

1 Birds help plants – a meta-analysis of top-down trophic cascades  
2 caused by avian predators

3

4

5 **Elina Mäntylä<sup>1\*</sup>, Tero Klemola<sup>1</sup> and Toni Laaksonen<sup>1,2</sup>**

6

7 <sup>1</sup>Section of Ecology, Department of Biology, University of Turku, FI-20014 Turku, Finland

8 <sup>2</sup>Finnish Museum of Natural History, P.O Box 17, FI-00014 University of Helsinki, Finland

9 \*Correspondence, e-mail: elkuma@utu.fi, phone: +358 2 333 5039, fax: +358 2 333 6550

10 **Abstract**

11

12 The tritrophic interactions between plants, herbivores and avian predators are complex and  
13 prone to trophic cascades. We conducted a meta-analysis of original articles that have studied  
14 birds as predators of invertebrate herbivores, to compare top-down trophic cascades with  
15 different plant responses from different environments and climatic areas. Our search found 29  
16 suitable articles, with a total of 81 separate experimental study set-ups. The meta-analysis  
17 revealed that plants benefited from the presence of birds. A significant reduction was  
18 observed in the level of leaf damage and plant mortality. The presence of birds also positively  
19 affected the amount of plant biomass, whereas effects on plant growth were negligible. There  
20 were no differences in the effects between agricultural and natural environments. Similarly,  
21 plants performed better in all climatic areas (tropical, temperate and boreal) when birds were  
22 present. Moreover, both mature plants and saplings gained benefits from the presence of  
23 birds. Our results show that birds cause top-down trophic cascades and thus they play an  
24 integral role in ecosystems.

25

26

27 **Keywords**

28

29 Herbivory, indirect effects, meta-analysis, predation, trophic interactions

## 30 **Introduction**

31

32 Ecosystems are usually seen as being controlled by either top-down (consumer-driven) or  
33 bottom-up (resource-driven) mechanisms (Hunter and Price 1992; Polis et al. 1997). If an  
34 ecosystem is productive enough to facilitate the existence of vertebrate predators, the  
35 “ecosystem exploitation hypothesis” predicts that predators keep the population sizes of the  
36 folivorous prey low, thus, enabling plants to grow and reproduce (Hairston et al. 1960;  
37 Oksanen et al. 1981; Oksanen and Oksanen 2000). Bottom-up controlled ecosystems, in  
38 contrast, are considered to be shaped more by inorganic resources than by predation  
39 (Slobodkin 1960; Polis and Strong 1996). In both top-down and bottom-up controlled  
40 systems there may occur trophic cascades; linear interactions inside ecosystem food webs that  
41 typically include a plant, an herbivore and a predator (Persson 1999; Schmitz et al. 2004).  
42 Information on trophic cascades may help to understand, for example, the effects of top  
43 predator removal on the remaining ecosystem or stability properties of communities that are  
44 disturbed by action of humans (Paine 1980; Pace et al. 1999). It is commonly thought that  
45 ecosystems are more complex, and thus clear evidence of trophic cascades more rare, in  
46 species-rich tropical areas and natural environments than in colder climates and agricultural  
47 monocultures (Strong 1992; Polis and Strong 1996).

48

49 Carnivorous birds are common in ecosystems throughout the world and there have been  
50 numerous studies showing that they can have negative effects on the population sizes of  
51 insects and other small herbivores (e.g. Holmes 1979; Fowler et al. 1991; Williams-Guillén et  
52 al. 2008). At the same time, herbivores can cause notable damage to plants (e.g. Marquis  
53 1984; Bejer 1988; Mattson et al. 1988). To combine these two interactions, an increasing  
54 number of studies have also examined the effect of bird predation on plant herbivores

55 cascading down to plants (e.g. Marquis and Whelan 1994; Strong et al. 2000; Van Bael et al.  
56 2003). Multitrophic studies are warranted because studies with two trophic levels (e.g. plant –  
57 herbivore or predator – herbivore) at a time do not necessarily reveal the interactions among  
58 all three (or more) trophic levels. This is because the separate two-trophic level studies are  
59 seldom conducted at the same time or the same place, or with species common to both  
60 interactions. A recent review assessed the importance of birds in reducing plant damage  
61 mainly in forests and agricultural environments in the tropics (Van Bael et al. 2008), and  
62 another one documented the top-down cascading effects of vertebrate insectivores in general  
63 (Mooney et al. 2010), but as yet there has been no analysis whether bird-driven trophic  
64 cascades differ among climatic areas, including temperate and boreal forests. In addition,  
65 plant characteristics which gain benefits from the presence of birds remain to be explored. To  
66 answer these questions, we conducted a meta-analysis of original studies on potential trophic  
67 cascades from birds to plants. A meta-analysis is the best way to combine the results of  
68 independent studies to discover if there is a shared pattern among them (Gurevitch and  
69 Hedges 2001).

70

71 Our analyses serve several purposes. First, we measure the overall effect size of the presence  
72 of birds cascading down to plants, and thereafter we resolve with subgroup analyses whether  
73 the strength of the effect varies according to the climatic area (tropical, temperate or boreal),  
74 or the type of environment (agricultural or natural). Thus, these analyses test ideas that  
75 predators would be more effective in creating top-down cascades in agricultural  
76 monocultures and in colder climates (Polis and Strong 1996). Second, we identify with  
77 subgroup analyses whether there are differences in plant responses between the different  
78 types of measures the researchers have studied (leaf damage, biomass, growth or mortality)  
79 or between the age of the plants studied (mature or sapling). These analyses help to evaluate

80 how long-lasting the effect is and to focus future research on the appropriate measures of  
81 plant performance. Third, there is interest in measuring the ecosystem services provided by  
82 birds, and the removal of herbivores from harvested plants is certainly a potential service  
83 with economic value (Sekercioglu 2006a, 2006b; Whelan et al. 2008).

84

85 Knowing the importance of birds to plants is also a key element in understanding co-  
86 evolution in the trophic interactions among birds, herbivores and plants. For example, recent  
87 studies have shown that birds can find an insect-rich tree on the basis of cues from the host  
88 plant, without seeing either the herbivores or the damaged leaves (Mäntylä et al. 2004, 2008a,  
89 2008b). This suggests that to reduce the amount of herbivory, plants may have evolved  
90 induced responses that attract birds. Alternatively, these signals may be unspecific to birds  
91 (Mäntylä et al. 2008a). This kind of co-evolution between plants and birds may change the  
92 way we think about other trophic interactions. The plant-bird interactions include the  
93 relationships between herbivorous insects and their host plants, already known to be complex  
94 (e.g. Agrawal 1999; Engelberth et al. 2004; Vehviläinen et al. 2006), between insects that try  
95 to hide from birds (e.g. Heinrich and Collins 1983) and birds that vary in their preference for  
96 different prey (e.g. Kaspari and Joern 1993; Lindström et al. 1999). Thus, to get a broader  
97 view on how co-evolution may work within these multitrophic systems, we need to know  
98 whether plants benefit from the presence of birds that remove herbivores from plants.

99

100

## 101 **Methods**

102

103 To obtain a comprehensive set of studies for our meta-analysis, we searched online databases:  
104 ISI Web of Science, Biological Abstracts and BIOSIS Previews; with different combinations

105 of the following keywords: bird\*, avia\*, herbivor\*, predat\*, interacti\*, insect\*, indirect\* and  
106 trophic\*. The last online search was conducted in June 2010. We also checked the references  
107 of papers already retrieved and previous review articles about tritrophic interactions that  
108 included birds.

109

110 The articles included in the meta-analysis had to fulfil the following requirements: 1) At least  
111 one of the predators in the studied system had to be a bird species; 2) The experiment needed  
112 to contrast two groups, one of which contained a substantially lower level of bird predation  
113 than the other (usually stated as experimental and control groups); 3) There had to be at least  
114 one measured response from the plants, e.g. the extent of leaf damage, or changes in biomass,  
115 growth or mortality; 4) Sample sizes and means, with their deviation terms, had to be  
116 indicated, for both experimental and control groups.

117

118 In the articles accepted to our meta-analysis, the researchers had in some cases measured a  
119 certain response several times either within single or successive growing seasons (in 11 of the  
120 29 articles). To avoid bias, we chose only one occasion from these experiments (in total 30  
121 experiments or study set-ups, which included 2–4 measurement occasions each). Several  
122 methods have been used to do the choice: e.g. the last measurement of the original studies  
123 (e.g. Gurevitch et al. 2000), the mean of all measurements (e.g. Rustad et al. 2001), or the  
124 value with the largest effect size (i.e. the difference among experimental and control group  
125 means) (e.g. Koricheva et al. 1998). The use of last measurement seemed biologically  
126 inappropriate here since it was always the researchers' decision when to end the experiment.  
127 The correlation between the mean and maximum effect sizes in our data was so strong ( $r =$   
128 0.98,  $N = 30$  experiments) that the results of the meta-analysis were essentially the same

129 using either one of these two measures. From these two we present the results with the largest  
130 effect size, because high instantaneous damage can be more critical to plants than the long-  
131 term average level of encountered herbivory (Doak 1992; Leimu and Lehtilä 2006).

132

133 For the article by Atlegrim (1989), we conducted a separate meta-analysis to combine the  
134 five relatively similar forest areas that had been reported separately and used the attained  
135 effect size value and variation for our analyses. If researchers had used several plant or bird  
136 species in the same experiment, they were all included separately in the analyses. Similarly,  
137 we also treated all experiments within a single study as independent studies if they had been  
138 conducted in different types of environments (e.g. moist and dry forest), or if they had studied  
139 mature plants and saplings separately. For the overall result of all studies (“one response per  
140 study set-up” group), we used only one measured plant response (with the largest absolute  
141 value of effect size) of each species, environment and/or plant age.

142

143 In total we found 29 original articles that met the criteria as indicated above (Table 1). A  
144 further four possible studies (Loyn et al. 1983; Ritchie 2000; Gruner 2004; Mooney and  
145 Linhart 2006) were also found relevant in their ecological context but these lacked the  
146 necessary data to conduct meta-analytic calculations. Our four criteria excluded large  
147 numbers of articles, where cascading effects on the plant level were not considered, even  
148 though they reported significant effects of the birds on their arthropod prey communities (e.g.  
149 Holmes 1979; Joern 1986; Fowler et al. 1991; Floyd 1996; Borkhataria et al. 2006). The 29  
150 articles included in the meta-analysis had a total of 81 different experiments or study set-ups,  
151 which were used as independent studies in the analysis. The “one response per study set-up”  
152 group had 44 study set-ups. This group was used for the analysis of the overall effect. The  
153 study habitats ranged from Neotropical forests to intertidal shores and from Hawaiian forests

154 to apple orchards, consisting of a wide range of study species. However, apart from four  
155 studies (Bock et al. 1992; Wootton 1992, 1995; Hooks et al. 2003), the plant species under  
156 study were low-growing woody shrubs, trees or forest stands. The most common trees were  
157 species of oak (*Quercus* spp.; Table 1). In several studies there were no efforts to specify the  
158 herbivores or birds and they were merely labelled as “leaf-chewing insects”, “arthropods” or  
159 “insectivorous birds”. Although the majority of studies had excluded birds from certain areas  
160 or plants with nets or cages (Table 1), there were two exceptions. Sanz (2001) instead used  
161 the addition of birds, and Murakami and Nakano (2000) used bird enclosures and bird  
162 enclosures to test their hypotheses. Although these two studies did not contain only  
163 enclosures, we hereafter, for the sake of simplicity, use terms “bird exclusion” and “bird  
164 enclosures” to indicate the “non-bird group” of each study. Exclosure sizes (mentioned only  
165 in 15 original articles) ranged from 0.1 to over 450 m<sup>2</sup>, and this did not correlate with the  
166 effect size of the plant response ( $r = 0.13$ ,  $N = 15$  experiments). The most common plant  
167 response surveyed was some measure of leaf damage, while some studies also measured  
168 biomass, growth or mortality. We also noted whether the study plants were mature or  
169 saplings (including seedlings). Two studies by Wootton (1992, 1995) were omitted from this  
170 category as he used aquatic study plants (algae), which cannot be categorised similarly as  
171 terrestrial plants examined in all other studies. In many cases, the researchers were also  
172 interested in other factors together with bird exclusion, e.g. fertilization, insecticides or  
173 invertebrate predators. However, because these factors were not of interest in this review, we  
174 used values of treatments that included only avian predators.

175

#### 176 *Studies not included in the meta-analysis*

177 Loyn et al. (1983) and Ritchie (2000) were not included in the meta-analysis because they did  
178 not give the required deviation terms. Loyn et al. (1983) found that other bird species than



179 bell miners (*Manorina melanophrys*) were useful to eucalyptuses, while the bell miners were  
180 not. Ritchie (2000) showed that bird exclosures had a small effect on grasses eaten by  
181 grasshoppers. Additionally, we were unable to use the studies of Gruner (2004) and Mooney  
182 and Linhart (2006), because they had reported their results as effect sizes, which were  
183 impossible to transform to correspond to our effect sizes. Gruner (2004) reported that the  
184 effects of bird exclusion on the dominant tree species in Hawaiian forests varied during the  
185 study but the difference between exclosure and control plots was never significant. Mooney  
186 and Linhart (2006) found that avian exclosures reduced pine wood growth as birds were  
187 connected to pine by a linear food chain via aphids, whereas effects on mistletoe were  
188 negligible due to more reticulate food web and birds as intraguild predators.

189

#### 190 *Statistical methods*

191 We used MetaWin v. 2.1 (Rosenberg et al. 2000) to calculate standardized effect sizes as a  
192 log response ratio [ $\ln R = \ln(\text{control mean}) - \ln(\text{experimental mean})$ ]. The use of  $\ln R$  (instead  
193 of Hedges'  $d$  or other measures of effect size) has recently become more common in  
194 biological studies because it assumes that effects can be multiplicative and is less sensitive to  
195 errors (Morris et al. 2007). We used random effect models and ran resampling tests with 4999  
196 iterations to get 95% bias-corrected bootstrap confidence intervals. Here, effect size values  
197 below zero indicated that the control group (birds present) was more beneficial to plants than  
198 the experimental group (birds absent). All studies were modified with a reversal marker  
199 column of MetaWin ('+' sign for measurements of growth or biomass, and '-' sign for  
200 measurements of leaf damage, mortality or infestation level), so that if plants benefited from  
201 birds then the effect size value was below zero. For the subgroup summary analyses, we  
202 calculated the heterogeneity statistic  $Q$ , in MetaWin. As with variance in ANOVA, the total  
203 heterogeneity  $Q_T$  can be partitioned into  $Q_M$ , the variation explained by the model and

204 reported in the results, and  $Q_E$ , the residual error variance (Rosenberg et al. 2000). A  
205 statistically significant variance among the effect sizes means that the variance is greater than  
206 expected by sampling error alone (Cooper 1998).

207

208 We used three methods, which are simple to interpret and often used in meta-analytical  
209 studies (Gurevitch et al. 1992; Kaplan and Denno 2007; Salo et al. 2007), to estimate if the  
210 available data suffer from publication bias. Publication bias can be studied by the funnel plot  
211 method, where the observed effect size is plotted against sample size (Palmer 1999). If there  
212 is no publication bias more variation should occur in effect sizes of smaller studies than in  
213 larger studies causing a funnel-shaped plot (Gates 2002). Additionally, Rosenthal's fail-safe  
214 number method can be used to test for selective reporting by calculating how many studies  
215 with a zero effect size would be needed to make the result of the meta-analysis non-  
216 significant (Rosenthal 1979). Finally, one more method involves visual estimation of the  
217 normal quantile plot where standardised effect size values are plotted against normal quantile  
218 values. If the points remain close to the line  $x = y$  there should not be publication bias.

219

220

221

## 222 **Results**

223

224 The plants generally benefited from bird presence (i.e. control plants were in better condition  
225 than plants inside bird enclosures) as the overall effect size and its confidence interval (CI)  
226 were clearly less than zero ( $\ln R = -0.367$ , 95% CI = -0.500 to -0.237). The variation in effect  
227 sizes (total heterogeneity) was statistically significant ( $Q_T = 61.59$ ,  $df = 43$ ,  $p = 0.033$ ),  
228 indicating greater total heterogeneity than can be expected by sampling error alone. This

229 could be expected in our meta-analysis because we compiled studies conducted in different  
230 places with different methods, species and response variables.

231

232 There were no significant differences in plant responses between natural and agricultural  
233 environments ( $Q_M = 0.64$ ,  $df = 1$ ,  $p = 0.45$ ) (Fig. 1a) or among different climatic areas ( $Q_M =$   
234  $0.34$ ,  $df = 2$ ,  $p = 0.87$ ) (Fig. 1b). Similarly, the effects of bird exclusion did not differ between  
235 mature plants and saplings ( $Q_M = 1.99$ ,  $df = 1$ ,  $p = 0.18$ ) (Fig. 1c). There were, however,  
236 significant differences among different plant responses ( $Q_M = 12.95$ ,  $df = 3$ ,  $p = 0.014$ ) (Fig.  
237 1d). Plants inside bird enclosures had significantly more leaf damage and mortality, and they  
238 lost more biomass than those outside the enclosures where birds were allowed to prey on  
239 herbivores (Fig. 1d). In contrast, there was no clear effect of bird exclusion on the growth of  
240 plants (Fig. 1d).

241

#### 242 *Publication bias*

243 As the data points of the 44 studies used in the overall effect meta-analysis stayed inside the  
244 95 % confidence limits, our data were normally distributed and thus did not show deviation  
245 that could be interpreted as evidence of publication bias (Electronic Supplemental Material  
246 1). The Rosenthal's fail-safe number method to test for selective reporting (i.e. publication  
247 bias) gave a result of 2125.3, which is very high, considering that our data consisted of only  
248 81 experiments and of those, only 44 were used in the combined overall analysis. According  
249 to the funnel plot method, there was slightly more variation in effect sizes among  
250 experiments with small sample sizes than among those with larger sample sizes (Electronic  
251 Supplemental Material 2)

252

253

**254 Discussion**

255

256 The results of our meta-analysis show that the effects of birds eating herbivorous insects and  
257 other small prey cascade down to the plant level. Although it has generally been thought that  
258 trophic cascades are stronger in simple ecosystems (agricultural environments and colder  
259 climatic areas) than in more complex ones (natural environments and warmer climatic areas)  
260 (Strong 1992; Polis and Strong 1996), our results do not support this hypothesis. Among the  
261 original research articles used in our study, the authors found evidence of trophic cascades in  
262 several natural systems: boreal (Atlegrim 1989; Sipura 1999; Strengbom et al. 2005; Mooney  
263 2007), temperate (Wootton 1992, 1995; Marquis and Whelan 1994; Forkner and Hunter  
264 2000; Murakami and Nakano 2000; Strong et al. 2000; Lichtenberg and Lichtenberg 2002;  
265 Mazía et al. 2004, 2009; Barber and Marquis 2009; Bridgeland et al. 2010; Garibaldi et al.  
266 2010), Mediterranean (Sanz 2001), and tropical (Van Bael et al. 2003; Van Bael and Brawn  
267 2005; Boege and Marquis 2006; Dunham 2008; Kalka et al. 2008). Similar evidence was  
268 found in agricultural systems in temperate (Mols and Visser 2002), as well as in tropical areas  
269 (Greenberg et al. 2000; Hooks et al. 2003; Van Bael et al. 2007; Kellermann et al. 2008; Koh  
270 2008). Thus, birds were beneficial to plants in multiple habitats, and the agricultural  
271 monocultures or species-rich tropics did not differ from natural regions or boreal forests,  
272 indicating that trophic cascades can also exist in more complex ecosystems.

273

274 When all predators of herbivores (avian, mammalian, invertebrate) are taken into  
275 consideration, meta-analyses of terrestrial tritrophic cascades have shown that predator-  
276 exclusion benefits herbivorous arthropods more than harms plants (Halaj and Wise 2001;  
277 Mooney et al. 2010), but that vertebrate carnivores usually have a stronger impact than  
278 invertebrate predators (Schmitz et al. 2000). Moreover, previous reviews of terrestrial trophic

279 cascades have often used a large variety of predators where the specific effects of one  
280 predator group (e.g. birds) are often confounded among the diversity of study set-ups (e.g.  
281 Shurin et al. 2002). Thus, our main result concerning the trophic cascade from birds to plants  
282 corroborates the importance of vertebrate predators in such cascades (see also e.g. Kalka et  
283 al. 2008). It must be noted that none of the experiments had extremely high densities of  
284 herbivores. Since carnivorous birds are usually considered generalist predators showing  
285 relatively slow numerical response to an increase in prey density, it is unlikely that birds  
286 could consume a considerable amount of herbivores in a high density situation, e.g., during  
287 outbreaks of forest lepidopterans (Hogstad 2005). However, Fayt et al. (2005) found out that  
288 at least three-toed woodpeckers can regulate bark beetles of spruces and Loyn et al. (1983)  
289 showed that some bird species can eradicate psyllids from eucalypt forest patches.

290

291 Plants outside bird exclosures had less leaf damage and mortality, and higher biomass than  
292 those inside the exclosures (Fig. 1d). By contrast, plant growth did not seem to be affected by  
293 avian exclosure (Fig. 1d), which may be due to the relatively short duration of most of the  
294 research projects reviewed (from 23 days to 36 months, median 12 months), combined with  
295 the plants' ability to compensate for losses due to herbivory (Schmitz et al. 2000). When  
296 researchers had measured several plant responses, leaf damage was usually the measure most  
297 affected (e.g. Marquis and Whelan 1994; Strong et al. 2000; Boege and Marquis 2006;  
298 Dunham 2008; Van Bael et al. 2007). This is not surprising given that leaf damage is the first  
299 sign of herbivory. However, measuring only the amount of damaged leaves/removed leaf area  
300 does not always explain how damaging herbivory is to the fitness of a plant over time. The  
301 study by Mols and Visser (2002) is a notable exception because they recorded the amount of  
302 fruits that apple trees (*Malus domestica*) produced, while in another agricultural study, Hooks  
303 et al. (2003) measured the biomass of broccoli heads (*Brassica oleracea*). Both studies found

304 that the presence of birds increased the crop of these plants. Additional studies with measures  
305 of plant fitness, particularly in natural environments, would offer more knowledge about the  
306 long-lasting effects of the bird-driven trophic cascades in multitrophic systems.

307

308 Mature plants and saplings showed a similar response to bird presence (Fig. 1c), although,  
309 young saplings tend to be dominated more by bottom-up than top-down effects (Hunter and  
310 Price 1992). While most of the studies used insects or other arthropods as herbivores and  
311 trees as plants, there were some exceptions. Two studies were made on an intertidal shore  
312 with algivorous limpets and sea urchins (Wootton 1992, 1995), with very pronounced effects  
313 due to bird exclusion. In addition to these, only two other studies were conducted on plants  
314 other than low-growing woody shrubs, trees or forest stands (Bock et al. 1992; Hooks et al.  
315 2003). Thus, our results mostly apply to how woody plants react to bird exclusion. It is  
316 however noteworthy that of the four studies with non-woody plants, only Bock et al. (1992)  
317 found no effect of avian exclusion, while the other three showed that birds reduced herbivore-  
318 damage. Other studies that found no evidence for plants deriving benefit from birds had, for  
319 example, examined plants that have strong chemical defences (*Salix myrsinifolia*; Sipura  
320 1999) and are thus avoided by herbivorous insects (Kolehmainen et al. 1995). The choice of  
321 bird species could also affect the results, as in Murakami and Nakano (2000) where  
322 nuthatches (*Sitta europaea*) preferred to search for insects from tree trunks rather than from  
323 leaves. More large-scale and/or long-term experiments with a larger assortment of birds,  
324 herbivores and plants would nevertheless be needed for a more comprehensive view of the  
325 generality of the mutualistic relationship between birds and plants.

326

327 As yet totally unexplored potential trophic cascades include for example the ones caused by  
328 birds of prey that eat small herbivorous mammals (such as voles). Many predator reduction

329 experiments have already been undertaken with voles or lemmings and their predators  
330 (reviewed in Sundell 2006). However, the plant responses are often not reported at all. If they  
331 are reported, they cannot be separated between the different predator groups (mammalian,  
332 avian or reptilian), because all predators are usually excluded (see e.g. Norrdahl et al. 2002;  
333 Aunapuu et al. 2008). Incorporating measures of plant responses to these studies would  
334 widen our understanding of the effects of birds in trophic cascades among different  
335 ecosystems.

336

337 Our test for publication bias with the funnel and normal quantile plots (Electronic  
338 Supplemental Material 1, 2) did not produce results of strong bias, and the Rosenthal's fail-  
339 safe number method showed that over two thousand studies with an effect size of zero would  
340 be needed to make our result non-significant. No review however can cover studies if they  
341 are unpublished, and thus, our results of the meta-analysis may be a small overestimate of the  
342 actual effect of birds helping plants (Kotiaho and Tomkins 2002). In any case, our meta-  
343 analytic data set provides strong support that birds are commonly beneficial to plants.

344

345 In conclusion, our meta-analysis supported the finding that plants benefit from birds that  
346 remove their herbivores and that globally there are no differences in this phenomenon  
347 throughout a variety of environments and climatic areas. This work and some other recent  
348 studies (Sekercioglu 2006a, b; Van Bael et al. 2008; Whelan et al. 2008) have thus shown  
349 that birds are beneficial to plants and form an integral part of ecosystems. In this light it is  
350 worrying that many bird populations are in heavy decline (e.g. Sekercioglu 2004; BirdLife  
351 International 2008). The ecosystem services provided by birds are important not only for the  
352 functioning of natural ecosystems but also for pest control in agriculture and forestry  
353 (Sekercioglu 2006a). If bird populations decline, these services are not easily replaced by any

354 other taxa, especially in the tropics where specialisation is high (Sherry 1984; Sigel et al.  
355 2010). This emphasises the societal value of birds and the need for conserving bird  
356 populations.

357

358

### 359 **Acknowledgements**

360

361 We would like to thank Pälvi Salo for help and advice. Thanks are also due to Christiaan  
362 Both, Leena Lindström, Lauri Oksanen, Cagan Sekercioglu, three anonymous reviewers and  
363 the graduate student seminar at the section of ecology (Univ. Turku), for giving valuable  
364 comments. Kevin O'Brien checked the language. The study was financially supported by the  
365 Jenny and Antti Wihuri Foundation (grant to E.M.), Academy of Finland (decision numbers  
366 111195 and 129143 to T.K.) and the Emil Aaltonen Foundation (grant to T.L.).

367

368

### 369 **References**

370

371 Agrawal AA (1999) Induced responses to herbivory in wild radish: Effects on several  
372 herbivores and plant fitness. *Ecology* 80:1713–1723. doi: 10.2307/176559

373 Atlegrim O (1989) Exclusion of birds from bilberry stands: impact on insect larval density  
374 and damage to the bilberry. *Oecologia* 79:136–139. doi: 10.1007/BF00378251

375 Aunapuu M, Dahlgren J, Oksanen T, Grellmann D, Oksanen L, Olofsson J, Rammul Ü,  
376 Schneider M, Johansen B, Hygen HO (2008) Spatial patterns and dynamic responses of  
377 arctic food webs corroborate the Exploitation Ecosystems Hypothesis (EEH). *Am Nat*  
378 171:249–262. doi: 10.1086/524951



- 379 Barber NA, Marquis RJ (2009) Spatial variation in top-down direct and indirect effects on  
380 white oak (*Quercus alba* L.). *Am Midl Nat* 162:169–179. doi: 10.1674/0003-0031-  
381 162.1.169
- 382 Bejer B (1988) The nun moth in European spruce forests. In: Berryman AA (ed) *Dynamics of*  
383 *forest insect populations: patterns, causes, implications*. Plenum Press, New York, pp  
384 211–231.
- 385 BirdLife International (2008) *State of the world’s birds: indicators for our changing world*.  
386 BirdLife International, Cambridge, UK.
- 387 Bock CE, Bock JH, Grant MC (1992) Effects of bird predation on grasshopper densities in an  
388 Arizona grassland. *Ecology* 73:1706–1717. doi: 10.2307/1940022
- 389 Boege K, Marquis RJ (2006) Plant quality and predation risk mediated by plant ontogeny:  
390 consequences for herbivores and plants. *Oikos* 115:559–572. doi: 10.1111/j.2006.0030-  
391 1299.15076.x
- 392 Borkhataria RR, Collazo JA, Groom MJ (2006) Additive effects of vertebrate predators on  
393 insects in a Puerto Rican coffee plantation. *Ecol Appl* 16:696–703. doi: 10.1890/1051-  
394 0761(2006)016[0696:AEOVPO]2.0.CO;2
- 395 Bridgeland WT, Beier P, Kolb T, Whitham T (2010) A conditional trophic cascade: Birds  
396 benefit faster growing trees with strong links between predators and plants. *Ecology*  
397 91:73–84. doi: 10.1890/08-1821.1
- 398 Cooper H (1998) *Synthesizing research: a guide for literature reviews*, 3<sup>rd</sup> edn. Sage,  
399 Thousand Oaks.
- 400 Doak DF (1992) Lifetime impacts of herbivory for a perennial plant. *Ecology* 73:2086–2099.  
401 doi: 10.2307/1941457
- 402 Dunham AE (2008) Above and below ground impacts of terrestrial mammals and birds in a  
403 tropical forest. *Oikos* 117:571–579. doi: 10.1111/j.2007.0030-1299.16534.x

- 404 Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH (2004) Airborne signals prime plants  
405 against insect herbivore attack. *Proc Natl Acad Sci USA* 101:1781–1785. doi:  
406 10.1073/pnas.0308037100
- 407 Fayt P, Machmer MM, Steeger C (2005) Regulation of spruce bark beetles by woodpeckers –  
408 a literature review. *Forest Ecol Manag* 206:1–14. doi: 10.1016/j.foreco.2004.10.054
- 409 Floyd T (1996) Top-down impacts on creosotebush herbivores in a spatially and temporally  
410 complex environment. *Ecology* 77:1544–1555. doi: 10.2307/2265550
- 411 Forkner RE, Hunter MD (2000) What goes up must come down? Nutrient addition and  
412 predation pressure on oak herbivores. *Ecology* 81:1588–1600. doi: 10.2307/177309
- 413 Fowler AC, Knight RL, Luke George T, McEwen LC (1991) Effects of avian predation on  
414 grasshopper populations in North Dakota grasslands. *Ecology* 72:1775–1781. doi:  
415 10.2307/1940976
- 416 Garibaldi LA, Kitzberger T, Mazía N, Chaneton EJ (2010) Nutrient supply and bird predation  
417 additively control insect herbivory and tree growth in two contrasting forest habitats.  
418 *Oikos* doi: 10.1111/j.1600-0706.2009.17862.x
- 419 Gates S (2002) Review of methodology of quantitative reviews using meta-analysis in  
420 ecology. *J Anim Ecol* 71:547–557. doi: 10.1046/j.1365-2656.2002.00634.x
- 421 Greenberg R, Bichier P, Cruz Angon A, MacVean C, Perez R, Cano E (2000) The impact of  
422 avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations.  
423 *Ecology* 81:1750–1755. doi: 10.2307/177321
- 424 Gruner DS (2004) Attenuation of top-down and bottom-up forces in a complex terrestrial  
425 community. *Ecology* 85:3010–3022. doi: 10.1890/04-0020
- 426 Gurevitch J, Hedges LV (2001) Meta-analysis. In: Scheiner SM, Gurevitch J (eds) *Design*  
427 *and analysis of ecological experiments*. Oxford University Press, New York, pp 347–369.

- 428 Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and  
429 predation: a meta-analysis of field experiments. *Am Nat* 155:435–453. doi:  
430 10.1086/303337
- 431 Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in  
432 field experiments. *Am Nat* 140:539–572. doi: 10.1086/285428
- 433 Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and  
434 competition. *Am Nat* 94:421–425. doi: 10.1086/282146
- 435 Halaj J, Wise DH (2001) Terrestrial trophic cascades: How much do they trickle? *Am Nat*  
436 157:262–281. doi: 10.1086/319190
- 437 Heinrich B, Collins SL (1983) Caterpillar leaf damage, and the game of hide-and-seek with  
438 birds. *Ecology* 64:592–602. doi: 10.2307/1939978
- 439 Hogstad O (2005) Numerical and functional responses of breeding passerine species to mass  
440 occurrence of geometrid caterpillars in a subalpine birch forest: A 30-year study. *Ibis*  
441 147:77–91. doi: 10.1111/j.1474-919x.2004.00338
- 442 Holmes RT, Schultz JC, Nothnagle P (1979) Bird predation on forest insects: an enclosure  
443 experiment. *Science* 206:462–463. doi: 10.1126/science.206.4417.462
- 444 Hooks CRR, Pandey RR, Johnson MW (2003) Impact of avian and arthropod predation of  
445 lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem.  
446 *Ecol Entomol* 28:522–532. doi: 10.1046/j.1365-2311.2003.00544.x
- 447 Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles  
448 of bottom-up and top-down forces in natural communities. *Ecology* 73:724–732.
- 449 Joern A (1996) Experimental study of avian predation on coexisting grasshopper populations  
450 (Orthoptera: Acrididae) in a sandhills grassland. *Oikos* 46:243–249. doi:  
451 10.2307/3565473

- 452 Kalka MB, Smith AR, Kalko EKV (2008) Bats limit arthropods and herbivory in a tropical  
453 forest. *Science* 320:71. doi: 10.1126/science.1153352
- 454 Kaplan I, Denno RF (2007) Interspecific interactions in phytophagous insects revisited: a  
455 quantitative assessment of competition theory. *Ecol Lett* 10:977–994. doi:  
456 10.1111/j.1461-0248.2007.01093.x
- 457 Kaspari M, Joern A (1993) Prey choice by three insectivorous grassland birds: reevaluating  
458 opportunism. *Oikos* 68:414–430. doi: 10.2307/3544909
- 459 Kellermann JL, Johnson MD, Stercho AM, Hackett SC (2008) Ecological and economic  
460 services provided by birds on Jamaican Blue Mountain coffee farms. *Conserv Biol*  
461 22:1177–1185. doi: 10.1111/j.1523-1739.2008.00968.x
- 462 Koh LP (2008) Birds defend oil palms from herbivorous insects. *Ecol Appl* 18:821–825. doi:  
463 10.1890/07-1650.1
- 464 Kolehmainen J, Julkunen-Tiitto R, Roininen H, Tahvanainen J (1995) Phenolic glucosides as  
465 feeding cues for willow-feeding leaf beetles. *Entomol Exp Appl* 74:235–243. doi:  
466 10.1007/BF02381787
- 467 Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed  
468 woody plants: a meta-analysis. *Annu Rev Entomol* 43:195–216. doi:  
469 10.1146/annurev.ento.43.1.195
- 470 Kotiaho JS, Tomkins JL (2002) Meta-analysis, can it ever fail? *Oikos* 96:551–553. doi:  
471 10.1034/j.1600-0706.2002.960316.x
- 472 Leimu R, Lehtilä K (2006) Effects of two types of herbivores on the population dynamics of  
473 a perennial herb. *Basic Appl Ecol* 7:224–235. doi: 10.1016/j.baae.2005.09.002
- 474 Lichtenberg JS, Lichtenberg DA (2002) Weak trophic interactions among birds, insects and  
475 white oak saplings (*Quercus alba*). *Am Midl Nat* 148:338–349. doi: 10.1674/0003-  
476 0031(2002)148[0338:WTIABI]2.0.CO;2

- 477 Lindström L, Alatalo RV, Mappes J (1999) Reactions of hand-reared and wild-caught  
478 predators toward warningly colored, gregarious, and conspicuous prey. *Behav Ecol*  
479 10:317–322. doi: 10.1093/beheco/10.3.317
- 480 Loyn RH, Runnalls RG, Forward GY, Tyers J (1983) Territorial bell miners and other birds  
481 affecting populations of insect prey. *Science* 221:1411–1413. doi:  
482 10.1126/science.221.4618.1411
- 483 Mäntylä E, Klemola T, Haukioja E (2004) Attraction of willow warblers to sawfly-damaged  
484 mountain birches: novel function of inducible plant defenses? *Ecol Lett* 7:915–918. doi:  
485 10.1111/j.1461-0248.2004.00653.x
- 486 Mäntylä E, Alessio GA, Blande JD, Heijari J, Holopainen JK, Laaksonen T, Piirtola P,  
487 Klemola T (2008a) From plants to birds: higher avian predation rates in trees responding  
488 to insect herbivory. *PLoS ONE* 3(7):e2832. doi: 10.1371/journal.pone.0002832
- 489 Mäntylä E, Klemola T, Sirkiä P, Laaksonen T (2008b) Low light reflectance may explain the  
490 attraction of birds to defoliated trees. *Behav Ecol* 19:325–330. doi:  
491 10.1093/beheco/arm135
- 492 Marquis RJ (1984) Leaf herbivores decrease fitness of a tropical plant. *Science* 226:537–539.  
493 doi: 10.1126/science.226.4674.537
- 494 Marquis RJ, Whelan CJ (1994) Insectivorous birds increase growth of white oak through  
495 consumption of leaf-chewing insects. *Ecology* 75:2007–2014. doi: 10.2307/1941605
- 496 Mattson WJ, Simmons GA, Witter JA (1988) The spruce budworm in eastern North America.  
497 In: Berryman AA (ed) *Dynamics of forest insect populations: patterns, causes,*  
498 *implications.* Plenum Press, New York, pp 309–330.
- 499 Mazía CN, Kitzberger T, Chaneton EJ (2004) Interannual changes in folivory and bird  
500 insectivory along a natural productivity gradient in northern Patagonian forests.  
501 *Ecography* 27:29–40. doi: 10.1111/j.0906-7590.2004.03641.x

- 502 Mazía CN, Chaneton EJ, Kitzberger T, Garibaldi LA (2009) Variable strength of top-down  
503 effects in *Nothofagus* forests: bird predation and insect herbivory during an ENSO event.  
504 *Austral Ecol* 34:359–367. doi: 10.1111/j.1442-9993.2009.01933.x
- 505 Mols CMM, Visser ME (2002) Great tits can reduce caterpillar damage in apple orchards. *J*  
506 *Appl Ecol* 39:888–899. doi: 10.1046/j.1365-2664.2002.00761.x
- 507 Mooney KA (2007) Tritrophic effects of birds and ants on a canopy food web, tree growth,  
508 and phytochemistry. *Ecology* 88:2005–2014. doi: 10.1890/06-1095.1
- 509 Mooney KA, Gruner DS, Barber NA, Van Bael SA, Philpott SM, Greenberg R (2010)  
510 Interactions among predators and the cascading effects of vertebrate insectivores on  
511 arthropod communities and plants. *Proc Natl Acad Sci USA* 107:7335–7340 doi:  
512 10.1073/pnas.1001934107
- 513 Mooney KA, Linhart YB (2006) Contrasting cascades: insectivorous birds increase pine but  
514 not parasitic mistletoe growth. *J Anim Ecol* 75:350–357. doi: 10.1111/j.1365-  
515 2656.2006.01054.x
- 516 Morris WF, Hufbauer RA, Agrawal AA, Bever JD, Borowicz VA, Gilbert GS, Maron JL,  
517 Mitchell CE, Parker IM, Power AG, Torchin ME, Vázquez DP (2007) Direct and  
518 interactive effects of enemies and mutualists on plant performance: a meta-analysis.  
519 *Ecology* 88:1021–1029. doi: 10.1890/06-0442
- 520 Murakami M, Nakano S (2000) Species-specific bird functions in a forest-canopy food web.  
521 *Proc R Soc B* 267:1597–1601. doi: 10.1098/rspb.2000.1184
- 522 Norrdahl K, Klemola T, Korpimäki E, Koivula M (2002) Strong seasonality may attenuate  
523 trophic cascades: vertebrate predator exclusion in boreal grassland. *Oikos* 99:419–430.  
524 doi: 10.1034/j.1600-0706.2002.12025.x
- 525 Oksanen L, Fretwell SD, Arruda J, Niemelä P (1981) Exploitation ecosystems in gradients of  
526 primary productivity. *Am Nat* 118:240–261. doi: 10.1086/283817

- 527 Oksanen L, Oksanen T (2000) The logic and realism of the hypothesis of exploitation  
528 ecosystems. *Am Nat* 155:703–723. doi: 10.1086/303354
- 529 Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse  
530 ecosystems. *Trends Ecol Evol* 14:483–488. doi: 10.1016/S0169-5347(99)01723-1
- 531 Paine RT (1980) Food webs: linkage, interaction strength and community infrastructure. *J*  
532 *Anim Ecol* 49:667–685.
- 533 Palmer AR (1999) Detecting publication bias in meta-analyses: A case study of fluctuating  
534 asymmetry and sexual selection. *Am Nat* 154:220–233. doi: 10.1086/303223
- 535 Persson L (1999) Trophic cascades: Abiding heterogeneity and the trophic level concept at  
536 the end of the road. *Oikos* 85:385–397. doi: 10.2307/3546688
- 537 Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web  
538 ecology: The dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316.  
539 doi: 10.1146/annurev.ecolsys.28.1.289
- 540 Polis GA, Strong DR (1996) Food web complexity and community dynamics. *Am Nat*  
541 147:813–846. doi: 10.1086/285880
- 542 Ritchie ME (2000) Nitrogen limitation and trophic vs. abiotic influences on insect herbivores  
543 in a temperate grassland. *Ecology* 81:1601–1612. doi: 10.2307/177310
- 544 Rosenberg MS, Adams DC, Gurevitch J (2000) METAWIN. Statistical software for meta-  
545 analysis. Version 2. Sinauer Associates, Inc, Massachusetts, MA.
- 546 Rosenthal R (1979) The “file drawer problem” and tolerance for null results. *Psychol Bull*  
547 86:638–641. doi: 10.1037/0033-2909.86.3.638
- 548 Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC,  
549 Gurevitch J, GCTE-NEWS (2001) A meta-analysis of the response of soil respiration, net  
550 nitrogen mineralization, and aboveground plant growth to experimental ecosystem  
551 warming. *Oecologia* 126:543–562. doi: 10.1007/s004420000544

- 552 Salo P, Korpimäki E, Banks PB, Nordström M, Dickman CR (2007) Alien predators are more  
553 dangerous than native predators to prey populations. *Proc R Soc B* 274:1237–1243. doi:  
554 10.1098/rspb.2006.0444
- 555 Sanz JJ (2001) Experimentally increased insectivorous bird density results in a reduction of  
556 caterpillar density and leaf damage to Pyrenean oak. *Ecol Res* 16:387–394. doi:  
557 10.1046/j.1440-1703.2001.00403.x
- 558 Schmitz OJ, Hambäck PA, Beckerman AP (2000) Trophic cascades in terrestrial systems: a  
559 review of the effects of carnivore removals on plants. *Am Nat* 155:141–153. doi:  
560 10.1086/303311
- 561 Schmitz OJ, Krivan V, Ovadia O (2004) Trophic cascades: the primacy of trait-mediated  
562 indirect interactions. *Ecol Lett* 7:153–163. doi: 10.1111/j.1461-0248.2003.00560.x
- 563 Sekercioglu CH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. *Proc*  
564 *Natl Acad Sci USA* 101:18042–18047. doi: 10.1073/pnas.0408049101
- 565 Sekercioglu CH (2006a) Ecological significance of bird populations. In: del Hoyo J, Elliott  
566 A, Christie DA (eds) *Handbook of the Birds of the World v.11*. Lynx Edicions,  
567 Barcelona, pp 15–51.
- 568 Sekercioglu CH (2006b) Increasing awareness of avian ecological function. *Trends Ecol Evol*  
569 21:464–471. doi: 10.1016/j.tree.2006.05.007
- 570 Sherry TW (1984) Comparative dietary ecology of sympatric, insectivorous neotropical  
571 flycatchers (Tyrannidae). *Ecol Monogr* 54:313–338. doi: 10.2307/1942500
- 572 Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, Broitman B, Cooper SD,  
573 Halpern BS (2002) A cross-ecosystem comparison of the strength of trophic cascades.  
574 *Ecol Lett* 5:785–791. doi: 10.1046/j.1461-0248.2002.00381.x



- 575 Sigel BJ, Robinson WD, Sherry TW (2010) Comparing bird community responses to forest  
576 fragmentation in two lowland Central American reserves. *Biol Conserv* 143:340–350. doi:  
577 10.1016/j.biocon.2009.10.020
- 578 Sipura M (1999) Tritrophic interactions: willows, herbivorous insects and insectivorous birds.  
579 *Oecologia* 121:537–545. doi: 10.1007/s004420050960
- 580 Slobodkin LB (1960) Ecological energy relationships at the population level. *Am Nat*  
581 94:213–236. doi: 10.1086/282124
- 582 Strengbom J, Witzell J, Nordin A, Ericson L (2005) Do multitrophic interactions override N  
583 fertilization effects on *Operophtera* larvae? *Oecologia* 143:241–250. doi:  
584 10.1007/s00442-004-1799-5
- 585 Strong AM, Sherry TW, Holmes RT (2000) Bird predation on herbivorous insects: indirect  
586 effects on sugar maple saplings. *Oecologia* 125:370–379. doi: 10.1007/s004420000467
- 587 Strong DR (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose  
588 ecosystems. *Ecology* 73:747–754. doi: 10.2307/1940154
- 589 Sundell J (2006) Experimental tests of the role of predation in the population dynamics of  
590 voles and lemmings. *Mammal Rev* 36:107–141. doi: 10.1111/j.1365-2907.2006.00083.x
- 591 Van Bael SA, Bichier P, Greenberg R (2007) Bird predation on insects reduces damage to the  
592 foliage of cocoa trees (*Theobroma cacao*) in western Panama. *J Trop Ecol* 23:715–719.  
593 doi: 10.1017/S0266467407004440
- 594 Van Bael SA, Brawn JD (2005) The direct and indirect effects of insectivory by birds in two  
595 contrasting Neotropical forests. *Oecologia* 143:106–116. doi: 10.1007/s00442-004-1774-1
- 596 Van Bael SA, Brawn JD, Robinson SK (2003) Birds defend trees from herbivores in a  
597 Neotropical forest canopy. *Proc Natl Acad Sci USA* 100:8304–8307. doi:  
598 10.1073/pnas.1431621100

- 599 Van Bael SA, Philpott SM, Greenberg R, Bichier P, Barber NA, Mooney KA, Gruner DS  
600 (2008) Birds as predators in tropical agroforestry systems. *Ecology* 89:928–934. doi:  
601 10.1890/06-1976.1
- 602 Vehviläinen H, Koricheva J, Ruohomäki K, Johansson T, Valkonen S (2006) Effects of tree  
603 stand species composition on insect herbivory of silver birch in boreal forests. *Basic Appl*  
604 *Ecol* 7:1–11. doi: 10.1016/j.baae.2005.05.003
- 605 Whelan CJ, Wenny DG, Marquis RJ (2008) Ecosystem services provided by birds. *Ann NY*  
606 *Acad Sci* 1134:25–60. doi: 10.1196/annals.1439.003
- 607 Williams-Guillén K, Perfecto I, Vandermeer J (2008) Bats limit insects in a Neotropical  
608 agroforestry system. *Science* 320:70. doi: 10.1126/science.1152944
- 609 Wootton JT (1992) Indirect effects, prey susceptibility, and habitat selection: impacts on  
610 birds on limpets and algae. *Ecology* 73:981–991. doi: 10.2307/1940174
- 611 Wootton JT (1995) Effects of birds on sea urchins and algae: A lower-intertidal trophic  
612 cascade. *Écoscience* 2:321–328.

**Table 1.** A summary of the studies used in the meta-analysis. Abbreviations are as follows: LD = leaf damage, GR = growth, BM = biomass, MO = mortality, DB = damaged berries and # exp. = the number of experiments included within the study. Experiments within a particular study were defined based on different plant / bird species, measurements of the same plant species, forest types, or plants of different age.

Author	Treatment	Measured	Plant age	Environment	Climate	Study region	# exp.	Plant
Atlegrim 1989	exclosures	LD	mature	natural	boreal	Sweden	1	<i>Vaccinium myrtillus</i>
Barber & Marquis 2009	exclosures	LD GR	mature	natural	temperate	MO, USA	2	<i>Quercus alba</i>
Bock et al. 1992	exclosures	LD	mature	natural	temperate	AZ, USA	2	perennial grassland
Boege & Marquis 2006	exclosures	LD GR BM	mature, sapling	natural	tropical	Mexico	8	<i>Casearia nitida</i>
Bridgeland et al. 2010	exclosures	GR	mature	natural	temperate	UT, USA	4	<i>Populus</i> spp.
Dunham 2008	exclosures	LD MO	sapling	natural	tropical	Ivory Coast	2	rainforest understory
Forkner & Hunter 2000	exclosures	LD	sapling	natural	temperate	GA, USA	2	<i>Quercus prinus</i> , <i>Q. rubra</i>
Garibaldi et al. 2010	exclosures	LD GR	sapling	natural	temperate	Argentina	8	<i>Nothofagus pumilio</i>
Greenberg et al. 2000	exclosures	LD	mature	agricultural	tropical	Guatemala	2	<i>Coffea arabica</i>
Hooks et al. 2003	exclosures	BM	mature	agricultural	tropical	HI, USA	2	<i>Brassica oleracea</i>
Kalka et al. 2008	exclosures	LD	sapling	natural	tropical	Panama	1	understory trees
Kellermann et al. 2008	exclosures	DB	mature	agricultural	tropical	Jamaica	1	<i>Coffea arabica</i> var. <i>tipica</i>
Koh 2008	exclosures	LD	sapling	agricultural	tropical	Malaysia	1	<i>Elaeis guineensis</i>
Lichtenberg & Lichtenberg 2002	exclosures	GR BM	sapling	natural	temperate	AR, USA	3	<i>Quercus alba</i>
Marquis & Whelan 1994	exclosures	LD BM	sapling	natural	temperate	MO, USA	2	<i>Quercus alba</i>
Mazía et al. 2004	exclosures	LD	mature	natural	temperate	Argentina	2	<i>Nothofagus pumilio</i>
Mazía et al. 2009	exclosures	LD GR	sapling	natural	temperate	Argentina	12	<i>Nothofagus pumilio</i>
Mols & Visser 2002	exclosures	BM	mature	agricultural	temperate	Netherlands	1	<i>Malus domestica</i>
Mooney 2007	exclosures	LD GR	mature	natural	boreal	CO, USA	3	<i>Pinus ponderosa</i>
Murakami & Nakano 2000	exclosures, cages	LD	mature	natural	temperate	Japan	3	<i>Quercus crispula</i>
Sanz 2001	nest-box addition	LD	mature	natural	Mediterranean	Spain	2	<i>Quercus pyrenaica</i>
Sipura 1999	exclosures	LD GR MO	mature	natural	boreal	Finland	8	<i>Salix phylicifolia</i> , <i>S. myrsinifolia</i>
Strengbom et al. 2005	exclosures	LD	mature	natural	boreal	Sweden	1	<i>Vaccinium myrtillus</i>
Strong et al. 2000	exclosures	LD BM	sapling	natural	temperate	NH, USA	2	<i>Acer saccharum</i>
Van Bael et al. 2003	exclosures	LD	mature, sapling	natural	tropical	Panama	2	tropical trees
Van Bael & Brawn 2005	exclosures	LD	mature	natural	tropical	Panama	4	tropical trees
Van Bael et al. 2007	exclosures	LD GR MO	mature	agricultural	tropical	Panama	4	<i>Theobroma cacao</i>
Wootton 1992	exclosures	BM	-	natural	temperate	WA, USA	1	algae
Wootton 1995	exclosures	BM	-	natural	temperate	WA, USA	1	algae

## Figure captions

**Figure 1** Effect sizes of meta-analyses (lnR) with 95 % confidence interval. **a** Environments: natural (N = 70) and agricultural (N = 11); **b** Climatic areas\*: tropical (N = 27), temperate (N = 39) and boreal (N = 13); **c** Plant age\*\*: sapling (N = 32) and mature (N = 47); **d** Measured plant responses\*\*\*: mortality (N = 4), biomass (N = 10), growth (N = 25) and leaf damage (N = 41).

\* The Mediterranean climatic area comprised only one study (Sanz 2001) and was omitted from this analysis.

\*\* Studies by Wootton (1992, 1995) were omitted from this analysis since the age of the aquatic study plants (algae) cannot be categorised in the same way as with terrestrial plants in other studies.

\*\*\* Kellermann et al. (2008) was the only study to measure damage to the berries and therefore it was left out of this analysis.

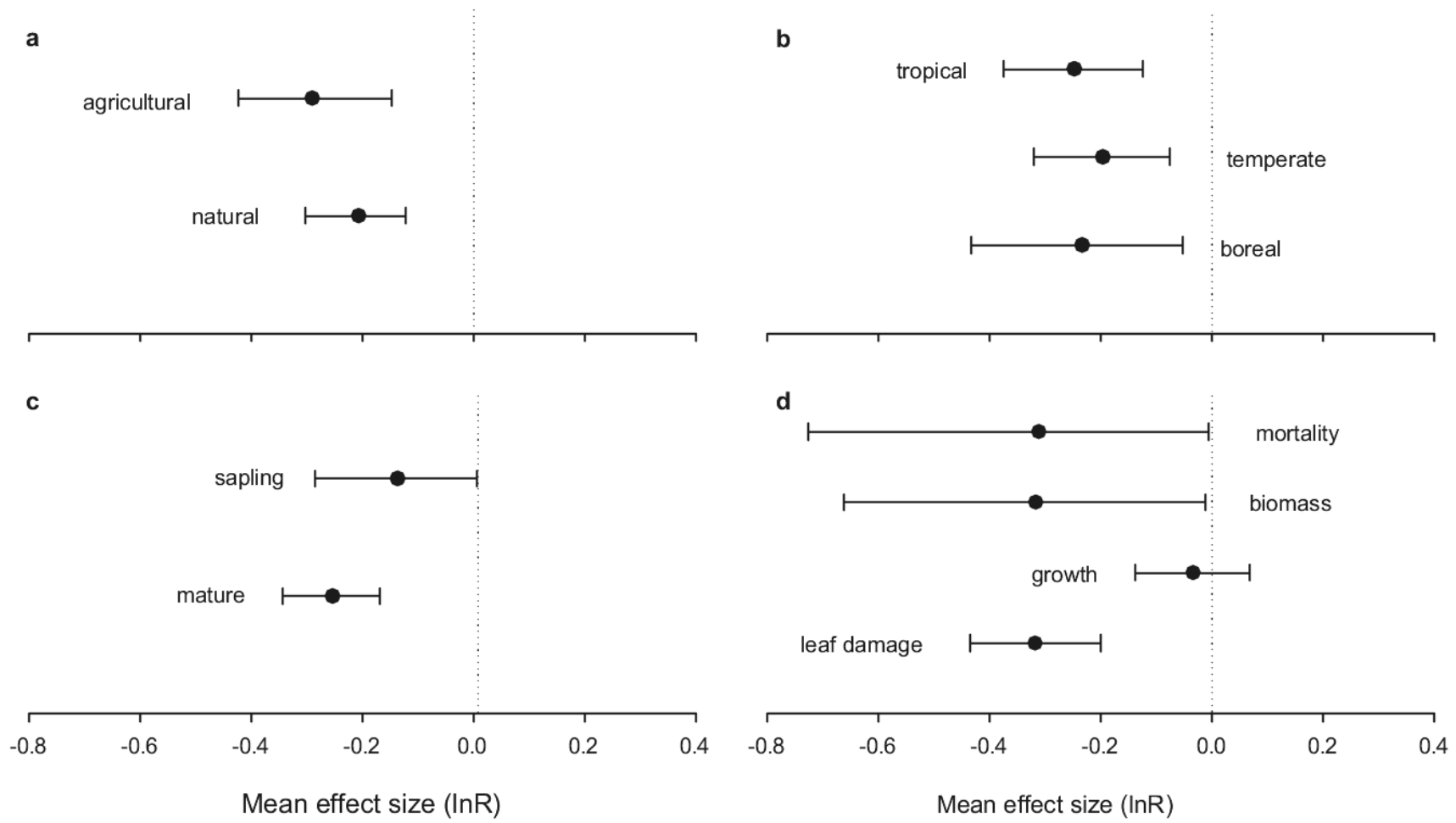
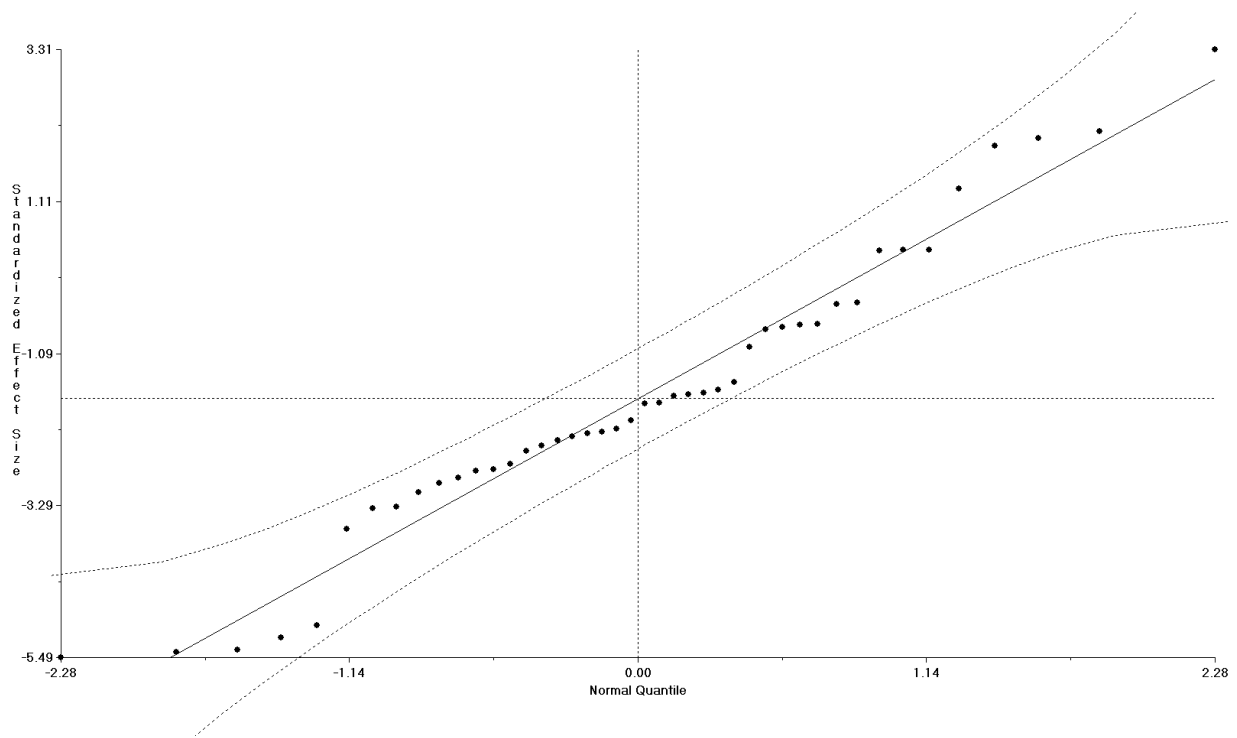


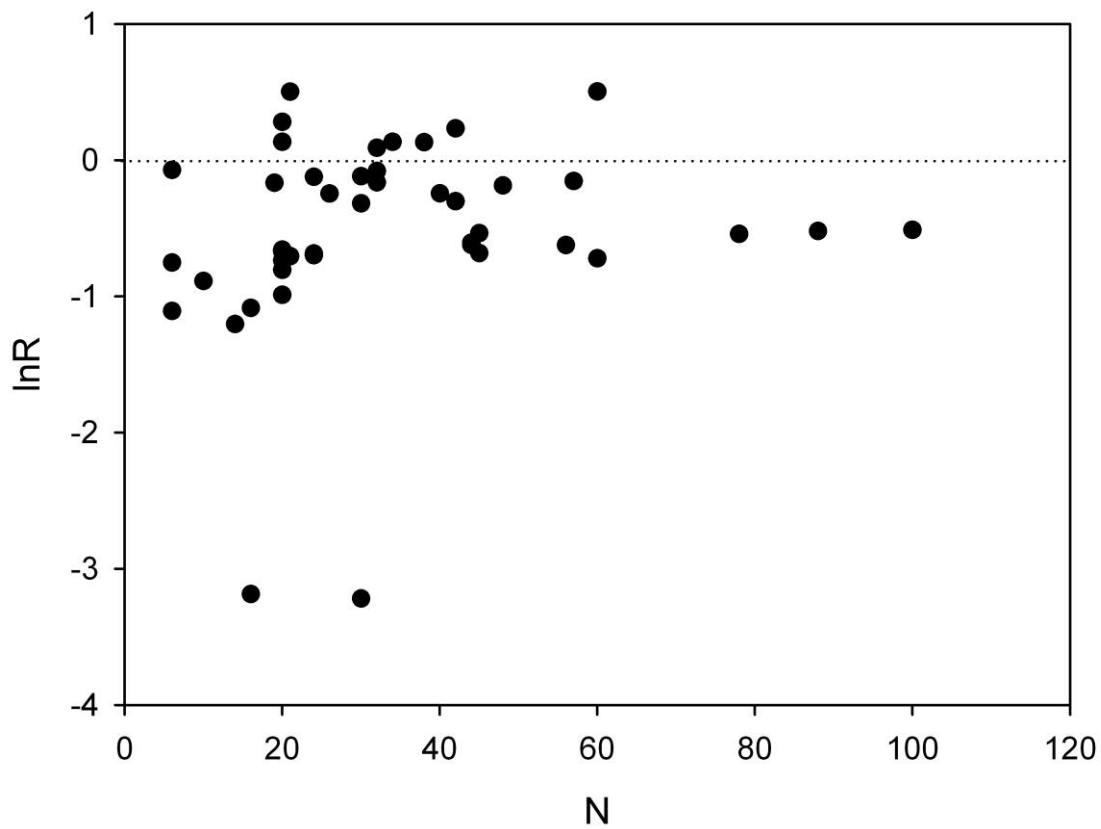
Figure 1

## Electronic Supplemental Material

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



**Electronic Supplemental Material 1** A normal quantile plot with 95 % confidence interval lines for examining publication bias of the studies used in the overall effect meta-analysis (N = 44).



**Electronic Supplemental Material 2** A funnel plot showing the relationship between the effect size ( $\ln R$ ) and sample size of the original studies ( $N = 44$ ).  $N$  is the combined sample size of treatment and control plots. The two outliers are the two studies of algae as plants (Wootton 1992, 1995).