

Contagious seed dispersal and the spread of avian-dispersed exotic plants

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Abstract Seed dispersal by avian frugivores has driven the invasive success of numerous exotic fleshy-fruited plant species around the world. Birds' movements are often directed toward food sources, producing seed shadows that are highly structured in space. The distribution of native fleshy-fruited plants in a landscape could thus form a spatial template for the contagious spread of exotic fleshy-fruited species in the early stages of invasion. We compared seed rain beneath fleshy-fruited and dry-fruited native-tree canopies in forested habitats and open fields in southeastern Michigan. We predicted that exotic seed rain would be highest beneath the canopies of fleshy-fruited plants, and that localities with higher densities of fruit-bearing fleshy-fruited plants would receive more exotic seed rain. Our results suggest that the seed shadows of exotic fleshy-fruited species are strongly influenced by the spatial distributions of native fleshy-fruited trees, and by the local

density of fleshy-fruited plants. Over 92 % of exotic seeds were dispersed beneath fleshy-fruited trees, whereas less than 8 % of exotic seeds were dispersed beneath dry-fruited trees. Exotic seed rain was positively related to the local density of fleshy-fruited plants in forest, but not in open fields. Our study shows how shared dispersal syndromes and frugivore behavior influence the seed shadows of avian-dispersed exotic plants, enabling spatially explicit predictions of invasive spread in their novel ranges.

Keywords Plant invasions · Novel mutualisms · Exotic fleshy-fruited plants · Ornithochory · Seed shadows · Spatially contagious seed dispersal

Introduction

A major goal of invasion ecology is to understand whether and how exotic species will expand their distributions in their novel ranges. Seed dispersal is the first stage of plant recruitment, and the behaviors of avian frugivores frequently play an important role in the patterns of establishment of fleshy-fruited plant species (Herrera et al. 1994; Zamora and Matías 2014). Some of the world's most problematic tree and shrub invasive species are fleshy-fruited plants that are dispersed by avian frugivores (Richardson et al. 2000; Gosper et al. 2005; Rejmánek 2014). Despite the crucial role of seed dispersal in plant invasions, we know very little about how dispersal mutualisms

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contribute to the patterns of spread of exotic plant populations (Westcott and Fletcher 2011).

Seed shadows produced by vertebrate dispersal differ from idealized, distance-dependent leptokurtic distributions because they reflect the movements of frugivores (Janzen 1970; Schupp et al. 2002; Carlo et al. 2013). The non-random movement of frugivores through the landscape can generate spatially contagious seed dispersal, i.e. disproportionately higher densities of seed rain beneath sites attractive to frugivores (Schupp et al. 2002). Such sites include locations where frugivores sleep, nest, lek, and perch (Beckman and Rogers 2013). The locations of fruit-bearing fleshy-fruited trees also strongly guide frugivore movements (Murray 1988; Clark et al. 2004; Carlo et al. 2013). Because frugivores usually consume the fruits of more than one plant species in short intervals of time, they can co-disperse non-random suites of co-fruiting plant species beneath such preferred sites (Loiselle 1990; Clark et al. 2004; Fedriani and Wiegand 2014). Nevertheless, few studies have documented contagious dispersal beneath heterospecific plants (Kwit et al. 2007).

In studies of native plant communities, the availability and abundance of fleshy fruits biases patterns of avian-dispersed seed rain at both landscape and local scales. For example, at landscape scales (25–700 m), the dispersal patterns of two avian-dispersed plant species were biased toward fleshy-fruited forested habitats (Carlo et al. 2013), which suggests that frugivore foraging behavior strongly influences large-scale patterns of seed dispersal. At local scales, frugivorous birds fly short distances when fruiting plants are abundant (Carlo and Morales 2008) and remain in fruiting trees after consuming fruits (Murray 1988). Heterospecific seed rain beneath fleshy-fruited shrubs and vines may thus often be proportional to the number of fruits removed by birds from those same shrubs and vines (Takahashi and Kamitani 2004).

Contagious seed dispersal could facilitate the spread of exotic fleshy-fruited plant species. Seed rain of avian-dispersed invasive species can be particularly high beneath favored perch sites (Ferguson and Drake 1999; Dean and Milton 2000; Bartuszevige and Gorchoff 2006; Deckers et al. 2008). Foraging frugivores could spread exotic species by dispersing exotic seeds to fruit sources far from the parent plant (Gosper et al. 2005). If frugivores prefer to forage in habitats favorable to exotic recruitment, frugivore foraging

could initiate positive feedback between exotic recruitment and seed dispersal (Bartuszevige and Gorchoff 2006), thereby accelerating the process of invasion. Although positive feedback of invasives themselves could drive later stages of invasion, other factors must determine frugivore movements at initial stages of invasion (Buckley et al. 2006). Determining what these factors are will enhance our predictive understanding of plant invasions (Westcott and Fletcher 2011).

Here we ask whether native fleshy-fruited plants can act as focal points for contagious dispersal of exotic species. If so, native fleshy-fruited plants could be particularly important landscape features influencing both range expansion of invasive species and local spread at early stages of the invasion process. In Australian subtropical forest, about a quarter of the invasive species are dispersed by birds, but native and invasive fleshy-fruited species have different fruiting phenologies, such that native plants serve as dispersal hubs when natives are fruiting and invasive plants serve as hubs when invasives are fruiting (White and Vivian-Smith 2011). In the Northeast and Midwest United States, however, most exotic fleshy-fruited plants are avian-dispersed (Silander and Klepeis 1999; Bartuszevige and Gorchoff 2006; McCay et al. 2009) and the fruiting phenology of exotics substantially overlaps with that of native species, such that native fleshy-fruited species may facilitate the contagious dispersal of fleshy-fruited exotics.

We compared the seed rain of fleshy-fruited plants, including seven exotic taxa, beneath the canopies of avian- and wind-dispersed native trees in forest and open fields in southeastern Michigan. To our knowledge, ours is the first study to compare the influence of avian-dispersed native plants to that of non-avian-dispersed native plants in guiding the seed rain patterns of fleshy-fruited exotics. We hypothesized that the seed shadows of exotic fleshy-fruited plants are determined by: (1) the spatial distribution of native fleshy-fruited plants in the landscape; and (2) the local densities of fleshy-fruited plants. We predicted, in turn, that: (1) native fleshy-fruited trees with mature fruits receive more exotic avian-dispersed seed rain beneath their canopies than do dry-fruited trees; and (2) localities with high densities of fleshy-fruited plants receive more avian-dispersed exotic seed rain than localities with low densities of fleshy-fruited plants. Our goal was to elucidate the mechanisms that

produce the seed shadows of avian-dispersed exotic plants to better predict their spread in their novel ranges.

Methods

Study system

The study was conducted at the University of Michigan E. S. George Reserve (ESGR) in Livingston County, Michigan (42° 28'N, -84° 00'W). Several invasive fleshy-fruited species are found at the site, including *Elaeagnus umbellata* (autumn olive), *Berberis thunbergii* (Japanese barberry), *Rosa multiflora* (multiflora rose), and *Lonicera* spp. (honeysuckles). The site is composed of hardwood forest, open fields, and wetlands.

The forest overstory is dominated by *Quercus* spp. (oaks), *Carya* spp. (hickories), *Acer* spp. (maples), and *Fagus grandifolia* (American beech). In forest stands where fleshy-fruited species are scarce, growth-suppressed maples dominate the midstory, and the understory is mostly open. In forest stands where fleshy-fruited species are abundant, the midstory is dominated by *Cornus florida* (flowering dogwood), *Sassafras albidum* (common sassafras), and growth-suppressed *Prunus serotina* (black cherry) in addition to maples, and the understory is a mix of open areas and thickets of *B. thunbergii*. A mix of native (e.g., *Juniperus virginiana*; Eastern redcedar) and exotic (e.g., *E. umbellata*, *R. multiflora*, and *Lonicera* spp.) woody colonizers, grasses, and other herbaceous plants compose the open fields.

We chose four focal native tree species for our study: two dry-fruited species, *Acer rubrum* (red maple) and *Acer saccharum* (sugar maple), and two fleshy-fruited species, *C. florida* and *J. virginiana*. *A. rubrum* and *A. saccharum* produce dry, wind-dispersed fruits (i.e., samaras) and are found in forest. *C. florida* is a small midstory tree that produces red berry-like drupes borne in close clusters of 3–6 fruits and is found in forest. *J. virginiana* is a coniferous tree that produces bluish berry-like fleshy cones (here referred to as “fleshy fruits” for simplicity) and is found in open fields. Fruits of both *C. florida* and *J. virginiana* tend to mature in early October, when sightings of frugivorous birds foraging on these species are also common (Bonilla personal obs.). In the site, *Turdus*

migratorius (American robin), *Catharus guttatus* (hermit thrush), and *Bombycilla cedrorum* (cedar waxwing) were the most common avian frugivores during our study period (Bonilla personal obs.). These are legitimate dispersers (sensu Jordano and Schupp 2000), which swallow whole fruits and either defecate or regurgitate whole seeds, and they forage on both *C. florida* and *J. virginiana* (Bonilla personal obs.).

Seed rain

To investigate whether the spatial distribution of native avian-dispersed plants in the landscape guided the seed rain of exotic fleshy-fruited plants, we monitored seed rain beneath our four focal native tree species. Seeds were collected on 0.25 m² PVC-framed traps with attached 1 mm² fiberglass mesh that were elevated 0.85 m from the ground. To the best of our knowledge, all ornithochorous seeds in our study area are larger than 1 mm. Seed traps were covered with a fixed wire 2.54 cm² mesh to prevent large mammals (e.g. deer and raccoons, which are known to eat *C. florida* seeds) from foraging in the traps.

We selected four focal individuals of each native tree species from each of three 50 × 50 m² plots within the Reserve ($N = 12$ focal individuals per species). Focal individuals of all native trees had similar heights [9.1 m ± 2.2 (SD)]. Two seed traps were placed beneath the canopy of each focal individual, and collections from the two traps were pooled to produce 0.5 m² of sampling area per focal tree. Focal trees were separated by >10 m from one another, and there was no overlap between the focal individuals' canopies and any other canopies in the midstory. We thus considered each focal tree individual an independent replicate for seed rain ($N = 48$). We tested this assumption by comparing a model that included only native tree species to predict seed rain to one that also included the random effect of plot, determining that the two models did not differ significantly (likelihood ratio test, $\chi^2 = 12.53$, $P = 0.13$).

The plots for *C. florida*, *A. rubrum*, and *A. saccharum* were located in forested areas, and the plots for *J. virginiana* were located in open fields. We estimated gap fraction for each forest plot by scanning the center and corners of the plot with a CI-110 plant canopy imager (CID Biosciences) and averaging the five gap fraction values. We found no significant

differences for gap fraction among the plots for the three forest species (ANOVA; $df = 2$; $F = 2.62$; $P = 0.15$).

Seed traps were placed in the field on September 2, 2013, before either *C. florida* or *J. virginiana* had mature fruits. Seeds were collected every 2 weeks until October 28, 2013, for a total of 8 weeks, which extended into the peak fruiting time of *J. virginiana* and past that of *C. florida*, as assessed by counts of conspecific seed rain. Only defecated and regurgitated avian-dispersed seeds were considered, which were those embedded in bird droppings with uric acid or lacking pulp, respectively. We identified seeds by comparing them with specimens collected in the field directly from fruiting trees and with seed guides (Martin and Barkley 1961; Young and Young 1992; Craves and Wloch 2012). Seeds of *Parthenocissus* spp. (Vitaceae), *Vitis* spp. (grapes; Vitaceae), and *Malus* spp. (crabapples; Rosaceae) were not identified to species because congeneric seeds are very similar morphologically; seeds of these genera were thus considered for analyses of all-species (i.e., native and exotic) seed rain only. To the best of our knowledge, no exotic species of *Parthenocissus* spp. or *Vitis* spp. were established in the ESGR at the time of our study, but *Malus* spp. has both native and exotic species established at the site. Our estimates of exotic seed rain are thus conservative.

Local density of fleshy-fruited plants

To investigate whether exotic seed rain was positively related to the local density of fleshy-fruited plants (native and exotic) with mature fruits, we surveyed the density of fall-fruiting fleshy-fruited plants by making a $10 \times 10 \text{ m}^2$ quadrat centered at each individual of the four focal tree species and systematically counting all of the fruiting trees and shrubs (excluding vines) in the quadrat. We counted only those plants with visible fruits, except for *P. serotina* and *S. albidum*, which were counted automatically when the diameter at breast height was >10 cm because mature individuals of these species often produce fruit at the top of the crown, which are difficult to observe from ground level (Bonilla pers. obs). Although *S. albidum* is a dioecious species and it was not possible to determine whether trees were fruit-producing females, there were only three *S. albidum* individuals in total and excluding them did not change our results.

Data analysis

Data analyses were conducted in JMP[®] Pro 11 (SAS Institute Inc. 1989–2007). We considered only heterospecific avian-dispersed seed rain in our analyses (i.e., we did not include conspecific seed rain beneath *C. florida* or *J. virginiana*). Analyses of seed rain that included time as a covariate revealed non-significant effects of collection date and did not qualitatively change the results. Seed rain data for the two seed traps beneath each focal individual were thus pooled across all collection dates. Seed rain comparisons across all focal native tree species and species-specific seed rain comparisons between the focal fleshy-fruited species were conducted using generalized linear models (GLMs) with a negative binomial distribution and log-link function. The negative binomial distribution was appropriate because our seed rain data were over-dispersed zero-inflated counts, which produced a positively skewed frequency distribution (Bliss and Fisher 1953). We used GLMs with a normal distribution and identity function to compare the local density of fleshy-fruited plants among focal native tree species and plots ($N = 48$). For both GLMs among all native tree species, *C. florida* was used as the reference group because it was the fleshy-fruited native tree found in forest and could thus be compared intuitively to the other fleshy-fruited species (*J. virginiana*) and to the dry-fruited species found in forest (*A. rubrum* and *A. saccharum*). GLMs with a normal distribution and identity function were also used to examine the relationships between seed rain and the local density of fleshy-fruited plants in each of the three plots ($N = 12$). For the latter, variables were log-transformed after adding 0.5 [$\log_e(x + 0.5)$] (Yamamura 1999). In all cases, error distributions for the models were chosen on the basis of visual examination of the data and comparisons among Akaike information criteria (AIC) of different models.

Results

Seed rain and dispersal syndrome of native tree species

We collected a total of 311 avian-dispersed seeds beneath our four focal native tree species (Appendix 1). At least seventeen taxa were present in the seed

rain, including nine native taxa, seven exotic taxa, and *Malus* spp. The sampled seed rain (i.e., all avian-dispersed seeds dispersed beneath the four focal tree species) consisted of 34 % *Parthenocissus* spp., 22 % *Vitis* spp., 14 % *E. umbellata*, and 6 % *Phytolacca americana* (American pokeweed), with each of the remaining species accounting for less than 5 %. Exotic seeds constituted 30 % of the sampled seed rain.

More seeds of all species and of exotic species in particular were dispersed beneath the fleshy-fruited tree species (*C. florida* and *J. virginiana*) than beneath the dry-fruited tree species (*A. rubrum* and *A. saccharum*) (Fig. 1; Appendix 2). Neither all-species nor exotic seed rain was significantly different beneath the canopies of *C. florida* and *J. virginiana* (Fig. 1; Appendix 2). Ninety-three percent of the sampled seed rain was dispersed beneath fleshy-fruited native trees (*C. florida* = 63 % and *J. virginiana* = 30 %), whereas 7 % was dispersed beneath dry-fruited native trees (*A. rubrum* = 5 % and *A. saccharum* = 2 %). Similarly, 92 % of the exotic seed rain was dispersed beneath fleshy-fruited native trees (*C. florida* = 30 %

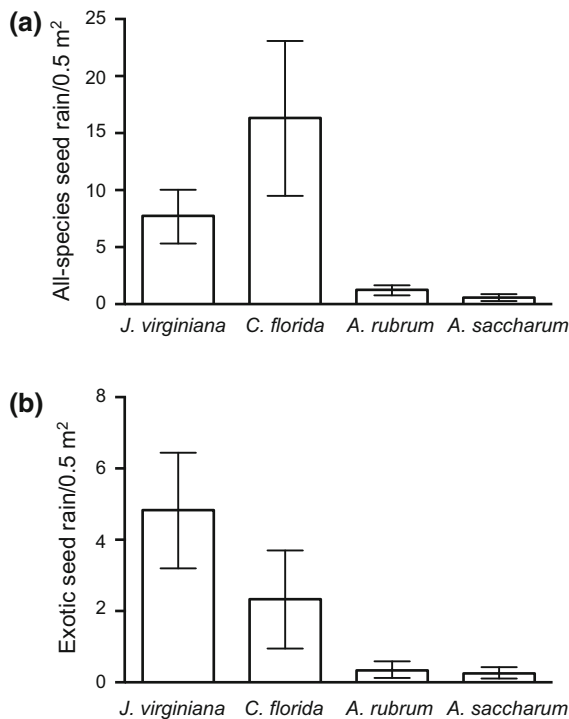


Fig. 1 Seed rain beneath the four focal native tree species over eight weeks for (a) all the avian-dispersed species (i.e., native and exotic), and (b) exotic avian-dispersed species only. Error bars indicate SE. See also Table 1, Appendix 2

and *J. virginiana* = 62 %), whereas 8 % was dispersed beneath dry-fruited trees (*A. rubrum* = 4.5 % and *A. saccharum* = 3.5 %). Our results suggested that the presence of mature fruits in the fleshy-fruited native tree species drove the overall patterns in seed rain. Conspecific seed rain was positively associated with heterospecific seed rain for both species (*C. florida*: $\chi^2 = 4.70$, $P < 0.03$; *J. virginiana* $\chi^2 = 4.77$ $P < 0.03$).

Seed rain and local density of fruit-bearing fleshy-fruited plants

We found nine species of fruit-bearing fleshy-fruited plants surrounding the focal native tree species. Exotic species were established at much higher densities than native species (Appendix 3). *B. thunbergii* was the most abundant species in *C. florida* and *A. rubrum* quadrats, whereas *E. umbellata* was the most abundant species in *J. virginiana* quadrats and the only fleshy-fruited species in *A. saccharum* quadrats. In addition, there were significantly higher densities of fruit-bearing fleshy-fruited plants in the quadrats surrounding *C. florida* than in the quadrats surrounding *J. virginiana*, *A. rubrum*, or *A. saccharum* (Fig. 2; Appendix 4).

Seed rain of all avian-dispersed species was positively related to the local density of fruit-bearing fleshy-fruited plants when considering all of the focal tree species, and when considering only the three tree species found in forest (Fig. 3). Exotic seed rain exhibited a positive relationship to the local density of

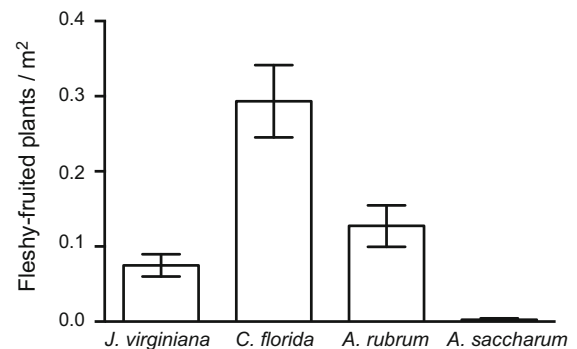


Fig. 2 The density of fruit-bearing fleshy-fruited plants in quadrats surrounding the four focal native tree species. Error bars indicate SE. Both tree species ($\chi^2 = 88.22$, $df = 3$, $P < 0.0001$) and the nested effect of plot ($\chi^2 = 67.06$, $df = 8$, $P < 0.0001$) were significant predictors. See also Appendix 4

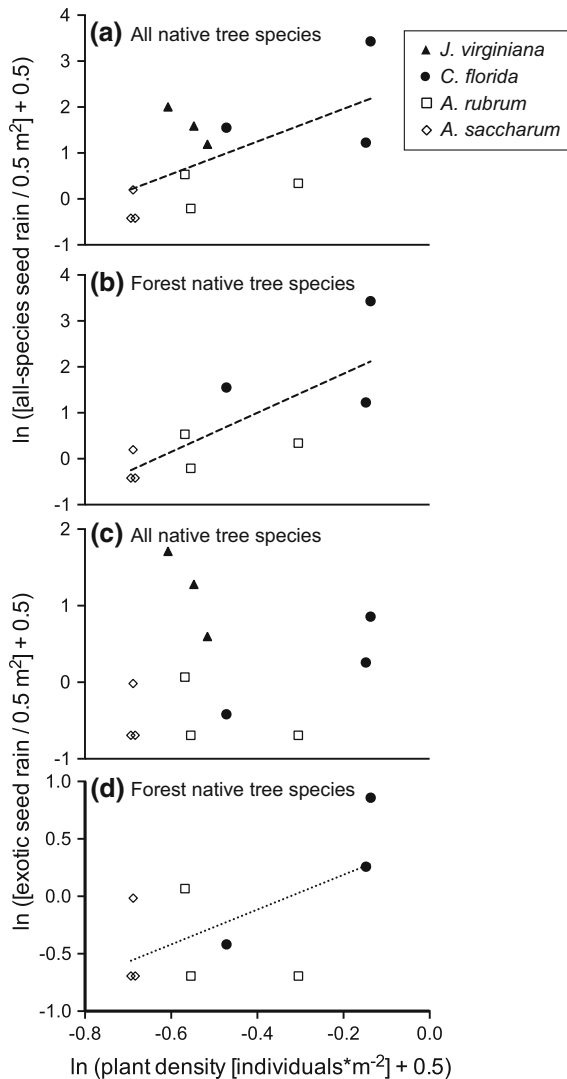


Fig. 3 Relationships between the density of fruit-bearing fleshy-fruited plants and the seed rain by GLMs for (a) all avian-dispersed species collected beneath all four native tree species (estimate = 3.70, SE = 1.35, $\chi^2 = 5.85$, $P = 0.016$), (b) all avian-dispersed species collected beneath the three native tree species found only in forest (estimate = 4.44, SE = 1.08, $\chi^2 = 9.46$, $P = 0.002$), (c) exotic avian-dispersed species collected beneath all four native tree species (estimate = 1.3, SE = 1.47, $\chi^2 = 0.74$, $P = 0.4$), and (d) exotic avian-dispersed species collected beneath the three native tree species found only in forest (estimate = 2.18, SE = 0.99, $\chi^2 = 3.82$, $P = 0.05$). Points represent the average seed rain over 8 weeks and average fruit-bearing fleshy-fruited plant density for each plot

fruit-bearing fleshy-fruited plants when considering only the three focal tree species found in forest, but not when including the fourth tree species (*J. virginiana*) found in open fields (Fig. 3).

Table 1 Effects of native tree species and the local density (individuals/m²) of fleshy-fruited (FF) plants on seed rain

Comparison	df	χ^2	P
All tree species			
All-species seed rain			
Tree sp.	3	364,577.08	<0.0001
FF plant density	1	6.05	0.014
Tree sp. × FF plant density	3	5.85	0.12
Exotic seed rain			
Tree sp.	3	152,021.26	<0.0001
FF plant density	1	6.10	0.014
Tree sp. × FF plant density	3	5.92	0.12
Tree species in forest			
All-species seed rain			
Tree sp.	2	408,669.66	<0.0001
FF plant density	1	5.67	<0.02
Tree sp. × FF plant density	2	1.51	0.5
Exotic seed rain			
Tree sp.	2	92,336.80	<0.0001
FF plant density	1	4.53	<0.033
Tree sp. × FF plant density	2	1.83	0.4

Generalized linear models for all-species seed rain and exotic seed rain beneath all tree species and beneath tree species located in forest only (*C. florida*, *A. rubrum*, and *A. saccharum*) after 8 weeks of sampling. The intercept of the model is the seed rain beneath *C. florida*. For estimates of coefficients, see Appendix 3

Relative influences of dispersal syndrome and local density of fruit-bearing fleshy-fruited plants on seed rain

When considering all four focal native tree species and only the three tree species located in forest in two-way models, the tree species and the local density of fleshy-fruited plants predicted seed rain from all species and exotic species (Table 1; Appendix 2). The effect of the surrounding fleshy-fruited plant density on seed rain was not different among the focal native tree species (Table 1; Appendix 2).

The composition of seed rain beneath the two fleshy-fruited native tree species, *C. florida* and *J. virginiana*, differed (Appendix 1), and these differences appeared driven by the species composition of the local assemblage of fruit-bearing fleshy-fruited plants. Seed rain beneath *C. florida* was dominated by *Parthenocissus* spp., *Vitis* spp., and *B. thunbergii*, whereas seed rain beneath *J. virginiana* was

dominated by *E. umbellata* and *P. americana* (Fig. 4; Appendix 5). The density of *B. thunbergii* was higher in the plots of *C. florida* than in those of *J. virginiana*, and the density of *E. umbellata* was higher in the plots of *J. virginiana* than in those of *C. florida* (Fig. 4; Appendix 5).

Discussion

Our results suggest that native fleshy-fruited plants act as hubs for the contagious dispersal of heterospecific avian-dispersed seeds, including exotic fleshy-fruited

species. The fleshy-fruited trees *C. florida* and *J. virginiana* together received 93 % of the sampled seed rain and 92 % of the exotic seed rain, whereas the dry-fruited trees *A. rubrum* and *A. saccharum* received just 7 and 8 %, respectively. At smaller spatial scales, the local density of fleshy-fruited plants also influenced the density and composition of seed rain, probably because frugivores move short distances among fleshy-fruited plants where food sources are abundant (Carlo and Morales 2008; Morales et al. 2012).

We propose that the biased movement of birds toward habitats with fleshy fruits will guide the dispersal of exotics in the initial stages of invasion. When fleshy-fruited native species vary in abundance at landscape scales, birds could facilitate dispersal of exotics to distant novel communities with fleshy-fruited plants. In a study in northern Spain, avian dispersal of a native species was directed toward forested habitats with fleshy fruits and away from non-fleshy forested habitats and open fields at long distances (150–700 m from the parent tree) (Carlo et al. 2013). The spatial distribution of avian-dispersed native plants could also influence the spread of invasives at large spatial scales. In our study, we found strong directionality in the patterns of avian dispersal toward fleshy-fruited trees across our $50 \times 50 \text{ m}^2$ plots. The density of seed rain was similar beneath the dry-fruited trees *A. rubrum* and *A. saccharum*, even though *A. rubrum* was located in areas with higher local densities of fruit-bearing fleshy-fruited plants. Seed rain was also higher beneath the fleshy-fruited *J. virginiana* than beneath the dry-fruited *A. rubrum*, even though similar local densities of fleshy-fruited plants surrounded the two species.

Once exotic individuals successfully establish in a novel community, the local fruiting neighborhood appears to influence their spread, creating contagious hubs of exotic plants by limiting dispersal distance. In fact, the spatial distributions of *E. umbellata* and *B. thunbergii* in our study site, which commonly form thickets near native fleshy-fruited plants (Bonilla pers. obs.), suggest that this could be a successful mechanism of invasion for these species. The local density of fleshy-fruited plants significantly influenced the quantity of seed rain beneath the three forest tree species (i.e., *C. florida*, *A. rubrum*, and *A. saccharum*). The stronger results when excluding *J. virginiana*, the tree species found in open fields, resulted from a marginal

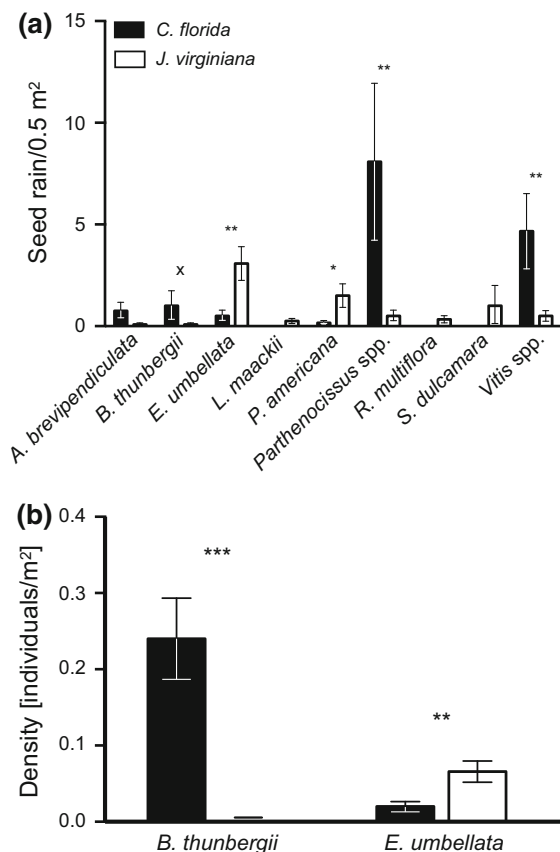


Fig. 4 Association between seed rain beneath *J. virginiana* and *C. florida* over 8 weeks and the local density of fruit-bearing fleshy-fruited plants. **a** Species-specific seed rain for species with a minimum of 3 seeds collected. **b** Local density of the exotic species *B. thunbergii* and *E. umbellata*. Error bars indicate SE. Significant comparisons by GLMs at $P < 0.05$ are denoted by an asterisk *, at $P < 0.005$ are denoted by two asterisks, and at $P < 0.0005$ are denoted by three asterisks. A marginally significant comparison ($P < 0.07$) is denoted by an “x.” See Appendix 5 for more details

negative relationship between *E. umbellata* seed rain beneath *J. virginiana* individuals and the local density of *E. umbellata* adults (not shown). This appeared to be caused by the birds' preference for perching in taller and isolated *J. virginiana* trees in the open fields (not shown), which may provide a better view of the surroundings, and hence protection from predators (McDonnell 1986). The local assemblage of fleshy-fruited plants also affected the species composition of seed rain beneath the two fleshy-fruited species, *C. florida* and *J. virginiana*. Similarly, in a New Zealand study, the quantity of invasive dispersal to islands was correlated with the density of avian-dispersed invasives on nearby land (Anderson et al. 2006).

Of course, the arrival of seeds does not necessarily mean that plants will successfully germinate and establish (Eriksson and Jakobsson 1998; Levine and Murrell 2003; but see Garcia et al. 2005). Once dispersed, biotic and abiotic conditions encountered by seeds will favor the recruitment of some species over others. At our site, *C. florida* is located in the forest, which should favor shade-tolerant species, whereas *J. virginiana* is located in open fields, which should favor desiccation-tolerant species. These differences probably contribute to the differences in fleshy-fruited species composition surrounding the two fleshy-fruited native tree species (Fig. 4; Appendix 5). In a recent study at our site, *E. umbellata* survival was found to be moisture-limited at seedling stages, but light-limited at adult stages (Brym et al. 2014). Dispersal to the partial shade beneath *J. virginiana* in open fields may nurse *E. umbellata* seedlings. The partial shade of the vegetation edge would then expand outwards as the invasion progresses from this central hub. In this way, the contagious dispersal of *E. umbellata* beneath avian food sources functions as "directed dispersal," guiding seeds disproportionately to sites favorable for establishment (Wenny 2001; Carlo and Tewksbury 2014).

Contagious dispersal results in high densities of seed rain, which should increase the probability of density-dependent mortality from competition, pathogens, and predation (Janzen 1970; Wenny 2001; Schupp et al. 2002; but see Augspurger and Kitajima 1992; Karubian et al. 2010). If exotic seeds and seedlings are partially released from natural enemies in the novel range (Maron and Vila 2001; Mitchell and Power 2003; Vila et al. 2005), however, contagious

co-dispersal of native and exotic fleshy-fruited species to the same sites could in fact be particularly advantageous for exotics. For example, in the Czech Republic, fungal pathogens had a greater negative impact on native than on exotic seeds in phylogenetically controlled comparisons (Dostál 2010). Fleshy-fruited exotics could also out-compete native species if avian frugivores disperse exotic seeds more effectively because they prefer to consume exotic fruits (Gosper et al. 2005; Buckley et al. 2006; Aslan and Rejmánek 2012). Contagious dispersal contributes to spatially aggregated plant populations, and competition between synchronously fruiting species for dispersers may be particularly strong where plants are aggregated (Carlo and Morales 2008). Further research is needed to determine whether contagious dispersal confers advantages to exotics over natives due to enemy release, frugivore preferences, or both.

Dispersal syndrome has been found to be one of the most important plant traits determining invasive success, and avian-dispersed exotic plants have been particularly successful at expanding their distributions, both in the region of our study site (Aronson et al. 2007) and around the world (Rejmánek 2014). This suggests that the contagious dispersal provided by avian frugivores has been associated with particularly successful establishment by exotic plants in novel communities. Paradoxically, contagious dispersal was initially conceived as a mechanism of dispersal limitation (Murray 1988; Schupp et al. 2002). Seeds that are dispersed heterogeneously in space may not reach sites that are favorable for recruitment. Yet here we have found that some of the most aggressive exotic fleshy-fruited plants in a temperate forest and field system exhibit seed shadows consistent with contagious dispersal by avian frugivores. Future research should explore whether directed dispersal to favorable habitats, release from natural enemies, frugivore preferences for exotics, or some combination of all three mechanisms can explain the invasion success of exotic fleshy-fruited plants.

Summary

We found that the patterns of avian dispersal for both native and exotic fleshy-fruited species are strongly influenced by the spatial distribution of native fleshy-fruited plants with mature fruits. We suggest two general mechanisms involved in range expansion of

avian-dispersed exotic species that operate at different spatial scales. First, at the landscape scale, habitats with high abundances of fleshy-fruited native plants could guide the spatial pattern of exotic seed rain in novel ranges. Second, at the local scale, contagious dispersal allows population expansion through positive feedback at invasion hubs. The potential for directed dispersal and enemy release could mean that contagious dispersal is particularly advantageous for avian-dispersed exotic species. Contagious dispersal of exotic avian-dispersed plants may be typical in the Northeast and Midwest United States and an important factor influencing the success of the exotic fleshy-fruited species that have invaded the region. Fleshy-fruited trees could thus be useful targets for management at early stages of invasion, by means of removal or sinks for exotic seeds in sites unfavorable for establishment.

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