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SHORT COMMUNICATION

Dispersal of invasive *Phytolacca americana* seeds by birds in an urban garden in China

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Abstract

Although seed dispersal is a key process determining the regeneration and spread of invasive plant populations, few studies have explicitly addressed the link between dispersal vector behavior and seedling recruitment to gain insight into the invasion process within an urban garden context. We evaluated the role of bird vectors in the dispersal of pokeweed (*Phytolacca americana*), a North American herb that is invasive in urban gardens in China. Fruiting *P. americana* attracted both generalist and specialist bird species that fed on and dispersed its seeds. The generalist species *Pycnonotus sinensis* and *Urocissa erythrorhyncha* were the most frequent dispersers. Seedling numbers of *P. americana* were strongly associated with the perching behavior of frugivorous birds. If newly recruited bird species use seedling-safe perching sites, the *P. americana* will regenerate faster, which would enhance its invasive potential. Based on our observations, we conclude that the 2 main bird vectors, *P. sinensis* and *U. erythrorhyncha*, provide potential effective dispersal agents for *P. americana*. Our results highlight the role of native birds in seed dispersal of invasive plants in urban gardens.

Keywords: dispersal patterns, frugivorous bird, *Phytolacca americana*, seed dispersal, urban ecosystem

INTRODUCTION

When exotic plant species are introduced to new habitats, whether or not they become invasive may depend on their interactions with resident organisms (Traveset & Richardson 2014). Invasion success could be limited by herbivory or competition (Cogni 2010). However, new mutualisms with pollinators or dispersers could facilitate invasion into new environments (Bascompte & Jordano 2007; Aslan 2011; Heleno *et al.* 2011).

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Often, fleshy-fruited invasive plants could easily form seed dispersal mutualisms with resident fauna, particularly birds (Aslan 2011; Gleditsch & Carlo 2011; Caughlin *et al.* 2012; Cruz *et al.* 2013). These mutualisms are usually diffuse, with many native birds interacting with an invasive plant species (Bascompte & Jordano 2007; Aslan 2011). Developing seed dispersal mutualisms with bird vectors not only enhances the regeneration potential of invasive plants in new habitats, but it also affects invasive spread (Gosper *et al.* 2005; Babweteera & Brown 2009). Generally, effective seed dispersal is quantified as the product of the number of seeds dispersed (quantity) and the recruitment probability of each dispersed seed (quality [Schupp 1993; Schupp *et al.* 2010; Hardesty 2011]). Most previous related studies have outlined the processes of effective seed dispersal for invasive plants in natural habitats and farmlands (Deckers *et al.* 2008; Babweteera & Brown 2009; Caughlin *et al.* 2012). The importance of exotic plants in urban contexts has, however, been underemphasized (Corlett 2005), which limits the general understanding of effective, bird-mediated dispersal of invasive plants.

Here, we evaluate the contribution of bird vectors to the effective dispersal of pokeweed (*Phytolacca americana L.*), a North American herb that is invasive in urban gardens in China. Specifically, we address the following questions: First, which frugivorous species are responsible for seed dispersal of *P. americana* and how do they differ in terms of seed removal? Second, where do the main dispersers perch after foraging and what potential contribution do they make to the recruitment of this invasive species?

MATERIALS AND METHODS

Species and study site

Phytolacca americana, a bird-dispersed herbaceous species, is native to North America that has been widely introduced in central Europe, the Mediterranean and East Asia (McDonnell *et al.* 1984; Orrock 2005). In 1935, *P. americana* was introduced as an ornamental herb to China and was soon recognized as an invasive species. The distribution of this invasive plant grew to spread to the southwestern, central and eastern areas of China (Li & Xie 2002). Individual plants are highly productive; an average female plant can bear more than 4500 fruits at one time (McDonnell *et al.* 1984; Orrock 2005).

We studied a population of invasive *P. americana* at the Sun Yatsen Memorial Botanical Garden in Nanjing, Jiangsu Province, China (32°5′N, 118°48′E; altitude: 30–50 m). The garden includes a fenced area of approximately 186 ha on the southern foot of the Purple Mountain in Jiangsu Province. The population consisted of 35 females distributed in a patch of fir trees (*Cunninghamia lanceolata*) that was surrounded by a patch of pine trees and a patch of broadleaf trees (Li *et al.* 2014).

Frugivorous bird diversity

We estimated the diversity of frugivorous birds during the fruiting season (from late August to early October) in 2012 and 2013. We established 3 transects (50 m × 3 km): one through the *P. americana* population and 2 parallel transects 100 m to each side of the first transect, which could reflect the detection pattern of frugivorous birds that surrounding the mother plant (Li *et al.* 2015). Transects were surveyed every 3 days, usually between the hours of 0630–1000 and 1530–1800. The observer only recorded the species of bird and number of individuals that were within a 30-m distance of transect. Because the urban garden is a disturbed and patchy habitat for birds, we defined generalist and specialist species by their habitat use. Habitat generalists referred to the species those that used multiple habitat types, such as fir, pinewoods, and broadleaf patches; while specialists primarily used a single habitat type (Babweteera & Brown 2009).

For analysis, we averaged the detections of each bird species across censuses. Three diversity indices were used to compare diversity between generalist and specialist species (Shannon–Wiener index, Pielou species evenness index and Simpson's dominance index; Sutherland *et al.* 2004).

Fruit consumption by birds

Ten fruiting mother plants were observed in 2012 and 2013 at the botanical garden. Observations were made from a blind placed at least 30 m from the plant. All surveys were conducted in good weather and continued until no fruit remained on the mother plants. For each bird that visited a mother plant, we recorded its species, fruit-handling behavior and the number of fruits foraged per visit. If a group of conspecific birds visited the plant, we focused on the most visible individual (Altmann 1974).

Post-foraging perching behavior of frugivorous birds and its effects on seedling distribution

We first used 10 × 10 m^2 habitat cells to grid the study site. Overall, 48 sampling cells were surveyed in the botanical garden, with the population of *P. americana* at the center. We then monitored 1-year-old seedlings in each cell to determine the seedling distribution for *P. americana.*

To evaluate the contribution of post-foraging perching behavior of frugivorous birds to seedling distribution, we monitored the perching behavior of 2 high-volume disperser bird species. Bird perching was observed using binoculars from high vantage points on the hills. Birds were selected randomly and tracked until visual contact was lost or until the focal bird could no longer be distinguished from conspecifics. During these observations, the habitat used by the birds and their position was recorded every 30 s (Spiegel & Nathan 2007; Breitbach *et al.* 2010).

After the field study, we first used the Kolmogorov–Smirnov test (SPSS 21.0, Chicago, IL) to determine whether data on seedling numbers were normally distributed. A semivariogram function was used to describe the spatial distribution of 1-year-old seedlings. Block kriging was applied to interpolate seedling distribution to a spatial surface map using GS + 3.1 (Quinn & Keough 2002). Seedling numbers in each habitat cell was analyzed using a generalized mixed effects model, with the activity of the 2 bird species and their interaction as fixed effects and the study year as a random effect. We used the function *glmer* in the package lme4 of R version 3.1.2 to fit the model. Because the seedling numbers and bird perching observations were count data, we used the Poisson distribution in *glmer*. We also used a random forest model (an ensemble machine-learning method for classification and regression that operates by constructing a multitude of decision trees) to plot the partial effect of perching bird species and year on seedling numbers, which included a location index representing the spatial locations of habitat cells (Random Forest R package, Breiman 2001).

RESULTS

Frugivorous bird diversity

In the fruiting season, 16 habitat generalist species (n = 314 individuals) and 9 specialist species (n = 40 individuals) were recorded within the *P. americana* habitat. Species diversity differed between generalists and specialists. The dominance for generalists was less than it was for specialists, whereas species richness and diversity were higher for generalists than for specialists (Simpson's dominance index: generalist, 0.10; specialist: 0.24; Shannon–Wiener diversity: generalist, 2.47; specialist, 1.79; species evenness index: generalist, 0.89; specialist, 0.81; Table S1).

Fruit consumption by frugivorous birds

During 180 h of observations, we recorded 157 visits by 9 species that foraged fruit in 2012 and 146 visits by these same 9 species in 2013. Foraging differed between generalists and specialists. Only 2 specialist species were recorded foraging fruit (2012, 7 visits; 2013, 11 visits) and their foraging frequency was less than that of the generalists. Furthermore, the most common species foraging for fruit did not change between the 2 years. The Chinese bulbul (*Pycnonotus sinensis*, 96 visits) and the red-billed blue magpie (*Urocissa erythrorhyncha*, 68 visits) were the most common frugivorous birds in both years.

Post-foraging perching behavior of frugivorous birds and its effects on seedling distribution

During the our census, 258 *P. americana* seedlings were found in the urban garden. All seedlings were aggregated within 80 m of the mother plants (Fig. 1a).

Over the 2 years of the study, we recorded 316 perching events for *U. erythrorhyncha* (2012, 175; 2013, 141) and 310 events for *P. sinensis* (2012, 170; 2013, 140; Fig. 1b,c). The random forest model identified a positive association between perching frequencies and seedling numbers (random forest: 60.43% of seedling numbers could be explained by 3 variables; Fig. 2). Moreover, the generalized linear mixed-effects model showed that the interaction between perching frequency of *U. erythrorhyncha* and *P. sinensis* was significant ($P < 0.001$; Table 2). This indicates that wherever the contribution of *U. erythrorhyncha* was low, the contribution of *P. sinensis* had a positive association with seedling count, and wherever the contribution of *U. erythrorhyncha* was high, there was a negative association between *P. sinensis* and seedling count.

DISCUSSION

We have shown that the invasive plant *P. americana* attracts native generalist and specialist birds to forage fruit and thereby establishes an effective seed dispersal system in urban environments in China (Table 1 and Table S1).

The seed removal pattern of *P. americana* differed in urban gardens and natural habitat (Table 1; Li *et al.* 2011 report only 3 species with 126 visits per year), which was affected by the habitat structure. First, disturbance rates in the urban garden consisting of artificial plants are higher than that in natural habitat (Li *et al.* 2014). This favors generalist species that have greater tolerance to disturbance, making them more likely to participate in the dispersal of invasive plants (Table 1 and Table S1). Second, in simple structural habitats in urban gardens, the relatively high dominance of dispers-

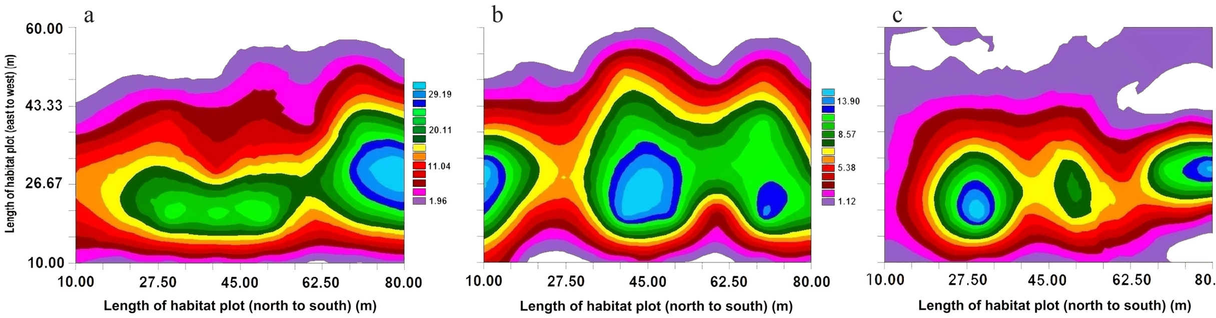

Figure 1 Distribution of (a) 1-year-old seedlings of pokeweed (*Phytolacca americana*) and perching frequency of generalist species (b) Chinese bulbul, *Pycnonotus sinensis,* and (c) red-billed blue magpie, *Urocissa erythrorhyncha,* in the Sun Yat-sen Memorial Botanical Garden, Jiangsu Province.
Colored contours are interpolated from the value of the consponding variable in the centroid of each 10 × 10 m habitat cell.

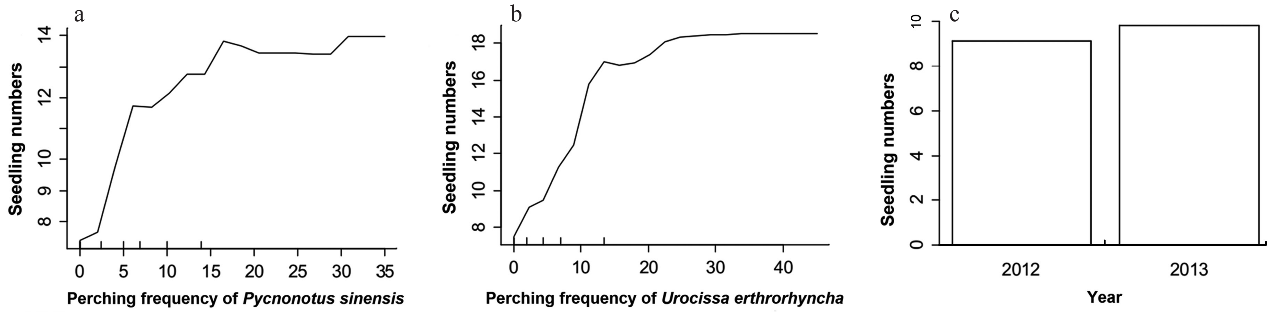

Figure 2 Random forest analysis results: (a) relationship between seedling numbers and perching frequency of the Chinese bulbul, *Pycnonotus sinensis*; (b) relationship between seedling numbers and perching frequency of the red-billed blue magpie, *Urocissa erythrorhyncha*; (c) relationship between seedling and sampling years

Table 1 Fruit consumption by frugivorous birds in the Sun Yatsen Memorial Botanical Garden, Jiangsu Province

Bird species	No. visits		Seeds ingested per visit	Feeding pattern
	2012	2013		
Habitat generalist				
Pycnonotus sinensis	52	44	6.4 ± 1.9	S
Urocissa erythrorhyncha	37	31	5.0 ± 1.9	S
Streptopelia orientalis	25	20	3.3 ± 0.8	S
Turdus merula	13	14	3.0 ± 0.8	S
Cyanopica cyana	12	15	2.3 ± 0.7	S
Phoenicurus auroreus	8	6	1.4 ± 0.5	S
Paradoxornis webbianus	3	5	2.8 ± 0.4	P
Habitat specialist				
Zoothera dauma	5	8	8.7 ± 1.7	S
Tarsiger cyanurus	2	3	1.8 ± 0.4	P

Feeding pattern: S, swallow; P, peck. Data are based on 10 mother plants.

Table 2 A generalized linear mixed-effects model showing the association between seedling numbers and bird activities in 2012 and 2013

Fixed effects	Estimate	Standard error	*z*-value	*P*-value
Factors				
Intercept	1.367	0.062	22.138	< 0.001***
Urocissa erythrorhyncha	0.070	0.004	19.350	< 0.001***
Pycnonotus sinensis	0.088	0.006	14.554	< 0.001***
Urocissa erythrorhyncha: *Pycnonotus sinensis*	−0.003	0.001	−9.328	< 0.001***
Random effects	Variance	Standard deviation		
Year	1.38E-17	3.72E-06		

*** $P < 0.001$

er species may facilitate a high seed removal rate (Breitbach *et al.* 2010; Schupp *et al.* 2010; Smith-Ramírez *et al.* 2013). This favors high seed removal by birds in urban gardens than previously observed in natural habitat (Table 1).

After foraging, dispersers must decide where to perch, which determines seed deposition and spatial distribution of 1-year-old seedlings (Schupp *et al.* 2010). In the case of *P. americana*, seedling distribution reflected a patchy pattern surrounding the birds' perch sites, which was mainly influenced by the post-foraging behaviors of the seed dispersers (Figs 1 and 2). The 2 most common disperser species (*P. sinensis* and *U. erythrorhyncha*) provided an apparent successful seed dispersal service that facilitates the spread of *P. americana* (Table 2, Fig. 2). Therefore, the invasive population of *P. americana* established an effective seed dispersal system in this urban habitat. Once exotic plants form an effective seed dispersal system in a new habitat, they can easily regenerate and become invasive because their seeds will be deposited into suitable sites (Lehouck *et al.* 2009; McConkey *et al.* 2011; Bueno *et al.* 2013; Smith-Ramírez *et al.* 2013). Our results highlight the capacity of invasive *P. americana* to interact with native frugivorous birds in urban Chinese habitats. Moreover, if the recruited vector species use seedling-safe sites for perching, the invasive plants are more likely to regenerate and invade new habitats.

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SUPPLEMENTARY MATERIALS

Table S1 Frugivorous birds observed in the neighborhood of invasive *Phytolacca Americana* in the fruiting season of 2012 and 2013

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