any one time. However, initial models were run to determine whether
234 effects of all diversity variables (from either plot or neighbourhood level) on bird predation
235 were dependent on the study area used or the time of observation (area x time x variable [1-
236 4]). As neither area nor time significantly interacted with any diversity variable at either spatial
237 scale, we performed all subsequent analysis on predation across all sampling points, retaining
238 area as a fixed factor in subsequent models (not in interaction with other variables) to account
239 for natural variation in bird activity between the two study areas.

240

241 For analysis at plot level, we first calculated the mean number of larvae damaged per plot and
242 ran generalized linear-models (GLM) with the binomial response variable (mean number of
243 larvae damaged per plot, number of larvae installed in each plot) against area and each variable
244 (1-4) or tree height variation separately (ie. area + variable[1-4] or area + tree height variation).
245 A similar approach was used at the neighbourhood scale, this time running models for
246 neighbourhood-level predictor variables (1-4) or tree species identity. Binomial GLMMs were
247 run for the response variable (number of damaged larvae per tree, number of larvae installed
248 per tree) against each individual predictor variable using plot as a random factor. Tree species
249 composition effects were assessed for mixtures at each species richness level separately but as

250 no significant differences were detected at either plot or neighbourhood level, we focus our
251 discussion on variables 1-4.

252

253 In order to determine which variables (at plot or neighbourhood level) best predicted bird
254 predation, we ranked univariate models on the basis of their AICc values (second-order
255 Akaike's Information Criterion) and used Akaike weights as an indicator of the weight of
256 evidence in support of a given model, compared to other candidate models (Anderson et al
257 2001; Burnham and Anderson 2004). Models with lower AICc values were therefore
258 considered to be better than other candidate models but could only be termed the single best
259 model if the Akaike weight exceeded 0.9 (Anderson et al 2001). Where Akaike weights did not
260 exceed this value, differences in the AICc were used as an indicator of the relative likelihood
261 of the model. Candidate models differing least from the best model ($\Delta AICc \leq 2$) are considered
262 to be well supported but those differing most ($\Delta AICc \geq 10$) can be omitted (Burnham and
263 Anderson 2004). In addition to model comparison, we also calculated R^2 values to estimate the
264 variance explained by fixed factors only (R^2_m) or, both fixed factors and random factors
265 together (R^2_c) (Nakagawa and Schielzeth 2013).

266

267 Different bird species might exhibit foraging preferences for individual tree species or the
268 insect prey they host (Holmes and Robinson 1981; Gabbe et al 2002). Therefore, we ran similar
269 analysis for each tree species separately to test the relative importance of components of
270 neighbourhood diversity in determining bird predation rates. In particular, for birch and alder
271 trees, we use AICc weighing to determine whether predation rates are driven more by changes
272 in neighbourhood diversity (variables 1-4), natural insect abundance (both exposed and
273 concealed insects) or insect herbivore damage (understood to enhance bird predation rates).
274 Further GLM and GLMM models were used to determine the effect of plot and neighbourhood

275 diversity variables (1-4) on tree height variation and insect herbivore damage (log transformed)
276 respectively. Effects of diversity on the presence/absence of exposed chewing and the
277 abundance of concealed-feeding insects on birch and alder were also examined using GLMMs
278 with a poisson error distribution specified for count data. All statistical tests were conducted in
279 R software version 2.15.2 (R Core Team 2012) using the lme4 package (Bates et al 2012).
280 Model residuals were examined for homogeneity of variance and we report AICc and Akaike
281 weights from the MuMIn package as well as Chi-squared and corresponding p-values from
282 ANOVA using the car package (Fox and Weisberg 2011).

283

284 RESULTS

285 *Bird species present in the study area*

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

296

297 *Patterns of bird predation*

298 The number of attacks on artificial larvae increased linearly over time ($\chi^2=48.0$, $df=1$, $p<0.001$).
299 This pattern was more pronounced in area 1 than in area 3 (time x area: $\chi^2=34.6$, $df=1$, $p<0.001$)

300 with overall number of attacks being higher in area 1 ($\chi^2=11.3$, $df=1$, $p<0.001$). However,
301 despite these patterns, no significant two-way or three-way interactions were detected between
302 time, area and each of the four main diversity variables at either spatial scale (Online Resource
303 3). Similarly, effects of tree height variation at the plot level and tree species identity on bird
304 predation were independent of area or time (Online Resource 3). Therefore, we conducted all
305 subsequent analysis on the total number of larvae damaged per tree across all sampling points
306 and excluding interaction terms with 'area' in further models.

307

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

314

315 *Plot-level analysis*

316 Bird predation was not significantly affected by plot tree species richness (Fig. 2a, Table 1) but
317 decreased with tree height variation within a plot (Fig. 2a inset, Table 1). The densities of pine,
318 birch and alder had opposite effects on bird predation (Fig. 3a, Table 1). The number of larvae
319 damaged significantly increased with the density of pine but decreased with increasing
320 proportions of birch or alder (Fig 3a, Table 1). Although tree height variation increased with
321 plot species richness ($F=12.6$, $df=1$, $p=0.001$), it did not depend on densities of alder ($F=0.9$,
322 $df=1$, $p=0.362$), birch ($F=1.5$, $df=1$, $p=0.234$) or pine ($F=0.2$, $df=1$, $p=0.667$). Model
323 comparisons based on AICc identified the density of pine as the variable best accounting for
324 bird predation at the plot level compared to other predictor variables and explained the most

325 variance (Table 1). The second-ranked predictor was birch density but as $\Delta AICc > 10$, this
326 model had essentially no support compared to the top model with pine density.

327

328 *Neighbourhood-level analysis*

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

336

337 Regardless of tree species diversity, tree species identity had a significant effect on the number
338 of larvae damaged per tree (Table 1). Of the 551 damaged larvae, 358 (65%) were on pine trees
339 (222 from pine monocultures), 129 (23%) on birch and 64 (12%) on alder (all *post hoc* pairwise
340 comparisons significant, $p < 0.001$). In model comparisons, the single best explanatory variable
341 for the number of artificial larvae damaged per tree was the species identity of the focal tree,
342 explaining the most variance (highest R^2_m value) compared to any other model (Table 1).
343 However, responses to diversity did not differ between the three species (tree species identity
344 x richness: $\chi^2=0.5$, $df=2$, $p=0.769$, tree species identity x pine density: $\chi^2=2.1$, $df=2$, $p=0.356$).
345 Only the effects of birch and alder density varied between the three focal tree species.
346 Increasing birch density in the neighbourhood had a strong negative effect on predation rates
347 on pine trees but only weak negative effects on predation on birch and alder (tree species
348 identity x birch density; $\chi^2=6.3$, $df=2$, $p=0.042$, Fig 3b). At the same time, predation of artificial
349 larvae on birch trees decreased with alder density but no relationship was observed for

350 predation on pine or alder focal trees (tree species identity x alder density; $\chi^2=11.0$, df-2,
351 $p=0.004$, Fig 3b). However, this pattern might be partially attributed to the fact that we did not
352 have any plots with a pine/alder two-species combination so proportions of alder around pine
353 trees rarely exceeded 33% (Fig. 3b).

354

355 *Tree species-specific analysis*

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

373

374 *Natural insect herbivory on birch and alder*

375 In a comparison of natural herbivory between the two broadleaved species, the percentage leaf
376 area damage was significantly higher on birch compared to alder trees ($\chi^2=24.8$, $df=1$,
377 $p<0.001$), but the presence of exposed insects or the abundance of concealed insect herbivores
378 did not differ between the two species ($p\geq 0.531$). Tree species richness surrounding focal trees
379 also had no significant effect on initial insect herbivore damage ($p\geq 0.180$) or the presence of
380 exposed chewing insects ($p\geq 0.918$) on either tree species. However, the abundance of
381 concealed insects was reduced with increasing neighbourhood tree species richness on birch
382 ($\chi^2=4.5$, $df=1$, $p=0.033$) but not on alder ($\chi^2=2.5$, $df=1$, $p=0.111$). Neighbourhood densities of
383 alder, birch or pine had no effect on insect herbivore damage, the abundance of concealed
384 insects or the presence of exposed insect herbivores ($p\geq 0.295$).

385

386 DISCUSSION

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

398

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

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

411

412 When the enemies hypothesis was first proposed, Root (1973) suggested that stronger top-
413 down control in diverse habitats is mediated by increased structural complexity where more
414 niches were available for predators to exploit. This mechanism was supported by Poch and
415 Simonetti (2013) who showed that bird predation rates were higher in more structurally
416 complex forest plantations that had a higher abundance and diversity of woody species in the
417 understory. However, we found that, despite increased structural complexity with tree species
418 richness, bird predation decreased with increases in tree height variation (Fig. 2a, inset).
419 Although greater structural complexity may enhance the number of niches a predator can
420 exploit, prey might be better concealed, increasing search time. As a result, structurally
421 complex habitats may be considered less suitable foraging locations. For example, willow
422 warblers, the most common bird species in the study area, have been shown to establish
423 territories more frequently in stands where trees are of a similar size (Stostad and Menéndez
424 2014). Therefore, structural heterogeneity may reduce rather than enhance bird predation

425 independently of plot species richness. As predator responses to structural complexity have
426 been shown to change in magnitude but not direction across spatial scales (Langellotto and
427 Denno 2004), bird predation at the neighbourhood level is unlikely to increase with structural
428 heterogeneity within the microhabitat. Thus, structural complexity can explain neither tree
429 species richness effects at plot and neighbourhood levels nor differential responses to tree
430 species richness between the two scales.

431

432 Instead, scale-dependence of tree species richness effects on bird predation may result from
433 differences in prey visibility that manifest themselves only at fine spatial scales. Bird predation
434 rates on insects have been shown to increase where plant cover is reduced (Groner and Ayal
435 2001). As tree species richness increases, presence of tree species differing in growth rates and
436 foliage structure may result in less horizontal canopy space used and thus, a more open canopy
437 (Lang et al 2011). This has previously been shown in the Satakunta experiment, with canopy
438 cover around birch trees decreasing with tree species richness (Muiruri et al. 2015). As a result,
439 artificial larvae may be more visible to birds when the focal trees are surrounded by
440 heterospecifics but these effects are likely to be restricted to small spatial scale and unlikely to
441 manifest at plot level. Improved visibility of insect prey on trees in more open forest stands
442 may present a key advantage as palatable caterpillars may be visually more cryptic or have
443 more cryptic behaviour compared to unpalatable insect prey, hiding amongst foliage and
444 feeding in such a way as to minimise their apparent damage (Heinrich and Collins 1983). Thus,
445 neighbourhood species richness effects on avian predation may be driven by differences in the
446 light environment minimising search time and the energetic costs of foraging.

447

448 At the plot level, the capacity for direct visual assessment of prey is hampered and birds may
449 instead rely on other indicators of a suitable foraging patch such as the presence or absence of

450 host tree species of their favoured prey (Wiens and Rotenberry 1981; Mason 1997). As insect
451 prey abundance can vary significantly over space and time, insectivorous birds often have to
452 visit different parts of the environment continually to assess prey availability to the detriment
453 of immediate foraging efficiency (Smith and Dawkins 1971). However, with the use of
454 different cues within each spatial scale, insectivorous birds might be able to efficiently explore
455 the landscape, concentrating their searches on selected patches for visible and easily accessible
456 prey. This strategy would enable birds to exploit new resources as soon as they become
457 available, minimising the time spent locating insect prey while maximising food intake for
458 adults and nestlings in accordance with the optimal foraging theory (Stephens and Krebs 1986).

459

460 *Effects of tree species density and identity*

461 Strong foraging preference of insectivorous birds for certain tree species have been well
462 documented in forests (Holmes and Robinson 1981; Gabbe et al 2002; Strode 2009). In this
463 experiment, we observed that predation was consistently higher on artificial larvae installed on
464 pine than on birch and alder. Moreover, different beak marks on damaged artificial caterpillars
465 indicated that different bird species were responsible for predation on pine and the broadleaf
466 tree species. Individual pecks on caterpillars installed on birch and alder (Fig. 1b) were likely
467 to be caused by small passerines such as the willow warblers, the most abundant bird species
468 in the study area. In contrast, the multiple large beak marks found on artificial larvae on pine
469 trees (Fig. 1c) were likely caused by the great tits, as confirmed by the camera trapping. This
470 generalist insectivorous bird has been shown to preferentially forage on pine trees (Eeva et al
471 1997) and is known to be a highly innovative, opportunistic forager capable of social learning
472 (Aplin et al 2015). Artificial larvae used in this experiment may have presented a new and
473 attractive resource for breeding birds which often try to find the largest, most profitable prey
474 for their nestlings (Diaz et al 1998; Naef-Daenzer et al 2000; Hino et al 2002) regardless of

475 nutritional quality (Brodmann and Reyer 1999). Opportunistic pecking by seed-eating birds
476 would also be consistent with damage seen on artificial larvae (Fig. 1c) as they may have
477 stronger beaks to pry seeds out of cones (van der Meij and Bout 2004).

478

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

489

490 Regardless of scale, increases in pine density (and reduced birch and alder density) consistently
491 increased the probability of predation on artificial larvae (Fig. 2). Passerine birds often conduct
492 concentrated searches for prey within microhabitats (Naef-Daenzer and Keller 1999) so any
493 trees neighbouring pine may also be more susceptible to attack by virtue of their proximity and
494 those neighbouring birch or alder, less so. However, insectivorous birds may also return
495 repeatedly to profitable patches (Naef-Daenzer and Keller 1999) and this might explain why
496 predation of artificial larvae increased during the experimental period. Experiments using the
497 same technique of model prey over the same duration usually find that predation increases
498 initially then decreases as birds learn that the artificial prey offer no nutritional reward (Mäntylä
499 et al 2008). We hypothesise that the continuous increase in predation in this experiment was

500 due to increased recruitment of 'naïve' birds from outside the study area. In particular, as birds
501 might develop a search image for a given prey item during feeding (Tinbergen 1960), the
502 newly-fledged birds of early broods observed outside experimental plots may be responsible
503 for the continued increase in predation rates.

504

505 *Effects of insect damage and natural prey abundance*

506 We hypothesised that focal trees with more insect herbivore damage or a higher abundance of
507 insect prey might experience higher predation rates. However, contrary to previous work
508 showing that birds prefer to forage on insect-damaged trees (Mäntylä et al 2008; Amo et al
509 2013), leaf area damage by insect herbivores had no effect on predation rates on either birch or
510 alder. Similarly, despite evidence suggesting concealed insects are under intense bird predation
511 (Xiong et al 2010), we also observed no effect of concealed insect herbivore damage on the
512 probability of larval attack on birch or alder trees. This is perhaps not surprising as, although
513 concealed-feeding insects are sedentary and therefore potentially easy targets for avian
514 predators, the concealed insects measured in this experiment (leaf rollers, folders and miners)
515 are quite small (<10mm) and the difficulty of localising prey within shelters also increases
516 search and handling time for birds for little reward in return. The only indication that density-
517 dependent predator-prey interactions occurred in this experiment was found on birch where
518 predation was higher on trees initially infested with exposed chewing insects (Online Resource
519 4). However, this could not explain the effects of tree species richness on bird predation
520 because there was no significant difference between natural herbivory on birch trees
521 surrounded by birches or by other tree species.

522

523 *Conclusions*

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

535

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540

541 REFERENCES

- 542 Amo L, Jansen JJ, van Dam NM, et al (2013) Birds exploit herbivore-induced plant volatiles
543 to locate herbivorous prey. *Ecol Lett* 16:1348–55. doi: 10.1111/ele.12177
- 544 Anderson DR, Link WA, Johnson DH, Burnham KP (2001) Suggestions for presenting the
545 results of data analyses. *J Wildl Manage* 65:373–378. doi: 10.2307/3803088
- 546 Andow DA (1991) Vegetational diversity and arthropod population response. *Annu Rev*
547 *Entomol* 36:561–586. doi: 10.1146/annurev.en.36.010191.003021

548 Aplin LM, Farine DR, Cockburn A, et al (2015) Experimentally induced innovations lead to
549 persistent culture via conformity in wild birds. *Nature* 518:538–541. doi:
550 10.1038/nature13998

551 Arvidsson B, Klaesson P (1986) Territory size in a Willow Warbler *Phylloscopus trochilus*
552 population in mountain birch forest in Swedish Lapland. *Ornis Scand* 17:24–30. doi:
553 10.2307/3676749

554 Barbosa P, Hines J, Kaplan I, et al (2009) Associational resistance and associational
555 susceptibility: having right or wrong neighbors. *Annu Rev Ecol Evol Syst* 40:1–20. doi:
556 10.1146/annurev.ecolsys.110308.120242

557 Bates D, Maechler M, Bolker B (2012) lme4: Linear mixed-effects models using Eigen and
558 Eigen. *J Stat Softw* 65:1–67. doi: 10.18637/jss.v065.i01

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

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

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

565 Brodmann PA, Reyer HU (1999) Nestling provisioning in water pipits (*Anthus spinoletta*):
566 Do parents go for specific nutrients or profitable prey? *Oecologia* 120:506–514. doi:
567 10.1007/s004420050884

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

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

573 Eeva T, Lehikoinen E, Pohjalainen T (1997) Pollution-related variation in food supply and
574 breeding success in two hole-nesting passerines. *Ecology* 78:1120–1131. doi:
575 10.1890/0012-9658(1997)078[1120:PRVIFS]2.0.CO;2

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

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

581 Giffard B, Barbaro L, Jactel H, Corcket E (2013) Plant neighbours mediate bird predation
582 effects on arthropod abundance and herbivory. *Ecol Entomol* 38:448–455. doi:
583 10.1111/een.12035

584 Giffard B, Corcket E, Barbaro L, Jactel H (2012) Bird predation enhances tree seedling
585 resistance to insect herbivores in contrasting forest habitats. *Oecologia* 168:415–24. doi:
586 10.1007/s00442-011-2089-7

587 Gripenberg S, Roslin T (2007) Up or down in space? Uniting the bottom-up versus top-down
588 paradigm and spatial ecology. *Oikos* 116:181–188. doi: 10.1111/j.2006.0030-
589 1299.15266.x

590 Groner E, Ayal Y (2001) The interaction between bird predation and plant cover in
591 determining habitat occupancy of darkling beetles. *Oikos* 93:22–31. doi:
592 10.1034/j.1600-0706.2001.930102.x

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

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

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

599 Howe A, Lövei GL, Nachman G (2009) Dummy caterpillars as a simple method to assess
600 predation rates on invertebrates in a tropical agroecosystem. *Entomol Exp Appl*
601 131:325–329. doi: 10.1111/j.1570-7458.2009.00860.x

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

605 Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett*
606 10:835–48. doi: 10.1111/j.1461-0248.2007.01073.x

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

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

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

615 Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-
616 structured habitats: a meta-analytical synthesis. *Oecologia* 139:1–10. doi:
617 10.1007/s00442-004-1497-3

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

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

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

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

627 Mäntylä E, Alessio GA, Blande JD, et al (2008) From plants to birds: higher avian predation
628 rates in trees responding to insect herbivory. *PLoS One* 3:e2832. doi:
629 10.1371/journal.pone.0002832

630 Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: a meta-analysis of top-down
631 trophic cascades caused by avian predators. *Oecologia* 165:143–151. doi:
632 10.1007/s00442-010-1774-2

633 Mason C (1997) Association between Willow Warbler *Phylloscopus trochilus* territories and
634 birch in woodlands in southeastern England. *Ibis (Lond 1859)* 139:411–412. doi:
635 10.1111/j.1474-919X.1997.tb04648.x

636 Metcalfe DB, Asner GP, Martin RE, et al (2014) Herbivory makes major contributions to
637 ecosystem carbon and nutrient cycling in tropical forests. *Ecol Lett* 17:324–32. doi:
638 10.1111/ele.12233

639 Muiruri EW, Milligan HT, Morath S, Koricheva J (2015) Moose browsing alters tree
640 diversity effects on birch growth and insect herbivory. *Funct Ecol* 29:724–735. doi:
641 10.1111/1365-2435.12407

642 Naef-Daenzer B, Keller LF (1999) The foraging performance of great and blue tits (*Parus*
643 *major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for

644 nestling growth and fledging weight. *J Anim Ecol* 68:708–718. doi: 10.1046/j.1365-
645 2656.1999.00318.x

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

649 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R² from
650 generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142. doi:
651 10.1111/j.2041-210x.2012.00261.x

652 Poch TJ, Simonetti JA (2013) Insectivory in *Pinus radiata* plantations with different degree
653 of structural complexity. *For Ecol Manage* 304:132–136. doi:
654 10.1016/j.foreco.2013.04.044

655 Riihimäki J, Kaitaniemi P, Koricheva J, Vehviläinen H (2005) Testing the enemies
656 hypothesis in forest stands: the important role of tree species composition. *Oecologia*
657 142:90–7. doi: 10.1007/s00442-004-1696-y

658 Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats:
659 the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124. doi:
660 10.2307/1942161

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

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

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

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

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

673 Smith JNM, Dawkins R (1971) The hunting behaviour of individual great tits in relation to
674 spatial variations in their food density. *Anim Behav* 19:695–706. doi: 10.1016/S0003-
675 3472(71)80173-2

676 Sobek S, Scherber C, Steffan-Dewenter I, Tschardt T (2009) Sapling herbivory,
677 invertebrate herbivores and predators across a natural tree diversity gradient in
678 Germany's largest connected deciduous forest. *Oecologia* 160:279–288. doi:
679 10.1007/s00442-009-1304-2

680 Sperber CF, Nakayama K, Valverde MJ, Neves FDS (2004) Tree species richness and density
681 affect parasitoid diversity in cacao agroforestry. *Basic Appl Ecol* 5:241–251. doi:
682 10.1016/j.baae.2004.04.001

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

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

688 Straub CS, Simasek NP, Dohm R, et al (2014) Plant diversity increases herbivore movement
689 and vulnerability to predation. *Basic Appl Ecol* 15:50–58. doi:
690 10.1016/j.baae.2013.12.004

691 Strode PK (2009) Spring tree species use by migrating Yellow-Rumped Warblers in relation
692 to phenology and food availability. *Wilson J Ornithol* 121:457–468. doi: 10.1676/05-
693 148.1

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

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

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

700 Vehviläinen H, Koricheva J, Ruohomäki K (2008) Effects of stand tree species composition
701 and diversity on abundance of predatory arthropods. *Oikos* 117:935–943. doi:
702 10.1111/j.2008.0030-1299.15972.x

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

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

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

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

711 Zou Y, Sang W, Bai F, Axmacher JC (2013) Relationships between Plant Diversity and the
712 Abundance and α -Diversity of Predatory Ground Beetles (Coleoptera: Carabidae) in a
713 Mature Asian Temperate Forest Ecosystem. *PLoS One* 8:e82792. doi:
714 10.1371/journal.pone.0082792

715

716

717 TABLE

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

Spatial scale	Variable	χ^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	5.2	1	0.022	255.2	0.00	0.46	0.14 (0.31)
	insects							
	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	0.0	1	0.825	260.2	4.43	0.04	0.12 (0.23)
	damage							
(Alder only)	Concealed insects	3.1	1	0.076	153.3	0.00	0.33	0.29 (0.35)
	Insect herbivore	2.4	1	0.124	154.0	0.67	0.24	0.29 (0.35)
	damage							
	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	0.0	1	0.825	156.5	3.16	0.06	0.26 (0.31)
	insects							

727

728

729 FIGURES

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

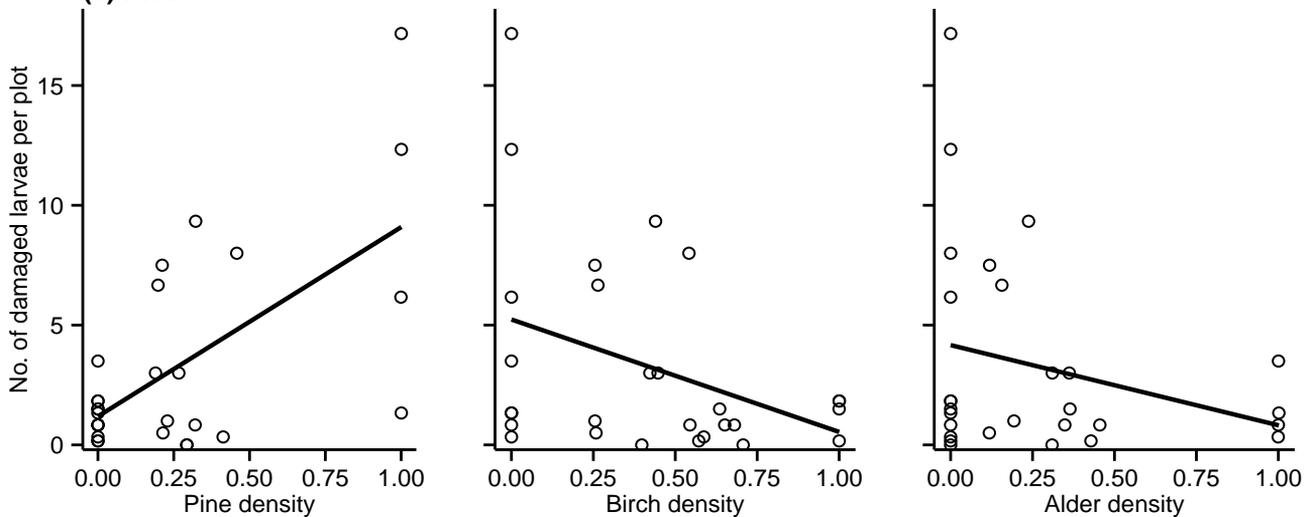
732

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

739

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

a**b****c**

(a) Plot**(b) Neighbourhood**