

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

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Received: 15 October 2009 / Accepted: 27 August 2010
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Abstract The tritrophic interactions between plants, herbivores and avian predators are complex and prone to trophic cascades. We conducted a meta-analysis of original articles that have studied birds as predators of invertebrate herbivores, to compare top-down trophic cascades with different plant responses from different environments and climatic areas. Our search found 29 suitable articles, with a total of 81 separate experimental study set-ups. The meta-analysis revealed that plants benefited from the presence of birds. A significant reduction was observed in the level of leaf damage and plant mortality. The presence of birds also positively affected the amount of plant biomass, whereas effects on plant growth were negligible. There were no differences in the effects between agricultural and natural environments. Similarly, plants performed better in all climatic areas (tropical, temperate and boreal) when birds were present. Moreover, both mature plants and saplings gained benefits from the presence of birds. Our results show that birds cause top-down trophic cascades and thus they play an integral role in ecosystems.

Keywords Herbivory · Indirect effects · Meta-analysis · Predation · Trophic interactions

Introduction

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

Carnivorous birds are common in ecosystems throughout the world, and there have been numerous studies showing that they can have negative effects on the population sizes of insects and other small herbivores (e.g. Holmes

Communicated by Chris Whelan.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-010-1774-2) contains supplementary material, which is available to authorized users.

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et al. 1979; Fowler et al. 1991; Williams-Guillén et al. 2008). At the same time, herbivores can cause notable damage to plants (e.g. Marquis 1984; Bejer 1988; Mattson et al. 1988). To combine these two interactions, an increasing number of studies have also examined the effect of bird predation on plant herbivores cascading down to plants (e.g. Marquis and Whelan 1994; Strong et al. 2000; Van Bael et al. 2003). Multitrophic studies are warranted because studies with two trophic levels (e.g. plant–herbivore or predator–herbivore) at a time do not necessarily reveal the interactions among all three (or more) trophic levels. This is because the separate two-trophic level studies are seldom conducted at the same time or the same place, or with species common to both interactions. A recent review assessed the importance of birds in reducing plant damage mainly in forests and agricultural environments in the tropics (Van Bael et al. 2008), and another one documented the top-down cascading effects of vertebrate insectivores in general (Mooney et al. 2010), but as yet there has been no analysis whether bird-driven trophic cascades differ among climatic areas, including temperate and boreal forests. In addition, plant characteristics which gain benefits from the presence of birds remain to be explored. To answer these questions, we conducted a meta-analysis of original studies on potential trophic cascades from birds to plants. A meta-analysis is the best way to combine the results of independent studies to discover if there is a shared pattern among them (Gurevitch and Hedges 2001).

Our analyses serve several purposes. First, we measure the overall effect size of the presence of birds cascading down to plants, and thereafter we resolve with subgroup analyses whether the strength of the effect varies according to the climatic area (tropical, temperate or boreal), or the type of environment (agricultural or natural). Thus, these analyses test ideas that predators would be more effective in creating top-down cascades in agricultural monocultures and in colder climates (Polis and Strong 1996). Second, we identify with subgroup analyses whether there are differences in plant responses between the different types of measures the researchers have studied (leaf damage, biomass, growth or mortality) or between the age of the plants studied (mature or sapling). These analyses help to evaluate how long-lasting is the effect and to focus future research on the appropriate measures of plant performance. Third, there is interest in measuring the ecosystem services provided by birds, and the removal of herbivores from harvested plants is certainly a potential service with economic value (Sekercioglu 2006a, b; Whelan et al. 2008).

Knowing the importance of birds to plants is also a key element in understanding co-evolution in the trophic interactions among birds, herbivores and plants. For example, recent studies have shown that birds can find an insect-rich tree on the basis of cues from the host plant, without seeing

either the herbivores or the damaged leaves (Mäntylä et al. 2004, 2008a, b). This suggests that, to reduce the amount of herbivory, plants may have evolved induced responses that attract birds. Alternatively, these signals may be unspecific to birds (Mäntylä et al. 2008a). This kind of co-evolution between plants and birds may change the way we think about other trophic interactions. Plant–bird interactions include the relationships between herbivorous insects and their host plants, already known to be complex (e.g. Agrawal 1999; Engelberth et al. 2004; Vehviläinen et al. 2006), between insects that try to hide from birds (e.g. Heinrich and Collins 1983) and birds that vary in their preference for different prey (e.g. Kaspari and Joern 1993; Lindström et al. 1999). Thus, to get a broader view on how co-evolution may work within these multitrophic systems, we need to know whether plants benefit from the presence of birds that remove herbivores from plants.

Materials and methods

To obtain a comprehensive set of studies for our meta-analysis, we searched online databases—ISI Web of Science, Biological Abstracts and BIOSIS Previews—with different combinations of the following keywords: bird*, avia*, herbivor*, predat*, interacti*, insect*, indirect* and trophic*. The last online search was conducted in June 2010. We also checked the references of papers already retrieved and previous review articles about tritrophic interactions that included birds.

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

In the articles accepted in our meta-analysis, the researchers had in some cases measured a certain response several times either within single or successive growing seasons (in 11 of the 29 articles). To avoid bias, we chose only one occasion from these experiments (in total 30 experiments or study set-ups, which included 2–4 measurement occasions each). Several methods have been used to, make the choice: e.g. the last measurement of the original studies (e.g. Gurevitch et al. 2000), the mean of all measurements (e.g. Rustad et al. 2001), or the value with the largest effect size (i.e. the difference among experimental and control group means) (e.g. Koricheva et al. 1998). The

use of the last measurement seemed biologically inappropriate here since it was always the researchers' decision when to end the experiment. The correlation between the mean and maximum effect sizes in our data was so strong ($r = 0.98$, $n = 30$ experiments) that the results of the meta-analysis were essentially the same using either one of these two measures. From these two, we present the results with the largest effect size, because high instantaneous damage can be more critical to plants than the long-term average level of encountered herbivory (Doak 1992; Leimu and Lehtilä 2006).

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

In total, we found 29 original articles that met the criteria as indicated above (Table 1). A further four possible studies (Loyn et al. 1983; Ritchie 2000; Gruner 2004; Mooney and Linhart 2006) were also found relevant in their ecological context, but these lacked the necessary data to conduct meta-analytic calculations. Our four criteria excluded large numbers of articles, where cascading effects on the plant level were not considered, even though they reported significant effects of the birds on their arthropod prey communities (e.g. Holmes et al. 1979; Joern 1986; Fowler et al. 1991; Floyd 1996; Borkhataria et al. 2006). The 29 articles included in the meta-analysis had a total of 81 different experiments or study set-ups, which were used as independent studies in the analysis. The "one response per study set-up" group had 44 study set-ups. This group was used for the analysis of the overall effect. The study habitats ranged from Neotropical forests to intertidal shores and from Hawaiian forests to apple orchards, consisting of a wide range of study species. However, apart from four studies (Bock et al. 1992; Wootton 1992, 1995; Hooks et al. 2003), the plant species under study were low-growing woody shrubs, trees or forest stands. The most common trees were species of oak (*Quercus* spp.; Table 1). In several studies, there were no efforts to specify the herbivores or birds and they were merely labelled as "leaf-chewing insects", "arthropods" or "insectivorous birds". Although the majority of studies had excluded birds from certain areas or plants with nets or cages (Table 1), there were two

exceptions. Sanz (2001) instead used the addition of birds, and Murakami and Nakano (2000) used bird enclosures and bird exclosures to test their hypotheses. Although these two studies did not contain only exclosures, we hereafter, for the sake of simplicity, use terms "bird exclusion" and "bird exclosures" to indicate the "non-bird group" of each study. Exclosure sizes (mentioned only in 15 original articles) ranged from 0.1 to over 450 m², and this did not correlate with the effect size of the plant response ($r = 0.13$, $n = 15$ experiments). The most common plant response surveyed was some measure of leaf damage, while some studies also measured biomass, growth or mortality. We also noted whether the study plants were mature or saplings (including seedlings). Two studies by Wootton (1992, 1995) were omitted from this category as he used aquatic study plants (algae), which cannot be categorised in the same way as the terrestrial plants examined in all other studies. In many cases, the researchers were also interested in other factors together with bird exclusion, e.g. fertilisation, insecticides or invertebrate predators. However, because these factors were not of interest in this review, we used values of treatments that included only avian predators.

Studies not included in the meta-analysis

Loyn et al. (1983) and Ritchie (2000) were not included in the meta-analysis because they did not give the required deviation terms. Loyn et al. (1983) found that other bird species than bell miners (*Manorina melanophrys*) were useful to eucalyptuses, while the bell miners were not. Ritchie (2000) showed that bird exclosures had a small effect on grasses eaten by grasshoppers. Additionally, we were unable to use the studies of Gruner (2004) and Mooney and Linhart (2006), because they had reported their results as effect sizes, which were impossible to transform to correspond to our effect sizes. Gruner (2004) reported that the effects of bird exclusion on the dominant tree species in Hawaiian forests varied during the study, but the difference between exclosure and control plots was never significant. Mooney and Linhart (2006) found that avian exclosures reduced pine wood growth as birds were connected to pine by a linear food chain via aphids, whereas effects on mistletoe were negligible due to more reticulate food web and birds as intraguild predators.

Statistical methods

We used MetaWin v. 2.1 (Rosenberg et al. 2000) to calculate standardised effect sizes as a log response ratio [$\ln R = \ln(\text{control mean}) - \ln(\text{experimental mean})$]. The use of $\ln R$ (instead of Hedges' d or other measures of effect size) has recently become more common in biological studies because it assumes that effects can be multiplicative and

Table 1 A summary of the studies used in the meta-analysis

Author	Treatment	Measured	Plant age	Environment	Climate	Study region	No. of experiments	Plant
Atlegrim (1989)	Exclosures	LD	Mature	Natural	Boreal	Sweden	1	<i>Vaccinium myrtillus</i>
Barber and 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 and 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 and 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 and Lichtenberg (2002)	Exclosures	GR BM	Sapling	Natural	Temperate	AR, USA	3	<i>Quercus alba</i>
Marquis and 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 and 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 and 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 and 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

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

LD Leaf damage, GR growth, BM biomass, MO mortality, DB damaged berries

is less sensitive to errors (Morris et al. 2007). We used random effect models and ran resampling tests with 4,999 iterations to get 95% bias-corrected bootstrap confidence intervals. Here, effect size values below zero indicated that the control group (birds present) was more beneficial to plants than the experimental group (birds absent). All studies were modified with a reversal marker column of MetaWin ('+' sign for measurements of growth or biomass, and '–' sign for measurements of leaf damage, mortality or infestation level), so that if plants benefited from birds then the effect size value was below zero. For the subgroup

summary analyses, we calculated the heterogeneity statistic Q , in MetaWin. As with variance in ANOVA, the total heterogeneity Q_T can be partitioned into Q_M , the variation explained by the model and reported in the results, and Q_E , the residual error variance (Rosenberg et al. 2000). A statistically significant variance among the effect sizes means that the variance is greater than expected by sampling error alone (Cooper 1998).

We used three methods, which are simple to interpret and often used in meta-analytical studies (Gurevitch et al. 1992; Kaplan and Denno 2007; Salo et al. 2007), to

estimate if the available data suffer from publication bias. Publication bias can be studied by the funnel plot method, where the observed effect size is plotted against sample size (Palmer 1999). If there is no publication bias more variation should occur in effect sizes of smaller studies than in larger studies causing a funnel-shaped plot (Gates 2002). Additionally, Rosenthal's fail-safe number method can be used to test for selective reporting by calculating how many studies with a zero effect size would be needed to make the result of the meta-analysis non-significant (Rosenthal 1979). Finally, one more method involves visual estimation of the normal quantile plot where standardised effect size values are plotted against normal quantile values. If the points remain close to the line $x = y$ there should not be publication bias.

Results

The plants generally benefited from bird presence (i.e. control plants were in better condition than plants inside bird enclosures) as the overall effect size and its confidence interval (CI) were clearly less than zero ($\ln R = -0.367$, 95% CI = -0.500 to -0.237). The variation in effect sizes (total heterogeneity) was statistically significant ($Q_T = 61.59$, $df = 43$, $P = 0.033$), indicating greater total heterogeneity than can be expected by sampling error alone. This could be expected in our meta-analysis because we compiled studies conducted in different places with different methods, species and response variables.

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

Publication bias

As the data points of the 44 studies used in the overall effect meta-analysis stayed inside the 95% confidence limits, our data were normally distributed and thus did not show deviation that could be interpreted as evidence of publication bias (Electronic supplemental material 1). The Rosenthal's fail-safe number method to test for selective reporting (i.e. publication bias) gave a result of 2,125.3, which is very high, considering that our data consisted of only 81 experiments and, of those, only 44 were used in the combined overall analysis. According to the funnel plot method, there was slightly more variation in effect sizes among experiments with small sample sizes than among those with larger sample sizes (Electronic supplemental material 2)

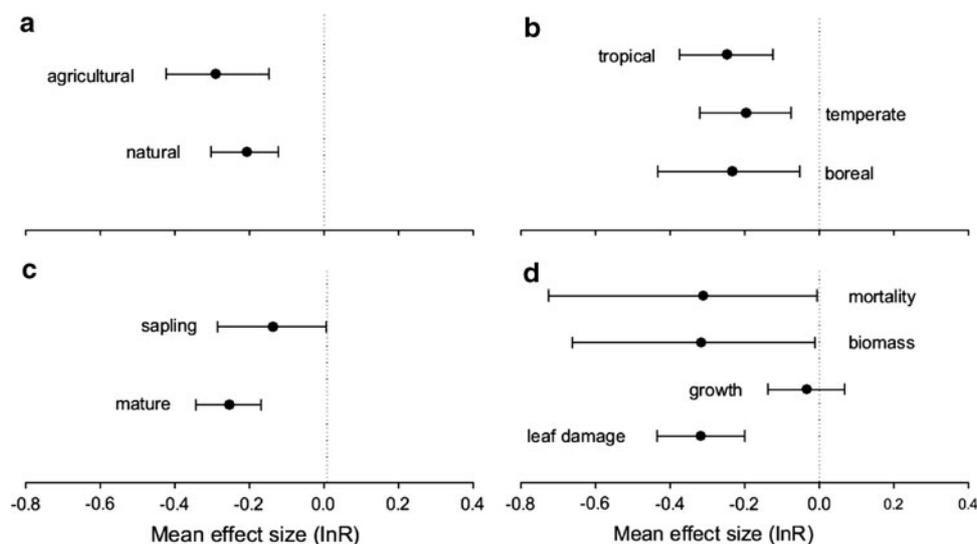


Fig. 1 Effect sizes of meta-analyses ($\ln R$) with 95% confidence interval. **a** Environments: natural ($n = 70$) and agricultural ($n = 11$); **b** climatic areas (the Mediterranean climatic area comprised only one study, Sanz 2001, and was omitted from this analysis): tropical ($n = 27$), temperate ($n = 39$) and boreal ($n = 13$); **c** plant age (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): sapling ($n = 32$) and mature ($n = 47$); **d** measured plant responses (Kellermann et al. 2008 was the only study to measure damage to the berries and therefore it was left out of this analysis): mortality ($n = 4$), biomass ($n = 10$), growth ($n = 25$) and leaf damage ($n = 41$)

Discussion

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

When all predators of herbivores (avian, mammalian, invertebrate) are taken into consideration, meta-analyses of terrestrial tritrophic cascades have shown that predator-exclusion benefits herbivorous arthropods more than harms plants (Halaj and Wise 2001; Mooney et al. 2010), but that vertebrate carnivores usually have a stronger impact than invertebrate predators (Schmitz et al. 2000). Moreover, previous reviews of terrestrial trophic cascades have often used a large variety of predators where the specific effects of one predator group (e.g. birds) are often confounded among the diversity of study set-ups (e.g. Shurin et al. 2002). Thus, our main result concerning the trophic cascade from birds to plants corroborates the importance of vertebrate predators in such cascades (see also, e.g., Kalka et al. 2008). It must be noted that none of the experiments had extremely high densities of herbivores. Since carnivorous birds are usually considered generalist predators showing relatively slow numerical response to an increase in prey density, it is unlikely that birds could consume a considerable amount of herbivores in a high density situation, e.g. during outbreaks of forest lepidopterans (Hogstad 2005). However, Fayt et al. (2005) found that three-toed woodpeckers (*Picoides tridactylus*) can regulate bark beetles of spruces and Loyn

et al. (1983) showed that some bird species can eradicate psyllids from eucalypt forest patches.

Plants outside bird exclosures had less leaf damage and mortality, and higher biomass than those inside the exclosures (Fig. 1d). By contrast, plant growth did not seem to be affected by avian exclosure (Fig. 1d), which may be due to the relatively short duration of most of the research projects reviewed (from 23 days to 36 months, median 12 months), combined with the plants' ability to compensate for losses due to herbivory (Schmitz et al. 2000). When researchers had measured several plant responses, leaf damage was usually the measure most affected (e.g. Marquis and Whelan 1994; Strong et al. 2000; Boege and Marquis 2006; Dunham 2008; Van Bael et al. 2007). This is not surprising given that leaf damage is the first sign of herbivory. However, measuring only the amount of damaged leaves/removed leaf area does not always explain how damaging herbivory is to the fitness of a plant over time. The study by Mols and Visser (2002) is a notable exception because they recorded the amount of fruits that apple trees (*Malus domestica*) produced, while in another agricultural study, Hooks et al. (2003) measured the biomass of broccoli heads (*Brassica oleracea*). Both studies found that the presence of birds increased the crop of these plants. Additional studies with measures of plant fitness, particularly in natural environments, would offer more knowledge about the long-lasting effects of the bird-driven trophic cascades in multitrophic systems.

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

birds, herbivores and plants would nevertheless be needed for a more comprehensive view of the generality of the mutualistic relationship between birds and plants.

As yet totally unexplored potential trophic cascades include, for example, the ones caused by birds of prey that eat small herbivorous mammals (such as voles). Many predator reduction experiments have already been undertaken with voles or lemmings and their predators (reviewed in Sundell 2006). However, the plant responses are often not reported at all. If they are reported, they cannot be separated between the different predator groups (mammalian, avian or reptilian), because all predators are usually excluded (see, e.g., Norrdahl et al. 2002; Aunapuu et al. 2008). Incorporating measures of plant responses to these studies would widen our understanding of the effects of birds in trophic cascades among different ecosystems.

Our test for publication bias with the funnel and normal quantile plots (Electronic supplemental materials 1, 2) did not produce results of strong bias, and the Rosenthal's fail-safe number method showed that over 2,000 studies with an effect size of zero would be needed to make our result non-significant. No review, however, can cover studies if they are unpublished, and thus our results of the meta-analysis may be a small overestimate of the actual effect of birds helping plants (Kotiahho and Tomkins 2002). In any case, our meta-analytic data set provide strong support that birds are commonly beneficial to plants.

In conclusion, our meta-analysis supported the finding that plants benefit from birds that remove their herbivores and that globally there are no differences in this phenomenon throughout a variety of environments and climatic areas. This work and some other recent studies (Sekercioglu 2006a, b; Van Bael et al. 2008; Whelan et al. 2008) have thus shown that birds are beneficial to plants and form an integral part of ecosystems. In this light, it is worrying that many bird populations are in heavy decline (e.g. Sekercioglu et al. 2004; BirdLife International 2008). The ecosystem services provided by birds are important not only for the functioning of natural ecosystems but also for pest control in agriculture and forestry (Sekercioglu 2006a). If bird populations decline, these services are not easily replaced by any other taxa, especially in the tropics where specialisation is high (Sherry 1984; Sigel et al. 2010). This emphasises the societal value of birds and the need for conserving bird populations.

Acknowledgements We would like to thank Pålvi Salo for help and advice. Thanks are also due to Christiaan Both, Leena Lindström, Lauri Oksanen, Cagan Sekercioglu, three anonymous reviewers and the graduate student seminar at the section of ecology (University of Turku), for giving valuable comments. Kevin O'Brien checked the English. The study was financially supported by the Jenny and Antti Wihuri Foundation (grant to E.M.), Academy of Finland (decision

numbers 111195 and 129143 to T.K.) and the Emil Aaltonen Foundation (grant to T.L.).

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