



Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania

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ABSTRACT

Aim Biological invasions pose one of the most severe threats to global biodiversity. Still, invasions can create positive ecological relationships and services, which can sometimes result in challenges for conservation efforts. A case in point is the invasion of alien plants that form mutualisms with native frugivorous birds. Here, we examined the correlation between honeysuckles (*Lonicera* spp.) and the bird communities in a landscape of central Pennsylvania during the fall months.

Location State College area in central Pennsylvania, USA.

Methods We conducted point counts to quantify the abundance of birds and fleshy-fruited plant species within a 187.5 km² landscape that included forested, urban and agricultural lands. We also compared fruit-removal rates for a native fruiting plant under low and high *Lonicera* densities.

Results The abundance of birds showed a strong positive association with *Lonicera* fruits, with the abundance of *Turdus migratorius* and *Dumetella carolinensis* showing the strongest correlations. We also found that fruit-removal rates were 30% larger for a native plant species in areas of high *Lonicera* density compared to a site with low density of *Lonicera*.

Main conclusions Our results suggest that *Lonicera* may currently serve as a main axis for the organization of bird communities and the networks of frugivore–plant interactions in central Pennsylvania. Since populations of key bird frugivores may be currently depending on *Lonicera* resources, we argue that control measures should account for the negative effects that the loss of this fruit resource could have on populations of native consumers in highly invaded regions.

Keywords

Biological invasions, *Dumetella carolinensis*, frugivory, *Lonicera*, mobile links, mutualisms, *Turdus migratorius*.

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INTRODUCTION

Biological invasions are considered one of the most severe threats to global biodiversity (Higgins *et al.*, 1999; Pimentel *et al.*, 2005). Biological invasions may alter the species composition, structure, nutrient cycling, primary productivity and hydrology of native communities and ecosystems (Vitousek, 1990), which can ultimately lead to species loss (Mack *et al.*, 2000; Olden, 2006). In contrast to these negative effects of biological invasions, Lugo (2004) suggests that biological invasions may aid in the recovery of an ecosystem after a

disturbance (i.e. external ecological memory; see also Lundberg & Moberg, 2003). The success of invading alien species has been attributed to factors that include an ability to thrive in conditions that may be adverse to native species, a capacity to outcompete native species, and an ability to form successful mutualisms with other exotics or native species (Luken *et al.*, 1997; Callaway & Aschehoug, 2000; Lugo, 2004; Aslan & Rejmánek, 2010). While the role of competition in biological invasions has been thoroughly documented (Callaway & Aschehoug, 2000; Mack *et al.*, 2000; MacDougall & Turkington, 2005), the role of mutualisms in determining the success

of an invasion has received considerably less attention (Richardson *et al.*, 2000; Rudgers *et al.*, 2005; Milton *et al.*, 2007), especially when it concerns a partnership between alien species and native ones (Kaiser-Bunbury & Müller, 2009). This lack of attention in the literature is intriguing because mutualistic services need to be received, such as pollination and seed dispersal by animals, in order for the alien plants to complete their life cycles or to become successful invaders (Richardson *et al.*, 2000).

An important fraction of invasive plant species bears fleshy fruits and are dispersed by fruit-eating animals (i.e. frugivores) (Richardson *et al.*, 2000; Kueffer *et al.*, 2009), which is not surprising given that most woody shrub and tree species world-wide are dispersed by frugivores (Herrera, 2003). Among mutualistic frugivores, birds are probably the most important seed dispersers for both native and alien woody species because of their high abundance, species diversity and mobility. The plant–frugivore mutualism can occur not only with local resident native bird species, but also include migratory species that have the potential to form dependencies that bridge distant communities at global scales (Levey, 1988; Levey & Stiles, 1992; Bascompte & Jordano, 2007). Abundant and generalistic migrant avian frugivores can thus function as ‘mobile links’ that connect species, communities and ecosystem processes in significant ways (Mills *et al.*, 1993; Lundberg & Moberg, 2003). Therefore, it is necessary to have a clearer understanding about the influences – and possible subsidies – that invasive alien fruiting species have on generalist frugivores that serve as mobile links, a perspective that is lacking in discussions on biological invasions and their consequences.

Increases of fleshy-fruited alien plants could potentially result in higher frugivore diversity and population densities, or in regional re-arrangements of avian frugivore communities (Boren *et al.*, 1999; Reichard *et al.*, 2001). In turn, changes in the frugivore community could trigger structural changes in local communities by affecting the distribution and availability of frugivory services and the structure of mutualistic networks (Terborgh *et al.*, 2008; Bascompte, 2009). Novel interdependencies are important to understand given that in this context, control and eradication of alien plants species could result in the severing of key novel mutualisms and negatively impact local native bird communities. The severing of novel mutualisms could cascade through the rest of the community and temporarily impact not only frugivore populations, but also other plant species that rely on shared frugivores for dispersal (Bascompte & Jordano, 2007; Carlo *et al.*, 2007; Terborgh *et al.*, 2008).

As estimated by The Nature Conservancy, the control of invasive species in the United States costs 120 billion dollars per year, with invasive plants affecting approximately 100 million acres. The invasion of Asian honeysuckle species (*Lonicera* spp.) has come to the forefront of these conservation initiatives in the eastern United States. The honeysuckle family (Caprifoliaceae) includes many species of shrubs and vines with Amur (*Lonicera maackii*) and Morrow's honeysuckle (*Lonicera morrowii*) being the most abundant in central

Pennsylvania. The first reported successful cultivation of Amur honeysuckle in the United States dates back to 1903 in the Arnold Arboretum at Harvard University (Luken & Theiret, 1996). The plant was not seen to be naturalized until the late 1950s when the first report of naturalization came out (Luken & Theiret, 1996). From the 1960s to the 1980s, Amur honeysuckle was used by the USDA Soil Conservation Service for land reclamation and to improve bird habitat owing to its high flower and fruit production (Luken & Theiret, 1996). Now according to the USDA, Amur honeysuckle is invasive in 27 states (banned or prohibited in two) and Ontario, while Morrow's honeysuckle is considered invasive in 29 states in the United States (banned or prohibited in three) and four provinces of Canada. In addition, both of these species have been shown to be consumed in high quantities by a wide range of bird species (Ingold & Craycraft, 1983; Reichard *et al.*, 2001; Bartuszevige & Gorcho, 2006).

To further our understanding of how plant invasions affect the environment, we need to look at all aspects of their ecology with mutualisms being a major component. Although understanding the distribution and abundance of animal populations is a complex multivariate problem, food resources are invariably one of the main explanatory factors (Morrison *et al.*, 2006). It will be expected that if the two partners of the *Lonicera*–bird mutualism depend and benefit from each other, then the distribution and abundance of one would predict the distribution of the other (McKey, 1975). This spatial concordance can be hypothesized to result in differential rates of frugivory at areas with high *Lonicera* abundance compared to sites with low or no *Lonicera* (competition or facilitation, Carlo, 2005). To study the concordance of bird and fruiting plant communities, we conducted a landscape-scale survey. We specifically examined the relationship of the bird community with the abundance and distribution of invasive *Lonicera* spp. in Centre County, Pennsylvania. In addition to the census, we conducted an experiment to determine the potential of *Lonicera* to affect fruit-removal rates of a native plant species. Our ultimate goal was to hint at how much the frugivorous bird communities are currently relying on *Lonicera* spp. invasions, and to discuss potential consequences of *Lonicera* eradication efforts.

METHODS

Point counts

Bird censuses and observations were conducted from 1 September through 31 October of 2009 to coincide with the fall fruiting peak of the fleshy-fruited community (Gorcho, 1987). To select point count locations, a rectangular grid was laid over a map of the State College area in Centre County, Pennsylvania (Fig. 1). The grid was made of 30 2.5 × 2.5 km squares and measured 15 × 12.5 km. The grid was centred at the Penn State University Campus (40°47'44"N 77°51'52"W) and extended in all directions to include urban environments, forested lands (e.g. State Game Lands and Mount Nittany) and



Figure 1 The grid used for determining the point count locations measured 15×12.5 km and was centred over the Penn State campus, along the main axis of the valley (Happy Valley) as shown in the aerial photograph. The actual point count locations are represented by the white dots near the centre of each cell.

agricultural fields. At the centre of each square, a point count was located in the map. Because the main goal of the study was to examine the relationship between fleshy fruits and birds, points that landed on agricultural fields, inaccessible lands, highways and other areas that lacked any woody vegetation were relocated to the nearest vegetation patch. Point counts were sampled in a random order, first in September and then a second time in October following the same order as in September. After arriving at a point count location, the observer waited 2 minutes before conducting a 5-minute count to reduce any disturbances caused by arrival. To minimize observer bias, one person (J. Gleditsch) conducted all point counts. The observer only recorded the species of bird and number of individuals that were within a 30-m distance of the point (excluding flyovers). The weather conditions, start and finish times, were also recorded.

Fleshy-fruit counts

A fruit census was also conducted at each bird point count location covering the same area as the point count (a circle with a radius of 30 m). The observer recorded the fruit

abundance (ripe and unripe) of each plant species using a rank scale following the method in Saracco *et al.*, 2004. Each plant species was assigned a fruit score with 0 = 0, 1 = 1–10, 2 = 10–100, 3 = 100–1000, 4 = 1000–10,000, 5 > 10,000 (Saracco *et al.*, 2004).

Fruit-removal experiment

We conducted a fruit-removal experiment using 78 potted black nightshade plants (*Solanum americanum* – greenhouse grown) bearing ripe fruit in September of 2009 at two sites in the State College area in Centre County, PA. The objective was to test for differences in fruit-removal rates for a native plant species in two contrasting backgrounds. One location was a forested area with the understory almost completely covered by *L. maackii* and *L. morrowii* (Thompson Woods Preserve, $40^{\circ}48'05''N$ $77^{\circ}50'17''$), while the other, also forested, had a much lower abundance of the aforementioned species and the same abundance of both native and other alien fleshy-fruited species (Sunset Park, $40^{\circ}48'19''N$ $77^{\circ}52'29''$). The two study sites were 3.2 km apart, and *S. americanum* and bird frugivores were relatively common at both sites with both transects oriented in similar directions, and had similar abiotic conditions (i.e. water availability, proximity to roads, and human usage).

In each site, thirteen fruit-removal points were established at 50-m intervals. Three pots, each with one *S. americanum* plant, were placed at each point. The number of fruit across the three plants was controlled to be 500 fruits (± 100). Any flowers and extra fruits were removed. A total of six infructescences were individually tagged with a fine wire (same method as in Carlo, 2005), with the total tagged crop ranging between 25 and 40 fruits. Tagged fruits were counted a total of four times at 5-day intervals. The stem density of fruiting shrubs was determined in a 3 m radius from each point. Survival analysis was used to test for differences in fruit-removal rates between sites, and *t*-tests were used to compare stem densities of fleshy-fruited plants within and across sites in JMP (SAS Institute., 2007).

Statistical analyses of bird and fleshy fruit surveys

For analysis, we averaged the detections of each bird species per point count across censuses. Given that the fruits of the two *Lonicera* species are almost identical, their fruit counts were combined for analyses by adding the mid-points of the abundance categories (i.e. 1 = 5.5, 2 = 55, 3 = 550, etc., with the highest possible category truncated at 10,000, see Carlo *et al.*, 2003). We performed first a non-metric multidimensional scaling (NMS, in PC-ORD, McCune & Mefford, 1999) ordination, with correlation distances and a varimax axis rotation, on the entire dataset using a matrix of 56 species (birds and fruit species) \times 30 rows (point counts). We used a random starting configuration for 15 runs with real data and 30 runs with randomized data. The instability criterion for accepting a solution was 0.0001 over the last 10 iterations.

We used correlation analyses to examine the relationship between frugivore abundance (response variable) and fruit abundance scores. For this, we looked at the correlation between individual and pooled bird species with the pooled fruit scores of plant species and the correlation between individual and pooled bird species with *Lonicera* spp. fruit scores. We also used general linear models (GLM, Poisson error distribution in R version 2.11.1, The R Foundation for Statistical Computing, 2010) to examine the influence of landscape variables on the abundance of *Turdus migratorius* and *Dumetella carolinensis*, the two most abundant avian frugivores. The percentages of three land cover types (forest, agriculture, urban) around the survey points were estimated using recent aerial photographs and ArcGIS software version 9.3 (ESRI, Redlands, CA, USA). Per cent land use types were calculated by constructing a 200 m radius circle around each point using ArcGIS software. A land cover diversity index was also constructed using the Simpson's diversity index (1-D) to examine how land cover diversity affected bird abundance (see also Alberti *et al.*, 2001 for use of diversity indices in land cover analysis). To calculate the Simpson's diversity index of land cover, we considered the number of patches of each land cover type in the formula as the number of 'individuals' and the land cover types as the 'species' (Krebs, 1989). To perform the GLMs, we constructed three different models for the three different land cover types since these values were not independent of one another (to avoid the interaction between the multicollinear landscape variables). Each GLM contained a land cover parameter, *Lonicera* fruit abundance, and the diversity index parameters with interactions up to the third degree. The GLMs were stepped by removing the least significant value until the lowest Akaike's information criterion (AIC) was achieved.

RESULTS

We recorded a total of 34 species of birds and at least 22 species of fleshy-fruited zoochorous plants (see Appendix S1 & S2 in Supporting Information). In censuses, frugivorous robins and catbirds were the two most abundant and frequently detected bird species, accounting for 31.7% (21.1% robins and 10.6% catbirds) of all detections. Catbirds were the most widespread and detected in 56.7% of counts, while robins were detected in 50% of counts (altogether detected in 70% of points; see Appendix S1). The most abundant fruit crop was by far *Lonicera* spp. with 53.6% of the total fleshy fruit crop in the landscape. Another alien fruiting species, *Ligustrum obtusifolium*, ranked second in total crop size with 10.1% (Fig. 2). *Lonicera* species were also the most widespread and were detected in 70% of the sample points, again trailed not so closely by *L. obtusifolium* at 33.3% of counts (see Appendix S2).

The community-wide NMS ordination shows that the most important bird and fruiting plant patterns in terms of species diversity and abundance are driven by the abundance patterns of bird and plant species that responded more strongly to NMS

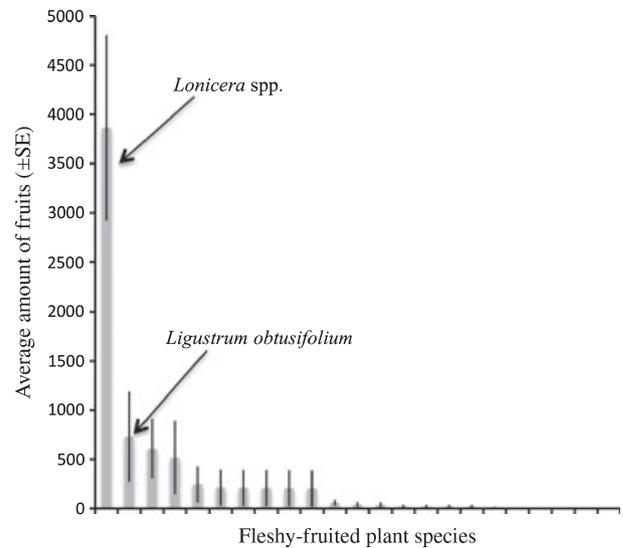


Figure 2 *Lonicera* spp. fruits were by far the numerically dominant fruit in the plant communities of a landscape in Central Pennsylvania. Bars are the average amount of fruit for each fleshy-fruited plant species. The number of species detected totals to 24, six of which are considered invasive.

axis-1. For example, six species of bird and six species of plants had strong correlations with axis-1 of the NMS ordination. Among birds, the American robin (*T. migratorius*) and the grey catbird (*D. carolinensis*) had the strongest positive correlations with NMS axis-1 (Fig. 3). For the fruiting plant community, NMS axis-1 was most strongly correlated with *Lonicera* and *L. obtusifolium* (Fig. 3). Of all bird and plant species, *Lonicera* had the highest correlation score on NMS axis-1, followed closely by American robins (Fig. 3). There were a total of three alien species of fruiting plants that had strong positive correlations with NMS axis-1, with only one native fruiting plant – *Cornus* spp. – showing a strong correlation with the main ordination axis.

In pairwise comparisons between fleshy fruit abundance and birds (i.e. that were important in the NMS ordination), we found the following. The abundance of catbirds, robins, and American goldfinches (*Carduelis tristis*) were positively correlated with *Lonicera* fruit, while counts of red-bellied woodpeckers (*Melanerpes carolinus*), downy woodpeckers (*Picoides pubescens*) and dark-eyed juncos (*Junco hyemalis*) were negatively correlated with *Lonicera* fruit (Table 1). However, when looking at the correlations between birds and all available fruits, we found that positive relationships were weaker (i.e. smaller correlation coefficients) than when considering only fruits of *Lonicera*. In fact, *Lonicera* fruit abundance rank was a very strong predictor of average bird abundance (Fig. 4a) while the combined crops of all fleshy-fruited plants did not explain bird abundance as well (Fig. 4b). Clearly, these pooled species correlations were largely driven by the numerical dominance of frugivorous catbirds and robins and their response to *Lonicera* fruits since the abundance of birds such as juncos, woodpeckers and others seem not to be as influenced by fruit abundance

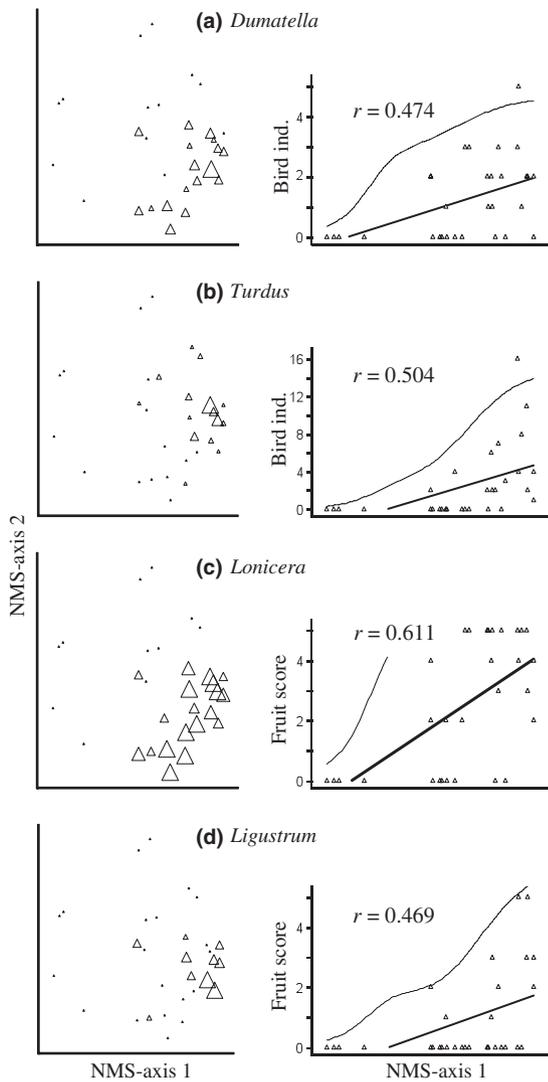


Figure 3 In a non-metric multidimensional scaling ordination (NMS), strong positive correlations of birds with axis-1 are mirrored by the correlations of the most abundant fruiting plant species. The left column is the spread of the points in the ordination with the size indicating the number of that species at that point. (a) The ordination of grey catbird (*Dumetella carolinensis*) showing its strong correlation with NMS axis-1. (b) The ordination of American robin (*Turdus migratorius*). (c) The ordination of *Lonicera* species (*L. maackii* and *L. morrowii*). (d) The ordination of Japanese Deciduous privet (*Ligustrum obtusifolium*). (Final Configuration: three dimensional; Stress = 15.22502; Instability = 0.00077; 400 iterations).

(Fig. 4c,d). The relationship between catbirds and *Lonicera* was so tight that not even a single catbird was detected at plots with few or no *Lonicera* fruits, despite that often such plots had other ornithochorous fruits present (e.g. *Elaeagnus umbellata*, *Rhamnus cathartica*, *Rosa multiflora*, *Berberis* sp., *L. obtusifolium*, *Vitis* sp.).

When looking at the influence of land cover types on the numerically dominant bird frugivores (i.e. catbirds and robins), we found that the land cover around each point did not have a significant effect on the frugivore abundance in any

Table 1 The three bird species that had the strongest positive correlations with axis-1 of a non-metric multidimensional scaling ordination (NMS) were also positively correlated with the fruit abundance of *Lonicera* spp., and to a lesser extent with the total fruit abundance (pooled fruiting species) in pairwise linear regressions. Represented are the species (both bird and plant) that were strongly correlated (positively and negatively) with NMS axis-1. The pairwise regressions are shown for *Lonicera* spp. and bird species, and for total fruit and bird species. Pairwise regressions between *Lonicera* and other fruiting species highly correlated with NMS axis-1 are also shown.

Species	Regression w/ <i>Lonicera</i> spp.*fruit		Regression w/ total fruit	
	r^2	P	r^2	P
<i>Dumetella carolinensis</i>	0.561	< 0.0001	0.376	0.0003
<i>Turdus migratorius</i>	0.171	0.023	0.131	0.049
<i>Carduelis tristis</i>	0.104	0.081	0.032	0.170
<i>Junco hyemalis</i>	0.047	0.246	0.177	0.020
<i>Melanerpes carolinus</i>	0.047	0.246	0.177	0.020
<i>Picoides pubescens</i>	0.018	0.476	0.164	0.026
<i>Ligustrum obtusifolium</i> *	0.096	0.095	–	–
<i>Phytolacca americana</i>	0.083	0.121	–	–
<i>Elaeagnus umbellata</i> *	0.127	0.053	–	–
<i>Malus</i> spp.	0.048	0.246	–	–
<i>Crataegus</i> sp.	0.065	0.092	–	–
<i>Prunus</i> spp.	0.066	0.171	–	–
<i>Rosa Multiflora</i> *	0.001	0.861	–	–

*Considered invasive in PA by the Pennsylvania Department of Conservation and Natural Resources.

of the three models (Table 2). The Simpson's diversity index used for land cover also showed no significant effect on frugivore abundance, except in the GLM model that included agriculture cover (Table 2). *Lonicera* fruit abundance was the only parameter that in all three models had a significant and strongest positive effect on frugivore abundance (Table 2). The results of our study point out that in the Centre County region, effects of landscape variables measured were weak and alien *Lonicera* fruit abundance was the best predictor of frugivore abundance.

Fruit-removal experiment

We found a significant difference in fruit-removal rates for *S. americanum* depending on the density of *Lonicera* in their neighbourhood. The higher rate of fruit removal occurred in Thompson Wood Preserve with a much higher *Lonicera* density, while the lower rates were found in Sunset Park, which had a lower *Lonicera* density (Kaplan–Meier: $\chi^2 = 53.6631$, d.f. = 1, $P < 0.0001$; Fig. 5). After 20 days, 96% of fruit had disappeared from tagged infructescences at Thompson Wood Preserve, while in Sunset Park, only 67% had been removed (Fig. 5). This represents almost a 30% difference between the site with a high and a low density of *Lonicera*. The two sites differed significantly in *Lonicera* density ($t = 4.6519$,

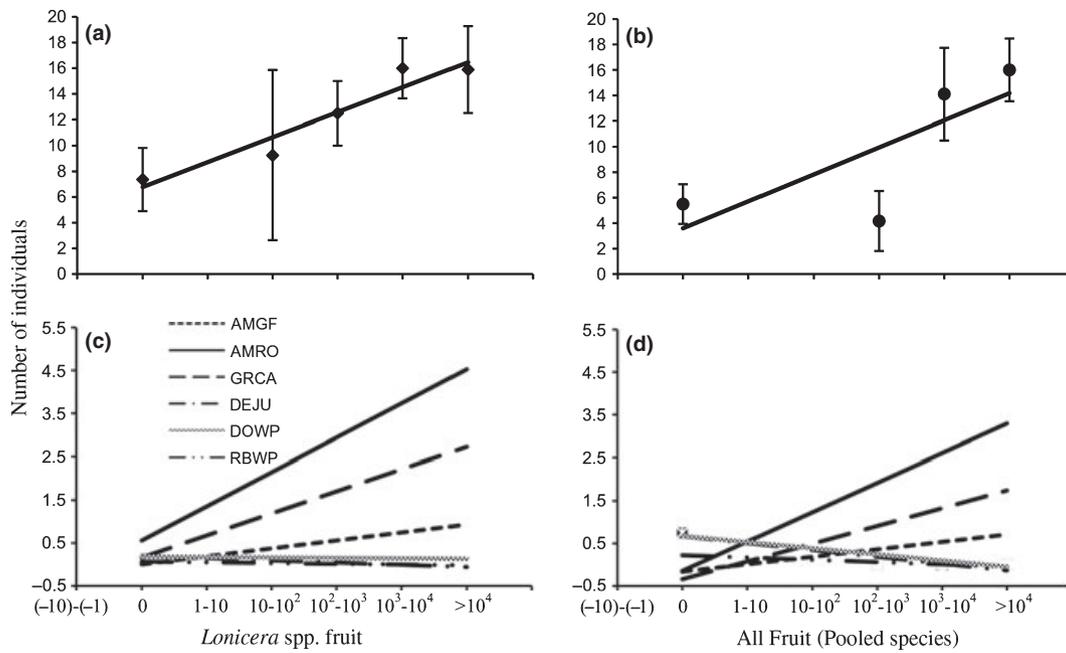


Figure 4 When the correlation of the total bird abundance and *Lonicera* spp. is compared to the bird abundance correlation with the fruit of all pooled plant species, it is evident that honeysuckle is the main driving factor for the abundance of birds. This correlation holds for some pairwise comparisons. (a) The linear correlation of average total number of birds with *Lonicera* spp. fruit abundance (with log(# of birds): $N = 30$, $r = 0.5149$, $P = 0.0036$). (b) The linear correlation of average total number of birds with total fruit abundance (with log(# of birds): $N = 30$, $r = 0.3999$, $P = 0.0285$). (c) Simple regression lines fitted between the average number of bird individuals of bird species correlated with non-metric multidimensional scaling (NMS) axis-1 (see Fig. 3, Table 1) and the fruit abundance of *Lonicera* spp. at point counts displays a stronger effect of *Lonicera* on frugivorous species than (d) the effect of pooled fruit abundance on such bird species.

$P = 0.0002$, d.f. = 26) with a mean stem density of 2.63 stems m^{-2} (± 0.52 SE) at Thompson Wood Preserve and a mean stem density of 0.17 stems m^{-2} (± 0.08 SE) at Sunset Park. Furthermore, Sunset Park had a significantly higher density of other fleshy-fruited shrubs (2.94 stems $m^{-2} \pm 0.64$) than *Lonicera* density ($t = 4.2814$, $P = 0.0004$, d.f. = 26). Between the two sites, the abundance of non-*Lonicera* fleshy-fruited plants did not differ significantly ($t = -0.7001$, $P = 0.4902$, d.f. = 26; Appendix S3).

DISCUSSION

In this study, we found that the fruit abundance of two invasive alien species of *Lonicera* (*L. morrowii* and *L. maackii*) in a central Pennsylvania landscape was a strong predictor of bird abundance (Table 1, Figs 3 & 4a). The *Lonicera*–bird correlations were strongest for native frugivorous bird species such as robins (*T. migratorius*) and catbirds (*D. carolinensis*). Some non-frugivorous species of bird such as woodpeckers showed strong negative correlations with *Lonicera* and likely reflect the disturbed and/or early-successional habitat characteristics that are favoured by *Lonicera* (Luken & Theiret, 1996). Because *Lonicera* fruits constitute a massive food resource that accounted for more than half of all fleshy fruits available on the landscape (Fig. 2), our findings suggest that novel interdependencies have formed between *Lonicera* and two of the most important native avian frugivores in the region.

Our results show that the composition of bird communities in the study area can be shaped in a predictable way largely by the availability of fruit from invasive *Lonicera* species (Figs 3 & 4, Table 1). Frugivore detectability patterns in association with the alien plant community could imply the emergence of important local interdependency of native birds on newcomer species. Conversely, frugivore seed dispersal may further strengthen the invasiveness of species like *Lonicera* on the landscape by creating high propagule pressures at already occupied sites, which is so typical of zoochorous dispersal patterns (Aukema & Martínez del Río, 2002; García *et al.*, 2009). The strength of the positive interaction between avian frugivores and alien fruiting plants is most prominent in the case of the catbird since the species was not detected at *Lonicera* fruit levels of < 100 fruits per plot. Strong correlations between robins and *Lonicera* were also found in this study and are in agreement with results of at least one other study (see Reichard *et al.*, 2001; Watling & Orrock, 2010). For example, in Pennsylvania, catbirds and robins have experienced significant increases in their populations during the last 43 years (354% and 215%, respectively; USGS Breeding Bird Survey, 2010) and it is a possibility that the *Lonicera* invasions may have progressed hand-in-hand with the growth and spread of local frugivore populations. It is possible then that rapid reductions and/or eradications of *Lonicera* could negatively impact bird populations in the region, especially of birds that rely heavily on fruit in the fall. For example, losses and/or

Table 2 The land cover type around point counts did not significantly affect the frugivore abundance according to stepped general linear model (GLM) analyses. Included in the table are the statistics for each parameter in each stepped GLM for each land cover type. The bolded parameters have a significant affect on frugivore abundance. *Lonicera* fruit abundance was the only parameter to have an affect across all three GLMs. The response variable was the abundance of the most common bird frugivores (*Turdus migratorius* and *Dumetella carolinensis*).

Model	Parameter	Estimate	SE	z-value	P > z	AIC
Agriculture	Agriculture cover (%)	1.4269	0.8292	1.7210	0.0853	161.97
	Lonicera fruit abundance	0.5287	0.0962	5.4930	< 0.0001	
	Diversity index	-1.2464	0.4474	-2.7860	0.0053	
	Ag: Lonicera	-0.6498	0.2676	-2.4280	0.0152	
	Ag: Lonicera: Diversity	0.5020	0.2167	2.3170	0.0205	
Forest	Forest cover (%)	0.2466	0.3370	0.7320	0.4643	156.79
	Lonicera fruit abundance	0.3881	0.0742	5.2280	< 0.0001	
	For: Diversity	-3.9410	2.2488	-1.7530	0.0797	
	For: Lonicera: diversity	0.4608	0.4880	0.9440	0.3449	
	Urban	Urban cover (%)	-1.1656	0.9030	-1.2910	
Lonicera fruit abundance	0.3075	0.0790	3.8940	< 0.0001		
Urb: Lonicera	1.0194	0.5110	1.9950	0.0461		
	Urb: Lonicera: Diversity	-0.7501	0.5207	-1.4410	0.1497	

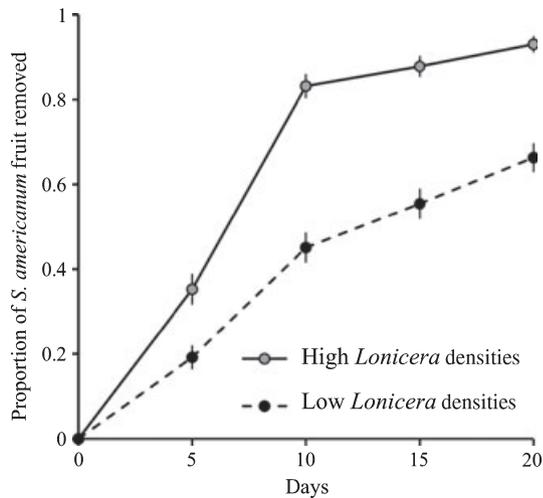


Figure 5 A higher fruit-removal rate was found for a bird-dispersed native nightshade species (*Solanum americanum*) in an area with a high *Lonicera* spp. stem density ($2.63 \text{ stems m}^{-2} \pm 0.52 \text{ SE}$) than in an area with a low density ($0.17 \text{ stems m}^{-2} \pm 0.08 \text{ SE}$).

declines in bird frugivore populations have been shown in studies that have experimentally removed fleshy fruits from habitats in the Block Islands (Parrish, 2000), longleaf pine savannas in South Carolina (Borgman *et al.*, 2004) and the Amazon (Moegenburg & Levey, 2003).

Frugivore populations can also be affected by changes in land uses such as shifts to agriculture, logging and fragmentation (Boren *et al.*, 1999; Cordeiro & Howe, 2003). Landscape disturbances and habitat loss also diminish fruit resources and create new environmental conditions for frugivores and fruiting plants (Brothers & Spingarn, 1992). However, in our models, we found weak or no effects of landscape variables on

the abundance of common avian frugivores, while *Lonicera* fruits had strong positive effects (Table 2). Human-modified landscapes normally have more favourable environments for alien species (Shea & Chesson, 2002), and with little doubt, *Lonicera* has taken advantage of the anthropogenic activities in Centre County. Studies have shown that *Lonicera* establishes best near urban environments and in open forest sites where the canopy has been disturbed (Luken & Theiret, 1996; Hutchinson & Vankat, 1997). In fact, our model detected that the interaction between per cent urban cover and *Lonicera* fruit abundance had a significant positive effect on frugivore abundance (Table 2). Therefore, in highly disturbed landscapes of central Pennsylvania, the fall fruit abundance of native plants may be too low to locally sustain fall frugivore abundances at the levels currently possible with *Lonicera* (see also Luken, 1997).

Mutualistic interactions that occur with high frequency in communities are key for shaping the structure of mutualistic networks (Carlo *et al.* 2007, Bascompte, 2009). For example, by organizing (i.e. attracting) the abundance patterns of two of the principal bird frugivore species in the region, *Lonicera* may be indirectly modulating the dispersal of other plant species that include natives and other aliens as well (Carlo & Aukema, 2005; Saracco *et al.*, 2005). This contention is supported by the results of our fruit-removal experiment with *S. americanum* in which removal rates were about 30% higher in areas of high density of *Lonicera* compared to areas with a lower density of the alien plant. However, it remains to be tested whether such increases in fruit removal translate into higher recruitment rates for other species in highly invaded areas. For example, a study by Hutchinson & Vankat (1997) showed that native species experienced recruitment limitation in highly invaded areas by *Lonicera*. Further studies are needed to assess whether the fruit-removal facilitation that *Lonicera* could provide can outweigh the concomitant recruitment limitations it also

poses, as well as the operative spatial scales of both negative and positive effects (Wiens, 1989). Because our experiment was conducted in only two locations, caution need to be taken in generalizing the results and in ruling out alternative explanations. For example, differences in removal rates could have been as a result of the effects of unaccounted variables at local levels such as the relative quality and availability of other fruiting species, or to large-scale landscape variables affecting bird abundance. However, these alternatives seem improbable since the sites had similar landscapes and communities of fleshy-fruited plant species (see results from GLM models and Appendix S3).

Our results advise caution to be taken in conducting control and eradication practices since reductions in *Lonicera* could negatively impact frugivore abundance, which could have undesirable ecological and economical consequences in both local and distant regions. Frugivore losses can affect pollination, gene flow and recruitment, thus affecting the long-term dynamics of plant communities, their self-organizing properties and their resilience by disrupting functional frugivory and seed dispersal networks (Cordeiro & Howe, 2003; Howe & Miriti, 2004; Şekercioğlu *et al.*, 2004; Bascompte & Jordano, 2007; Terborgh *et al.*, 2008; García *et al.* 2010). By keeping abundant populations of mobile link organisms, such as catbirds and robins, the capacity of an ecosystem to recover from disturbances increases by enhancing the external ecological memory (Lundberg & Moberg, 2003). In the case of migratory frugivores, the severing of functional mutualisms will be felt not only in breeding grounds but also in stopover and wintering sites. Many migrants become opportunistic frugivores during fall migrations since insects become scarce as temperatures drop (Smith & Hatch, 2008), and abundant fruit crops such as *Lonicera* can provide critical support. However, Rodewald *et al.* (2010) found that *Lonicera* invasions can increase nest predation in urban environments, suggesting potential 'ecological-trap' effects of *Lonicera*. Additional research across relevant temporal and spatial scales is needed to fully understand the outcome of frugivore–*Lonicera* relationships.

Biological invasions are complex nonlinear phenomena in which alien species can have unexpected and/or counterintuitive effects in invaded communities, even with some effects being positive (Lugo, 2004; Didham *et al.*, 2005; Sax & Gaines, 2008). Thus, the ecological complexity, particularly the presence of novel mutualistic relationships between natives and well-established and widespread alien species, need to be well understood before incurring in costly eradication practices. For example, some successful eradication of well-established alien species can result in unexpected trophic cascades that shift communities to states that could be even less ecologically desirable than before the eradication (Bergstrom *et al.*, 2009). We argue that in the case of *Lonicera*, control can be locally targeted to favour the dispersal and establishment of native species where it seems fit. However, a widespread and rapid eradication of large patches of dense *Lonicera* across the landscape might pose a greater immediate threat to

biodiversity if control programs do not account for the loss of resources for bird mutualists and other consumers. Control measures should go hand-in-hand with the replacement – in ecological time – of critical food resources and services provided by ecologically or aesthetically undesirable alien plant communities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Bird community data.

Appendix S2 Plant community data.

Appendix S3 Fruiting plant community at the two fruit-removal sites.

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BIOSKETCHES

Jason Gleditsch's main research interests include bird–plant interactions focusing on how invasive species affect avian behaviour, breeding and migration. Other research interests include: invasion ecology, ecological interactions in human-dominated landscapes, avian biodiversity and conservation.

Tomás Carlo's main research areas are the study of patterns of seed dispersal by fruit-eating animals. Specifically, looking at the community-wide consequences that seed dispersal by vertebrates has on the organization and patterning of plant communities. Other research areas include: how alien species affect newly invaded ecosystems, applications of network theory to model animal–plant interactions, the role of generalist consumers in ecological communities, ecological interactions in human-dominated landscapes, parasitic plant biology and ecology, biodiversity and conservation in the Caribbean and isotopic ecology.

Author contributions: J.G. and T.C. conceived the ideas; J.G. collected the data; J.G. and T.C. analysed the data; and J.G. and T.C. led the writing.

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