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# Trophic cascade effects of avian predation on a willow in an urban wetland

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**Abstract** Trophic cascades play a crucial role in ecosystem functioning. In this study, we tested the effects of avian predation on willows (*Salix warburgii*) and associated arthropods in an urban wetland. We excluded birds by netting around willow branches for 20 months from September–November 2010 to June 2012. We compared the leaf count, leaf area, leaf biomass, bud count, catkin (flower) count and herbivory from pairs of bird-exclusion and no-exclusion branches on 11 trees. Simultaneously, we compared herbivorous and predatory arthropod abundances associated with bird-exclusion and no-exclusion branches. Another nine trees were used as reference branches to assess whether the bird exclusion impacted other branches of the same trees (i.e., no-exclusion branches). Bird exclusion resulted in increased herbivory 1 year after the treatment, followed by a reduced leaf count, leaf area, leaf biomass, bud count and catkin count in the second year. The bird-exclusion branches exhibited greater spider abundance than the no-exclusion branches. However, herbivorous arthropod abundances were similar between the branch types. The reference branches had similar values in all plant traits and for all arthropod abundances to those of the no-exclusion branches. This study demonstrated the branch-level effects of trophic cascades on willows via the

exclusion of birds and a resulting reduction in herbivory. However, whether and how the arthropods mediate such effects require further investigation. This study adds to the limited empirical data demonstrating the effects of trophic cascades on plant reproduction. Our findings highlight the importance of bird conservation in urban wetlands.

**Keywords** Arthropod · Food web · Indirect effect · Plant–herbivore · Top-down control

## Introduction

Trophic cascades, defined as the propagation of indirect mutualism between non-adjacent levels in a food chain (Persson 1999), can influence primary productivity (e.g., Silliman and Bertness 2002), herbivore abundance (e.g., Marquis and Whelan 1994; Sipura 1999) and species composition (e.g., Marquis and Whelan 1994; Schmitz et al. 2006), as well as food web dynamics (e.g., Casini et al. 2009). Trophic cascades occur in a variety of ecosystems, including lakes and streams (e.g., Huryn 1998), marine and intertidal zones (Silliman and Bertness 2002; Casini et al. 2009), grasslands (e.g., Spiller and Schoener 1994; Schmitz et al. 2006), forests (e.g., Marquis and Whelan 1994; Sipura 1999; Mooney 2007; Böhm et al. 2011) and agricultural systems (e.g., Greenberg et al. 2000). Given their broad ecological implications, trophic cascades have been well studied, and efforts have been made to draw general rules on factors governing the presence and strength of trophic cascades from existing research (Shurin et al. 2002; Borer et al. 2005; Mäntylä et al. 2011). For example, based on a meta-analysis of 114 studies, Borer et al. (2005) found strong and weak cascades associated with the same combination of invertebrate herbivores and endothermic

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vertebrate predators in aquatic and terrestrial systems, respectively. Therefore, trophic cascades are complex ecological processes that require empirical studies across systems and species combinations to reveal their governing principles.

In terrestrial environments, herbivorous arthropods often exert a large impact on plant growth, reproduction and life history traits (Crawley 1989; Coley and Barone 1996). On the other hand, avian predation has been shown to suppress arthropod abundance, thereby reducing herbivory (Marquis and Whelan 1994; Sipura 1999; Böhm et al. 2011). A recent meta-analysis of 81 experiments from 29 articles revealed widespread effects of trophic cascades caused by avian predation on plants via the suppression of invertebrate herbivores (Mäntylä et al. 2011). For example, Marquis and Whelan (1994) caged white oak (*Quercus alba* L.) saplings with nylon gill netting in a deciduous forest for 2 years to prevent avian predation. As a result, the plants suffered twice the damage from herbivores as the control plants and consequently produced less aboveground biomass.

However, many system- or species-specific characteristics, such as light and nutrient conditions, plant chemistry, and interspecific interactions among herbivores, predators and parasites/parasitoids, can also influence the outcomes of trophic cascades. A plant's secondary compounds not only can be harmful to insects but also can attract herbivores' predators and parasitoids (Vet and Dicke 1992; Van Bael et al. 2003). Furthermore, the ability to produce secondary compounds is closely linked to species life history and microenvironment elements such as light and nutrient conditions (e.g., Dudt and Shure 1994). For example, willow (*Salix* spp.) is known to develop secondary compounds that can be used as toxins and deterrents to help reduce herbivory (Fritz et al. 2001; Hjältén et al. 2007; Boeckler et al. 2011), which may explain Sipura's (1999) finding that avian predation reduced leaf damage in *Salix phylicifolia* but not in *Salix myrsinifolia*, the latter of which produced 50-fold more defensive phytochemicals. Interspecific interactions can also complicate the processes of trophic cascades. For example, the dieback of eucalypt forests in Australia is sometimes associated with an increasing abundance of the bird known as the bell miner *Manorina melanophrys*. Such negative cascading effects from birds to plants may be explained by a series of interspecific interactions. Specifically, Loyn et al. (1983) showed that the displacement of avian predators, from territorial to nomadic insectivorous birds, could lead to the suppression of herbivorous insects (psyllids) that damage eucalypt trees. Steinbauer et al. (2015) further suggested that herbivory by some psyllid species can induce higher foliage quality, which benefits psyllid species more attractive to bell miners. The territorial behavior of bell miners against other avian insectivores then helps sustain psyllid populations. However, as leaf

quality declines with leaf age and parasitoid abundance increases with psyllid abundance, trophic interactions continue to change. These examples illustrate the complex and dynamic processes involved in any given trophic cascade.

Urbanization has become a dominant force driving ecosystem patterns and processes worldwide (Vitousek et al. 1997; Alberti et al. 2003). However, a recent literature review noted that the effects of land-cover change, which is frequently associated with urbanization, on trophic ecology are rarely examined for more than a single trophic interaction; furthermore, of the different ecosystem types analyzed, wetlands represented only four of the 341 studies (Herrera and Doblas-Miranda 2013). The degree of urbanization has been shown to correlate with decreased species richness and increased functional homogeneity in avian communities (Rottenborn 1999; McKinney 2006; Devictor et al. 2007). These changes are likely to influence trophic cascades involving avian predation. In fact, avian predation was found to be a dominant force controlling arthropods on plants in urban areas (i.e., the Phoenix area) of the Sonoran Desert (Faeth et al. 2005). However, few empirical studies address trophic cascades in urban ecosystems, particularly wetland habitats.

In this study, we examined the top-down effects of avian predation on willows (*Salix warburgii*) and associated arthropods in a riparian habitat amid the Taipei metropolis (area size ca. 2,324 km<sup>2</sup>, population ca. 6.7 million; Taiwan Ministry of Interior Monthly Bulletin, March 2015). We conducted a branch-level, 20-month manipulative field experiment using bird exclusion to test the effects of avian predation on leaf count, leaf area, leaf biomass, bud count, catkin (flower) count, herbivory and arthropod abundance associated with the willows. As pioneer species, willows are well adapted to disturbance, and therefore they form a critical component of woody vegetation in riparian habitats. They provide a range of ecological functions by stabilizing streambanks, providing nutrient input and supporting diverse animal communities (Naiman and Décamps 1997; Wigington and Beschta 2000; Dhondt et al. 2008; Kuzovkina and Volk 2009). Despite the fact that many willow species are known to develop strong chemical defenses against herbivory (e.g., Hjältén et al. 2007; Boeckler et al. 2011), natural predators of herbivores have been found to help willows in several cases, including one involving predatory birds (e.g., Sipura 1999) and one involving carnivores (e.g., Ripple and Beschta 2012). Arthropod predators such as spiders have also been reported to respond to increases in herbivores on willows (Nakamura et al. 2005), suggesting they may also play a role in reducing herbivory. To our knowledge, trophic cascades in willows have not been investigated in an urban setting. Furthermore, the effects of trophic cascades on plant reproduction are also rarely evaluated (but see Mols and Visser 2002; Hooks et al. 2003),

and the majority of existing studies have focused on biomass, mortality or growth (Mäntylä et al. 2011).

To examine whether avian predation has a positive effect on willows in the Taipei urban wetland, we ask the following questions:

1. Does bird exclusion increase herbivore abundance on the willows?
2. Does bird exclusion increase herbivory of the willows?
3. Does bird exclusion reduce the leaf count, leaf area, leaf biomass, bud count and catkin count of the willows?

Finally, because predatory arthropods may mediate the relationship between birds and herbivores, we also assessed bird exclusion's effects on the abundance of the predatory arthropods.

## Materials and methods

### Study system

The study was conducted between September 2010 and June 2012 in a riparian area along the Xindian River in northern Taiwan (25°00'52"–25°01'00"N, 121°29'24"–121°29'29"E; Supplementary Fig. S1). The annual mean temperature is 23 °C and annual precipitation is 2,405 mm at the site (data from 1981 to 2010; Taiwan Central Weather Bureau, <http://www.cwb.gov.tw>, accessed in October 2013). The study site is under tidal influence, the lower portions of certain willows are periodically submerged in water during high tide. The mean water level is between 1.1 and 1.4 m at high tide, and between –0.6 and –0.9 m at low tide (Taiwan Central Weather Bureau, <http://www.cwb.gov.tw>, accessed in October 2012). The vegetation consists of subtropical broad-leaved trees and shrubs such as paper mulberry (*Broussonetia papyrifera*), small-leaved mulberry (*Morus australis* Poir.), macaranga (*Macaranga tanarius*), small Philippine Acacia (*Acacia confusa*), zebra grass (*Miscanthus* spp.), and water willow (*Salix warburgii*). Common avian predators at the site include the tree sparrow (*Passer montanus*), Chinese bulbul (*Pycnonotus sinensis*), Japanese white-eye (*Zosterops japonica*), magpie (*Pica pica*), crested myna (*Acridotheres cristatellus*), vinous-throated parrotbill (*Paradoxornis webbianus bulomachus*) and brown shrike (*Lanius cristatus lucionensis*) (P. C. W., personal observation). The nearest distances from the edge of the study site to paved trails and permanent buildings are approximately 50 and 380 m, respectively. Because of tidal influence and legal regulations (the entire wetland falls within the Taipei City Waterbird Refuge), recreational users are not allowed to enter the study site. Throughout the

study period, only one branch was cut down by a human (the tree was excluded from the study). Therefore, direct human disturbances to our experiment were limited.

### Experimental design

We included 11 *S. warburgii* trees in the bird-exclusion experiment and an additional nine trees as a reference set (Supplementary Fig. S1, Table S1). The trees were ca. 3–13 m in height and 7–101 cm diameter at breast height. All selected trees were >10 m apart from one another to ensure that their crowns did not touch. On each of the 11 experimental trees, two branches of similar height were selected from the lower canopy layer and randomly assigned to either the bird-exclusion or no-exclusion treatment. On each of the nine reference trees, one branch was selected from the lower canopy layer and assigned to the no-exclusion treatment (herein “reference” branch). All branches were located 1–2 m above the ground and shaded by other branches from above. Each branch was ca. 150–200 cm in length and 120–200 cm in width, and trees typically had eight to 30 branches (P. C. W., personal observation). The purposes of including the reference branches were: (1) to serve as a second control in addition to the no-exclusion treatment against which to test the bird-exclusion effect, and (2) to detect whether netting and sparkling strips on the bird-exclusion branches also affected the no-exclusion branches on the same trees.

Birds were excluded by enclosing an entire branch with nylon netting (mesh size 27 mm, string thickness 0.12 mm, black), which allowed arthropods access but prohibited even the smallest birds from accessing the branch. The netting was lightweight and stretched in multiple directions, and it was set up in a way that minimized direct contact with the leaves. Trees were checked one to three times every month to ensure that the netting worked properly. To reduce the chance of birds getting caught in the netting, we also attached sparkling strips on the nettings. Therefore, the bird-exclusion treatment comprised both netting and sparkling strips, whereas the no-exclusion treatment (for both the no-exclusion branches on the experimental trees and the reference branches on the reference trees) had neither netting nor sparkling strips. To reduce shading effects from netting on plant traits and the activities of arthropods and birds (e.g., Dudt and Shure 1994; Veteli et al. 2003; Mäntylä et al. 2008), both bird-exclusion and no-exclusion treatments were applied to naturally shaded lower canopy branches, and a pre-test of three different netting types was conducted to identify the netting with the lowest light reduction (6 % reduction in lux inside the netting; Supplementary Table S2).

The netting on the experimental trees was set up between September and November 2010. Due to logistical

constraints, the reference trees were included 1 year later, in October 2011. The sampling schedule was designed based on the willows' phenology. At our study site, *S. warburgii* started shedding leaves in late November–early December, and their inflorescences appeared in late February–April, with new leaves beginning to sprout in March. Therefore, leaf count, leaf area, leaf biomass and leaf damage were sampled during the September–November 2010 growing season (pre-treatment samples for experimental trees), and again during the October 2011 and June 2012 growing seasons (post-treatment samples for all trees), whereas buds and catkins were sampled during the March 2011 (post-treatment samples for experimental trees) and February 2012 (post-treatment samples for all trees) budding/flowering seasons.

### Leaf count, leaf area, leaf biomass, bud count and catkin count

To estimate leaf area and leaf biomass, we randomly selected ten leaves (>20 cm apart from one another) from each branch. The leaves were cut at the petiole, put in a cooler and transferred back to the laboratory in <12 h. In the laboratory, dust and animal traces such as silks, eggs and feces were washed off the leaves, and the leaves were dried with paper towels. The leaves were then scanned, and the images were analyzed in ImageJ (<http://rsbweb.nih.gov/ij/>) to determine the leaf area. The leaves were dried in an oven at ca. 50 °C for >48 h to constant weight (dry weight). The means of the ten leaves were calculated to quantify the leaf area and leaf biomass of a specific branch. Leaf count, bud count and catkin count, which were total numbers of leaves, buds and catkins on each branch, respectively, were recorded in the field during sampling.

### Leaf damage

We estimated leaf damage using the scanned images of the ten leaves sampled to calculate leaf area and leaf biomass for each branch. We first estimated whole leaf area by filling the chewed holes on the leaf scans in Adobe Illustrator. Damaged leaf area was calculated as the difference between filled leaf area and unfilled leaf area (i.e., damaged leaf area = whole leaf area – unfilled leaf area), and the degree of herbivory was quantified as the percentage of the damaged leaf area (i.e., damaged leaf area/whole leaf area). We did not estimate leaf damage for branches that did not have any leaves at the time of sampling.

### Arthropod abundance

Arthropods were surveyed in September–November 2010 (pre-treatment samples for experimental trees), and in October 2011 and June 2012 (post-treatment samples for all trees). At our study site, aphids occurred only in the spring.

Hence, we performed two additional aphid surveys in March 2011 (post-treatment samples for experimental trees) and February 2012 (post-treatment samples for all trees). We grouped herbivores into three categories: Lepidoptera larvae, sap suckers including lace bugs (Hemiptera: Tingidae) and *Icerya seychellarum* (Westwood 1855), and aphids (Hemiptera: Aphididae). Spiders (Araneae) were sampled to represent predatory arthropods because they were the most commonly seen predatory taxon. Arthropods were surveyed between 7 a.m. and 5 p.m. on sunny days. All Lepidoptera larvae, sap sucker and spider individuals on a branch were counted and standardized by total leaf area on a branch (i.e., leaf count × mean leaf area; square meters). For one branch, we had a leaf count of 62 but did not obtain the mean leaf area; we used the overall mean leaf area (13.73 cm<sup>2</sup>) across all samples to estimate this branch's total leaf area. Aphids formed aggregates and were difficult to count in large groups. In these cases, our counts were based on conservative estimates. The estimated aphid numbers were standardized by total bud count on a branch. We excluded data points where no leaves or buds were present on the branch at the time of arthropod sampling.

### Statistical analyses

The generalized linear mixed model with a repeated-measure design was used to test the effects of bird exclusion on plant traits (i.e., leaf count, leaf area, leaf biomass, bud count, catkin count), herbivory (i.e., percent leaf damage) and arthropod abundance. Willows are dioecious, therefore we included sex of the tree as a fixed effect. Because data on reference trees were available only 1 year after the initiation of the bird-exclusion treatment, we constructed two sets of models, one for experimental trees only and one for both experimental and reference trees. Comparisons between the bird-exclusion and no-exclusion branches for each time period were made in the first set of models; comparisons between bird-exclusion and reference trees and between no-exclusion and reference trees were made for each time period in the second set of models. Leaf area, leaf damage and arthropod abundance were modeled as a Poisson distribution; leaf count, leaf biomass, bud count and catkin count were modeled as a negative binomial distribution. We followed the procedures outlined in Bolker et al. (2009) for fitting the full models. Specifically, we observed that the residuals (on the linked scale) generally followed a normal distribution and were independent of the predicted values of the response variable; furthermore, the Pearson  $\chi^2$ /probability density function values were <1.5 for all models (a value = 1 for zero over-dispersion), indicating that the Poisson or negative binomial distribution was appropriate for the data.

**Table 1** Effects of bird exclusion on leaf count, leaf area, leaf biomass and leaf damage in *Salix warburgii*

Effect	Num. <i>df</i>	Den. <i>df</i>	Leaf count		Den. <i>df</i> <sup>a</sup>	Leaf area (cm <sup>2</sup> )		Leaf biomass (mg)		Den. <i>df</i> <sup>b</sup>	Leaf damage (%)	
			<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>
Experimental trees												
Bird exclusion	1	30	5.71	0.02	29	33.54	<0.0001	2.00	0.17	16	8.34	0.01
Time	2	29	2.06	0.15	29	7.23	0.003	4.65	0.02	22	0.26	0.77
Bird exclusion × time	2	30	1.70	0.20	29	11.4	0.0002	0.77	0.47	16	2.34	0.13
Tree sex	1	30	0.1	0.76	29	1.78	0.19	0	0.97	16	0.14	0.71
Experimental and reference trees												
Bird exclusion	2	20	5.90	0.01	19	20.49	<0.0001	2.03	0.16	6	4.71	0.06
Time	1	35	0.03	0.88	35	5.94	0.02	3.14	0.09	28	0.02	0.88
Bird exclusion × time	2	20	0.36	0.70	19	6.82	0.01	0.48	0.62	6	1.08	0.40
Tree sex	1	20	0.05	0.83	19	2.25	0.15	0.02	0.89	6	0.17	0.70

Num. Numerator

<sup>a</sup> Data on leaf area/biomass are not available for one branch, hence the lower denominator (*Den.*) *dfs* for these two traits compared to the leaf count

<sup>b</sup> Leaf damage is only estimated for branches with non-zero leaf area, hence the lower *Den. df* compared to the other traits

## Data availability

The original data, including all plant traits and arthropod counts, can be found in Supplementary Table S1, along with basic tree information.

## Results

### Leaf count, leaf area and leaf biomass

Leaf count, leaf area and leaf biomass were similar between the bird-exclusion and no-exclusion branches during the pre-treatment period as well as in the first year after treatment (Table 1; Fig. 1a, c, e). However, the bird-exclusion branches had 90 % fewer leaves, a 74 % smaller leaf area and a 72 % lower leaf biomass than the no-exclusion branches in the second year (Fig. 1a, c, e). A similar trend existed between the bird-exclusion and reference branches (Table 1; Fig. 1b, d, f). The bird-exclusion branches had 94 % fewer leaves, an 87 % smaller leaf area and an 80 % lower leaf biomass than the reference branches in the second year, but there were no differences in any of the leaf traits between the two in the first year (Fig. 1b, d, f). The no-exclusion branches and the reference branches had similar numbers of leaves with similar leaf areas and biomasses (Fig. 1b, d, f), all of which were higher than those for the bird-exclusion branches, indicating that bird exclusion had negative, branch-level effects on willow leaves that did not extend to other branches on the same trees.

### Leaf damage

Percent leaf damage was similar between the bird-exclusion and no-exclusion branches during the pre-treatment

period (Table 1; Fig. 2a). The bird-exclusion branches had 2.6 times the leaf damage compared to the no-exclusion branches in the first year after the treatment (Fig. 2a). By the second year, the bird-exclusion and no-exclusion branches had similar levels of leaf damage (Fig. 2a). However, the bird-exclusion branches had significantly smaller leaf areas in the second year (Fig. 1c), so a similar percentage of leaf damage may have had a disproportionately large impact on the bird-exclusion branches. The reference branches had similar levels of leaf damage to that of both the bird-exclusion and no-exclusion branches (Table 1; Fig. 2b).

### Catkin and bud count

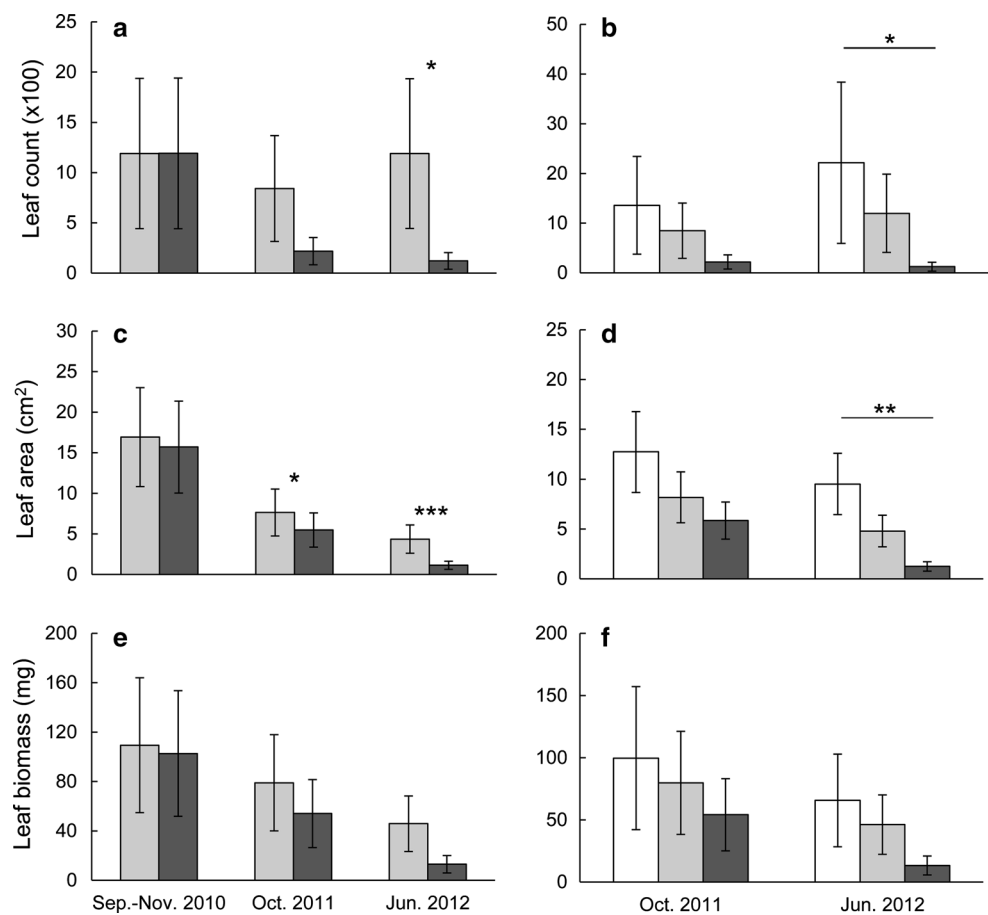
Both catkin and bud counts exhibited similar patterns. The bird-exclusion branches had fewer catkins and buds than the no-exclusion branches in the second but not the first year after the experiment began (Table 2; Fig. 3a, c). In fact, only one and two of the 11 bird-exclusion branches produced catkins and buds, respectively, in the second year, compared to seven of the 11 no-exclusion branches that produced catkins and buds. The reference branches had catkin/bud counts that were similar to those of the no-exclusion branches but higher than those of the bird-exclusion branches (Table 2; Fig. 3b, d), suggesting that the negative effects of bird exclusion on willow catkins and buds were limited to the bird-exclusion branches and did not extend to other branches on the same tree.

### Arthropod abundance

The Lepidoptera larvae, sap sucker and aphid abundances were similar between the bird-exclusion and no-exclusion



**Fig. 1** Leaf count (**a, b**), leaf area (**c, d**) and leaf biomass (**e, f**) of *Salix warburgii* on the bird-exclusion (black bars), no-exclusion (gray bars) and reference (open bars) branches. Sample sizes are 66 and 62 for leaf count (**a, b**), which comprise 11 bird-exclusion, 11 no-exclusion and nine reference branches for each time period; sample sizes are 65 (**c, d**) and 61 (**e, f**) for leaf area/biomass, which comprise 11 bird-exclusion branches in September–November 2010 and in June 2012, and ten bird-exclusion branches in October 2011, along with 11 no-exclusion and nine reference branches for each time period. Error bars SE, asterisks significant differences in contrast comparisons (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )



branches across all time periods (Table 3; Fig. 4a, c, e). Spider abundance was similar between the bird-exclusion and no-exclusion branches during the pre-treatment period but increased on the bird-exclusion branches 1 year after the experiment began (Fig. 4g). The reference branches had arthropod abundances similar to both the bird-exclusion and no-exclusion branches across all taxa (Table 3; Fig. 4b, d, f, h). Given the large variability associated with arthropod abundance values, it is difficult to assess the effects of bird exclusion on these values. Nevertheless, across all taxa, there appeared to be a trend of higher arthropod abundances on the bird-exclusion branches during the post-treatment period.

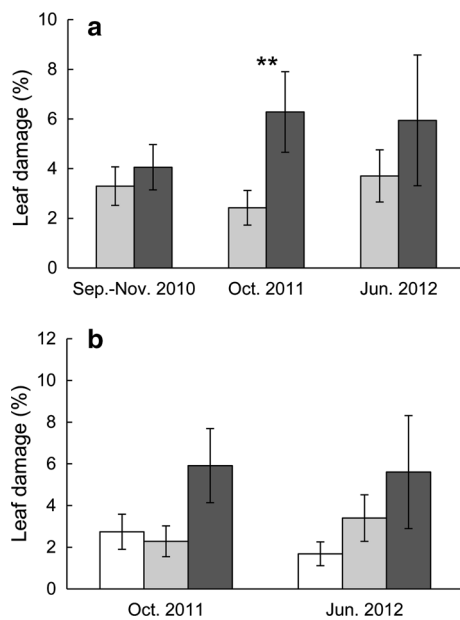
## Discussion

This study provided empirical findings of the effects of trophic cascades from avian predation on willows in an urban ecosystem. By excluding birds from branches, we demonstrated branch-level cascading effects, which did not extend to the entire tree. Furthermore, to our knowledge this is one of the few studies that has demonstrated cascading effects on plant reproduction (but see Mols and Visser 2002; Hooks et al. 2003). Because willows are strong

colonizers in frequently disturbed ecosystems (Naiman and Décamps 1997; Wigington and Beschta 2000), the number of propagules they produce is likely to affect their long-term biomass and the associated ecosystem services that they provide. Therefore, our results suggest that protecting birds is likely to produce indirect benefits for wetland vegetation in urban ecosystems.

## Shading effects of netting

Netting inevitably shaded the branches despite our efforts to choose netting materials that would have low impacts on a plant's microenvironment (Supplementary Table S2). On the one hand, shading has been shown to reduce plant allocation to phenolics, increase foliar quality for herbivorous insects, and even lower birds' ability to locate insects on branches (e.g., Dudt and Shure 1994; Sipura and Tahvanainen 2000; Mäntylä et al. 2008). On the other hand, Sipura and Tahvanainen (2000) demonstrated that herbivorous beetles were more abundant on willows growing in open habitats than on clones placed under shade trees in the field. Furthermore, beetle larvae in the field performed equally well, if not better, on willows growing in open habitats than under shade. Some of these discrepancies



**Fig. 2** Leaf damage of *S. warburgii* on the bird-exclusion (black bars), no-exclusion (gray bars) and reference (pen bars) branches. **a** Experimental trees, **b** experimental and reference trees. Sample sizes are 45 (**a**) and 41 (**b**), which comprise 11 bird-exclusion and 11 no-exclusion branches in September–November 2010, six bird-exclusion and eight no-exclusion in October 2011, two bird-exclusion and seven no-exclusion in June 2012, and nine reference branches for each time period. Error bars SE, asterisks significant differences in contrast comparisons (\* $P < 0.05$ , \*\* $P < 0.01$ )

may be explained by the differences between laboratory and field conditions. For example, Sipura and Tahvanainen (2000) suggested that fluctuating temperature, which is associated with open habitats in the field, might be important to beetle development. Such environmental heterogeneity is often controlled or eliminated in laboratory settings. Although we were not able to quantitatively assess the effects of shade in our study, we did observe that specific leaf weight (SLW; leaf dry weight divided by leaf

area) was similar for the netted (bird-exclusion) and unnetted (no-exclusion and reference) branches. In October 2011, approximately 1 year after netting, the SLWs of the bird-exclusion, no-exclusion and reference branches were  $6.5 \pm 0.6$  mg/cm<sup>2</sup> (mean  $\pm$  SE,  $n = 6$ ),  $6.8 \pm 0.3$  mg/cm<sup>2</sup> ( $n = 8$ ), and  $6.9 \pm 0.4$  mg/cm<sup>2</sup> ( $n = 9$ ), respectively; in June 2012, approximately 1.5 years after netting, the SLWs of the bird-exclusion, no-exclusion and reference branches were  $6.2 \pm 1.1$  mg/cm<sup>2</sup> ( $n = 2$ ),  $6.0 \pm 0.3$  mg/cm<sup>2</sup> ( $n = 7$ ) and  $6.1 \pm 0.5$  mg/cm<sup>2</sup> ( $n = 9$ ), respectively. Because SLW tends to change with the microenvironment (e.g., Niinemets and Kull 1994; Veteli et al. 2003), this observation indirectly suggests that the shading effect of the netting may be minor in relation to the willows. Nevertheless, we caution that the observed magnitudes of effects related to bird exclusion should not be entirely attributed to avian predation.

### Bird-exclusion effect on arthropods

We were not able to demonstrate clear impacts of bird exclusion on the abundances of three major groups of herbivorous insects, Lepidoptera larvae, sap suckers (lace bugs and *I. seychellarum*) and aphids. Given the large variability associated with the arthropod abundance values, our ability to detect treatment effects was limited. There are at least two explanations for the large variability in arthropod abundance values. First, our sample size was likely low for some of the herbivores, particularly aphids. Of the three morphological aphid types, we tentatively identified one as the large willow aphid (*Tuberolachnus salignus*), which is known to cause serious damage to willow growth and biomass (Collins et al. 2001). Unfortunately, these aphids often move from branch to branch in a matter of a few days, making it extremely difficult to quantify their effects on a particular branch. Second, as part of the Salicaceae family, willows are known for using a broad range of phenolics as anti-herbivore defenses (Dudt and Shure

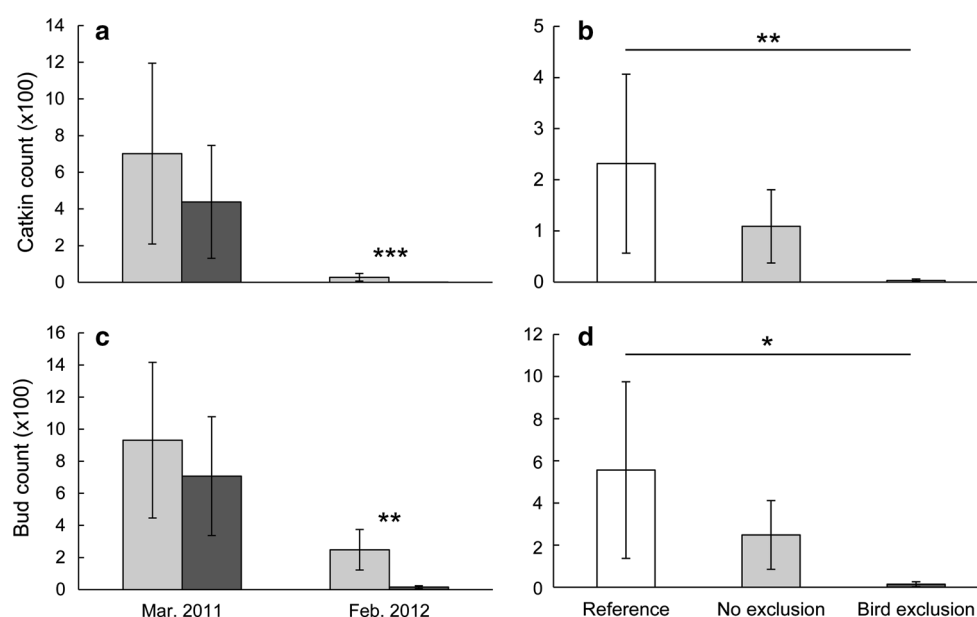
**Table 2** Effects of bird exclusion on catkin and bud count in *S. warburgii*

Effect	Num. <i>df</i>	Den. <i>df</i>	Catkin count		Bud count	
			<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Experimental trees						
Bird exclusion	1	20	45.42	<0.0001	8.34	0.009
Time	1	19	29.19	<0.0001	25.56	<0001
Bird exclusion × time	1	20	31.28	<0.0001	5.67	0.03
Tree sex	1	20	2.76	0.11	0.00	0.96
Experimental and reference trees <sup>a</sup>						
Bird exclusion	2	27	7.40	0.003	5.14	0.01
Tree sex	1	27	0.37	0.55	0.03	0.87

<sup>a</sup> Catkins and buds of the reference trees were sampled only once, in February 2012, thus, the time and interaction effects were dropped



**Fig. 3** Catkin (**a, b**) and bud counts (**c, d**) of *S. warburgii* on the bird-exclusion (black bars), no-exclusion (gray bars) and reference (open bars) branches. Sample sizes are 44 (**a, c**) and 31 (**b, d**), which comprise 11 bird-exclusion and 11 no-exclusion branches in March 2011 and in February 2012, and nine reference branches in February 2012. Error bars SE, asterisks significant differences in contrast comparisons (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )



**Table 3** The effects of bird exclusion on arthropod abundances in *S. warburgii*

Effect	Num. df	Den. df	Lepidoptera larvae <sup>a</sup>		Sap suckers <sup>a</sup>		Spiders <sup>a</sup>		Num. df	Den. df	Aphids <sup>b</sup>	
			F	P	F	P	F	P			F	P
Bird exclusion	1	17	1.48	0.24	0.42	0.52	3.20	0.09	1	11	1.9	0.20
Time	2	22	2.83	0.08	2.91	0.08	7.64	0.003	1	15	1.44	0.25
Bird exclusion × time	2	17	1.17	0.34	0.65	0.53	1.64	0.22	1	11	1.73	0.22
Tree sex	1	17	0.37	0.55	0.11	0.74	1.20	0.29	1	11	0.37	0.56

<sup>a</sup> Abundance of Lepidoptera larvae, sap suckers or spiders is the number of individuals per square meter of total leaf area on a branch

<sup>b</sup> Aphid abundance is the number of individuals per bud on a branch

1994; Fritz et al. 2001; Boeckler et al. 2011; Yoneya et al. 2012); consequently, even under the same nutrient and bird-exclusion treatments, strongly versus weakly defended willows can experience very different levels of herbivory (e.g., Sipura 1999). Because our study site is in a wetland under daily tidal influence and experiences occasional summer storms, the willows studied may exhibit high plasticity in their foliar chemistry and resource allocation ability. Such species- and site-specific characteristics can all contribute to the large variability in herbivore abundance. Despite the weak statistical power in each test, we did find a general trend towards higher arthropod abundance on the bird-exclusion branches across all taxa examined, including predatory spiders, suggesting that bird exclusion likely benefited arthropods.

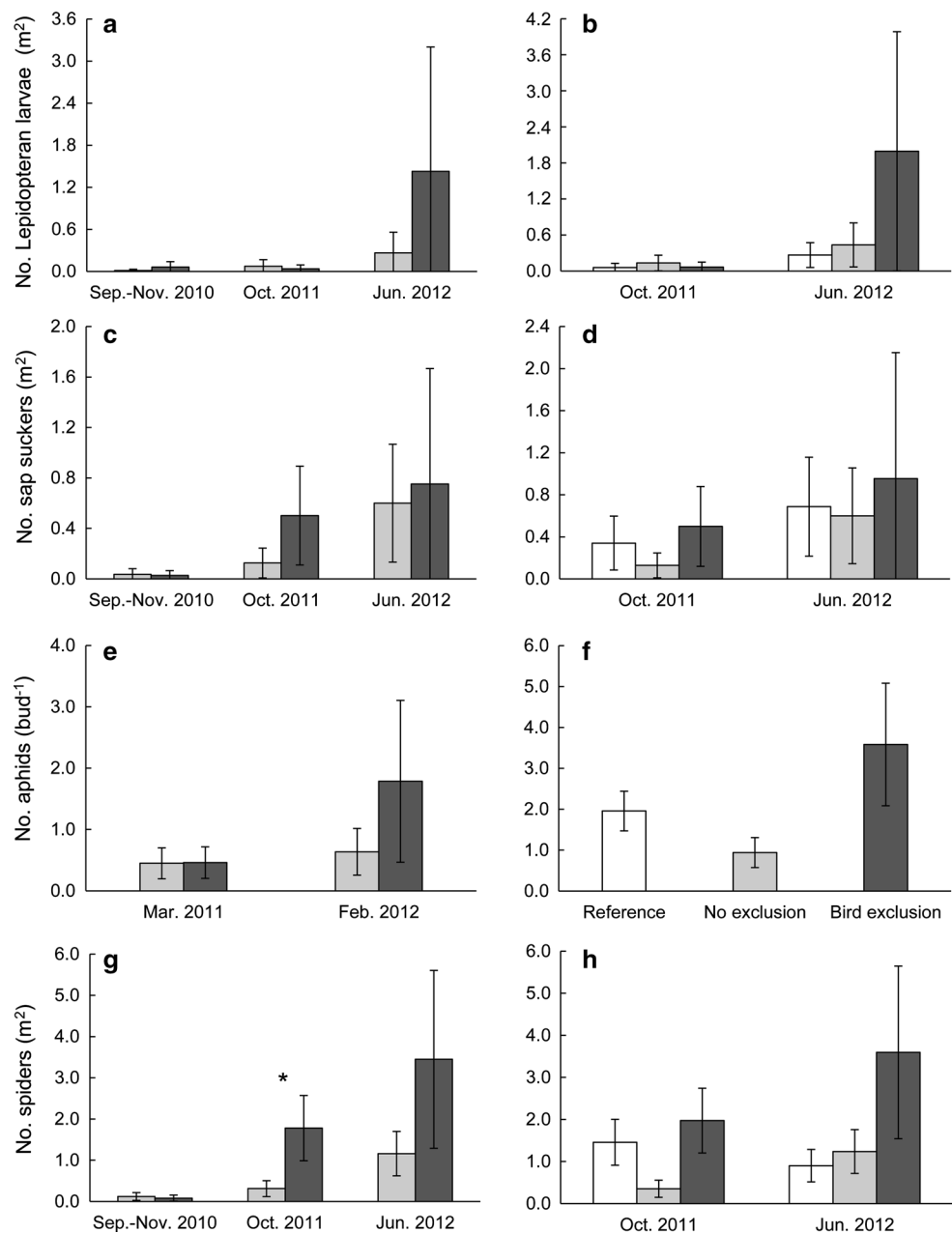
Interestingly, we did not find that the increase in spiders on the bird-exclusion branches helped reduce willow leaf damage or improve leaf performance, suggesting that spiders may not be very effective predators of herbivorous insects. Nevertheless, the degree to which bird exclusion

was mediated by the increase in spiders, which would require experiments that exclude spiders only, birds only and both, remains unclear.

### Branch-level versus tree-level response

In a study by Stolter (2008) poplar trees increased chemical defenses and reduced the palatability of new grown twigs, and they decreased chemical defenses and increased palatability of heavily browsed twigs at the same time. In another study by Crutsinger and Sanders (2005), the absence of aphid-tending ants doubled herbivory in the willow *Salix hookeriana* at the branch level. These studies suggest that trees and tree-dwelling arthropods can exhibit branch-level patterns that influence local herbivory. Therefore, branch-level bird exclusion may or may not result in whole-tree effects. Indeed, the reference and no-exclusion branches had similar values in all plant traits and for arthropod abundances, and they both had more leaves, buds and catkins, and larger leaf areas

**Fig. 4** The arthropod abundances on the bird-exclusion (black bars), no-exclusion (gray bars) and reference (open bars) branches of *S. warburgii*. **a, b** Lepidoptera larvae, **c, d** sap suckers, **e, f** aphids, **g, h** spiders. The sample sizes are 46 (**a, c, g**), 31 (**e**), 42 (**b, d, h**), and 18 (**f**), which comprise 11 bird-exclusion and 11 no-exclusion branches in September–November 2010 and in March 2011, seven bird-exclusion and eight no-exclusion branches in October 2011, two bird-exclusion and seven no-exclusion branches in February 2012 and in June 2012, and nine reference branches for each time period. Error bars SE, asterisks significant differences in contrast comparisons (\* $P < 0.05$ )



than the bird-exclusion branches. This suggests that bird-exclusion effects are likely limited to local branches and do not extend to other branches of the same tree. Although not statistically significant, the reference trees seemed to perform slightly better than the experimental trees (e.g., more leaves, buds, catkins). Therefore, it is still possible that bird exclusion on certain branches had a small effect on the no-exclusion branches. However, this pattern could also be explained by the generally larger trees that we used as a reference set (median heights for the reference and experimental trees were 10 m ranging from 4 to 13 m, and 5 m ranging from 3 to 7 m, respectively). We

did not intentionally select bigger trees as reference points; however, by the time we had the resources to add reference trees to our experiment, we had already netted the most readily available trees on site, leaving us with limited options for our reference trees. In many ecosystems, whole-tree manipulation can be challenging. However, as we demonstrated in this study, branch-level responses may not be easily scaled to the entire tree. We suggest that observational studies such as comparing areas with different levels of bird abundance, or manipulative experiments using multiple-branch treatments, may be considered in future studies where whole-tree manipulation is difficult.

## Temporal scale of trophic cascades

In the meta-analysis by Mäntylä et al. (2011), the authors found that despite the fact that plants outside bird exclosures exhibited less leaf damage and mortality, and higher biomass than those inside the exclosures, plant growth did not seem to be affected by bird exclosures. They speculated that the relatively short duration of most of the studies reviewed, from 23 days to 36 months (median of 12 months), may explain the lack of cascading effects on plant growth. Similarly, an earlier review by Borer et al. (2005) noted that the length of the study period can affect the outcome of trophic cascades. Our study lasted 20 months, which is a relatively long duration compared to previous studies. We found that different plant traits indeed responded to bird exclusion at different temporal scales. Specifically, bird exclusion caused higher leaf damage 1 year after netting. However, it was not until the second year that we saw the negative effects of bird exclusion on leaf, bud and catkin counts, suggesting that adult trees may exhibit delayed cascading effects. This study illustrates the importance of the temporal scale in designing trophic cascade studies.

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