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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Fruit removal rate depends on neighborhood fruit density, frugivore abundance, and spatial context

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Abstract Fleshy-fruited plants depend fundamentally on interactions with frugivores for effective seed dispersal. Recent models of frugivory within spatially explicit networks make two general predictions regarding these interactions: rate of fruit removal increases (i.e., is facilitated) as densities of conspecific neighborhood fruits increase, and fruit removal rate varies positively with frugivore abundance. We conducted a field experiment that constitutes the first empirical and simultaneous test of these two primary predictions. We manipulated neighborhood abundances of arrowwood (*Viburnum recognitum* and *Viburnum dentatum*) fruits in southern New England's maritime shrub community and monitored removal rates by autumn-migrating birds. Focal arrowwood plants in neighborhoods with high conspecific fruit density sustained moderately decreased fruit removal rates (i.e., competition) relative to those in low-density neighborhoods, a result that agrees with most field research to date but contrasts with theoretical expectation. We suggest the spatial contexts that favor competition (i.e., high-abundance neighborhoods and highly aggregated landscapes) are considerably more common than the relatively uniform, low-aggregation fruiting landscapes that promote facilitation. Patterns of arrowwood removal by avian frugivores generally varied positively with, and apparently in response to, seasonal changes in migratory frugivore abundance. However, we suggest that dense stands of arrowwood concentrated frugivore activity at the neighborhood scale, thus counteracting geographic patterns of frugivore abundance. Our results underscore the importance of considering spatial context (e.g., fruit distribution and aggregation, frugivory hubs) in plant-avian frugivore interactions.

Keywords Avian frugivory · Maritime plant community · Neighborhood effects · Stopover ecology · *Viburnum*

Introduction

Seed dispersal produces important ecological and evolutionary consequences for plants and their communities (Levin et al. 2003; Levine and Murrell 2003). Consider, for example, a temperate shrub producing fleshy fruits to compensate its primarily avian frugivores for seed dispersal services. The interactions between this shrub and its frugivores influence not only the outcome of the crucial mobile phase of its reproduction [i.e., its seed shadow (Janzen 1971)], but their aggregate across the community of individuals governs subsequent plant community demographics (e.g., Debussche et al. 1982; Jordano 1994; Lázaro et al. 2005). Plants depend fundamentally on these interactions for effective seed dispersal, and the patterns of fruit consumption by frugivores regulate the frequency of these interactions (Schupp 1993; Russo et al. 2006; Schupp et al. 2010). But the dependence is mutual: the distribution of plants and their fruit resources can dictate the distribution and behavior of frugivores [e.g., activity and feeding decisions (Rey 1995; Moegenburg and Levey 2003; Borgmann et al. 2004)]. Certainly, frugivores respond to the intrinsic qualities of fruits adapted to encourage fruit selection and removal (reviewed in Herrera 2002).

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However, factors extrinsic to an individual plant often influence frugivore distribution and behavior profoundly, rendering them largely context dependent. How this context dependence influences the strength and direction of species interactions in general is a key gap in our current ecological knowledge (Agrawal et al. 2007).

Context dependence is nearly ubiquitous in interactions among species (Agrawal et al. 2007), and the extent to which frugivores remove and disperse fruit is no exception (Schupp et al. 2010). Indeed, a given plant's spatial context may effectively determine its dispersal success (Herrera 1984b). In particular, the distribution, density, and species composition of the surrounding fruiting neighborhood can influence patterns of frugivory (and seed dispersal) by altering frugivore abundance and foraging behavior (Levey et al. 1984; Sargent 1990; Saracco et al. 2005). However, the influence of a fruiting neighborhood on fruit removal apparently lacks generality; in some cases, neighborhood fruit facilitates (i.e., increases) fruit removal by attracting frugivores (Sargent 1990; Takahashi and Kamitani 2004) while in others it decreases fruit removal when plants compete for frugivores (Moore and Willson 1982; Manasse and Howe 1983). Identifying generalities within this context dependence is crucial to developing a predictive understanding of seed dispersal efficiency (Carlo et al. 2007; Schupp et al. 2010).

Carlo et al. (2007) suggest that the influences of fruiting neighborhoods on fruit removal may be better understood within the context of a network governed predominantly by the spatial patterning of fruiting plants and the availability of frugivores. Specifically, their frugivory network model expands the concept of plant-frugivore interactions as hierarchical mutualistic networks (e.g., Jordano 1987, 2003) to incorporate the spatial arrangements of plants explicitly, whereby the movements of frugivores establish the linkage among plants (i.e., the network topology). They implicate two primary factors that largely determine the outcome of the complex interactions between plants and frugivores: the spatial patterning of fruiting plants and the availability of frugivores. Spatial patterns of particular import include the density of fruiting neighborhoods at the local scale and plant aggregation (i.e., the clumpiness of, or non-uniformity in, plant and fruit distributions) at larger, landscape scales. The models of Carlo et al. (2007) emphasized frugivore abundance and assumed frugivores consumed only fruits. The more general situation is that frugivores vary in foraging efficiency and fruit preferences, and may switch among alternative prey (e.g., Carnicer et al. 2009); thus, "frugivore activity" better describes the product of both frugivore abundance and the extent to which the frugivores are consuming fruits. Fruiting plant spatial patterns, fruit properties [e.g., quantity and nutritional quality, phenology (reviewed in Levey et al. 2002)], and frugivore activity can produce inequalities in visitation among plants; if inequalities are severe, network topologies may be dominated by "hubs"—plants, species, or neighborhoods that receive the majority of frugivory and seed dispersal services (Carlo et al. 2007). Simulations of avian frugivory within this spatially explicit framework (Morales and Carlo 2006; Carlo et al. 2007; Carlo and Morales 2008) predict that fruit removal increases (i.e., facilitation occurs) from a given plant as a function of (1) increasing densities of conspecific fruit in the neighborhood surrounding that plant, and (2) increasing frugivore activity (Fig. 1). However, at typical levels of frugivore activity in highly aggregated landscapes (i.e., when fruits are distributed very non-uniformly on the landscape), fruit removal increases with neighborhood fruit density only to a point; in these landscapes, decreased fruit removal from a given plant (i.e., competition) may be expected at high conspecific neighborhood fruit densities (Carlo and Morales 2008) (Fig. 1). Our field experiment constitutes the first empirical and simultaneous test of these predictions and their potential interaction.

We evaluated these predictions with two field experiments conducted during autumnal bird migration in the maritime shrub community of southern New England. The maritime shrub community is well suited to evaluate frugivory network theory because of its abundant fruit availability but low fruiting plant diversity (Enser and Lundgren 2006). Additionally, generalist avian frugivores predominate

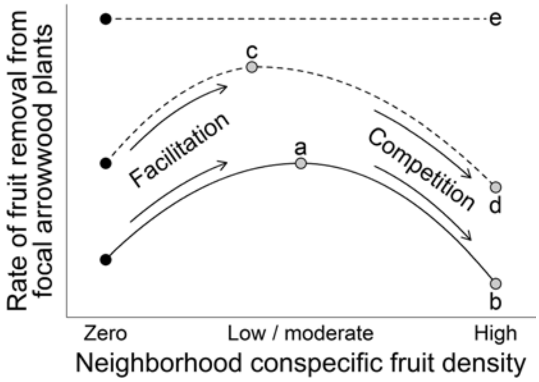

Fig. 1 Hypothesized changes in fruit removal rate from focal arrowwood (*Viburnum* sp.) plants at different neighborhood fruit density and frugivore activity scenarios. At low to moderate frugivore activity (*solid lines*), fruit removal increases from focal plants surrounded by neighborhoods containing conspecific fruit relative to focal plants with no neighborhood fruit. However, increased removal occurs only up to some unknown low or moderate neighborhood density (e.g., *points a*, *c*) beyond which fruit removal from focal plants decreases due to competition for frugivores. At very high neighborhood densities (e.g., *points b*, *d*), removal rates may fall below that incurred in the absence of neighborhood fruit. Sufficiently high frugivore activity may diminish or eliminate any effect of neighborhood fruit density if most (or all) available fruits are consumed (*line e*). Note that the exact form of the predictions (e.g., curvilinear or otherwise) between neighborhood fruit density and fruit removal rate is not crucial in this case

and exhibit seasonal (Able 1977; Mizrahi et al. 2010; Svedlow et al. 2012) and predictable geographic variation in abundance (Baird and Nisbet 1960; Able 1977). Songbirds are the primary consumers of fruits on Block Island during fall and the majority of these birds are stopping to refuel during migration. Migration is an especially pertinent study context in which to test the stated predictions, as migrating songbirds at stopover sites have a strong impetus to assess and acquire food resources efficiently; autumn migration is also the critical period of interactions between the majority of fleshy-fruited plants and their dispersers in this temperate maritime shrub system. Finally, simulations of avian frugivory (Morales and Carlo 2006; Carlo et al. 2007; Carlo and Morales 2008; Morales and Vázquez 2008) occur in a predominantly tropical context; thus we empirically evaluate their applicability in a temperate system.

Our field experiments examined differential fruit removal from individual northern and southern arrowwood (*Viburnum recognitum* and *Viburnum dentatum*, respectively) plants relative to neighborhood fruit density and frugivore abundance. Arrowwood is the most important fruit resource for migratory birds within this maritime shrub community (Parrish 1997a; Smith et al. 2007; Bolser et al. 2013). We evaluated two specific predictions related to the effects of local neighborhood (i.e., 50 m^2) and frugivore activity on fruit removal patterns. First, focal arrowwood plants surrounded by neighborhoods containing natural abundances of conspecific fruits will experience increased rates of fruit removal relative to focal plants surrounded by neighborhoods from which we removed all conspecific fruit (Fig. 1, points a, c); however, if neighborhood fruit density is sufficiently high (the precise threshold is uncertain), rates of fruit removal from focal plants will be reduced, via competition for limited frugivore activity, relative to focal plants in neighborhoods without arrowwood (Fig. 1, points b, d). Second, fruit removal rates on focal arrowwood plants will vary positively with temporal (seasonal) and geographic patterns of frugivore activity; however, high frugivore activity could decouple fruit removal rates from neighborhood fruit density and result in a high and constant rate of fruit removal, regardless of fruit density (Fig. 1, line e).

Materials and methods

Study site

The field experiment took place on Block Island (41°28′N, 71°31′W), a 25-km^2 glacially deposited landmass located approximately 15 km south of the Rhode Island mainland. The species composition and structure of the maritime shrub community are dictated, in large part, by exposure to salt spray and wind (Enser and Lundgren 2006). Autumnal migrating songbirds rest and refuel extensively in the maritime shrub community of Block Island, consuming large quantities of fruit (Parrish 1997a) and playing a key role in the dispersal of fruiting species (Thompson and Willson 1979). The high-energy fruits of northern and southern arrowwood are used nearly ubiquitously by migrant frugivores, which prefer them to fruits of co-occurring plant species (Parrish 1997a, b; Smith et al. 2007; Bolser et al. 2013).

Plot establishment and neighborhood manipulation

In autumn 2009, we thoroughly searched the maritime shrub community and identified 16 arrowwood-dominated stands of adequate size within which to establish a single 5 × 20-m plot (Fig. 2). Plots were separated by sufficient distances to expect independence; the distance between a plot and its nearest neighboring plot averaged 272 m and 449 m on northern and southern Block Island, respectively, with a minimum separation of 65 m. Our plots ranged over 7.5 km of latitude, nearly the entire latitudinal span (8.7 km) of the maritime shrub community on

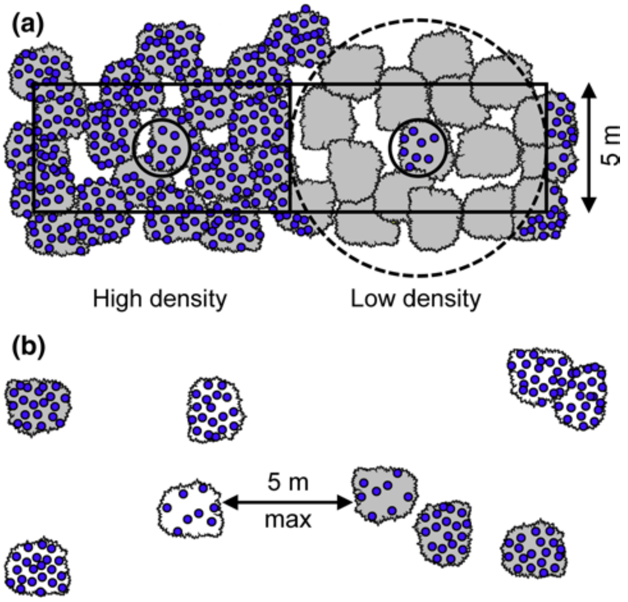

Fig. 2 **a** In autumn 2009 arrowwood plots, all arrowwood was removed within a low-density subplot and a 5-m radius circle around the treatment subplot center (*broken circle*) to ensure a fruitless conspecific neighborhood. Fruit counts occurred on eight representative arrowwood infructescences (*filled circles*) in the center (*solid circle*) of each subplot. **b** In autumn 2010 arrowwood pairs, a northern arrowwood shrub (*Viburnum recognitum*; unshaded shrubs) was located adjacent to and within 5 m of a southern arrowwood shrub (*Viburnum dentatum*; shaded shrubs). Fruit counts were carried out on eight representative arrowwood infructescences (*filled circles*) evenly distributed on each focal plant

Block Island. We expected these uncommonly large stands of arrowwood to concentrate frugivore activity [i.e., that each plot would act essentially as a frugivory hub; sensu Carlo et al. (2007)]. Consistent with its general distribution on Block Island (Online Resource 1), northern arrowwood dominated all northern plots and southern arrowwood dominated six of seven southern plots; northern arrowwood was more abundant on a single southern plot. To decouple the effect of the geographic location of plots from a potential preference for arrowwood species, we conducted a second experiment the following year (autumn 2010; see below).

To assess neighborhood effects, we paired subplots (i.e., one half of each plot; 5 × 10 m) within plots to control for (1) avian migrants' expected non-uniform use of the maritime shrub community, and (2) heterogeneity in the species composition and physiognomy of the surrounding maritime shrub community. In each subplot, we monitored avian fruit removal from eight well-separated, representative arrowwood infructescences (cymes) within a 1-m radius (ca. 3 m^2) subplot "center"; we removed all other conspecific fruit within each subplot center. Subsequently in each plot, we removed all arrowwood fruits outside of the subplot center from one subplot, selected at random (hereafter, "low-density subplot"; Fig. 2a). In the other subplot, arrowwood fruits outside of the subplot center were retained at their natural density (hereafter, "high-density subplot"; Fig. 2a). The availability of arrowwood on Block Island dictated our use of only two density treatments: uniformly dense arrowwood stands were too small to evaluate more densities and maintain a reasonable neighborhood size and too few to incorporate them into an incomplete block approach. Hence we did not attempt to delineate the shape of the functional relationship between neighborhood density and fruit removal (Fig. 1) as this was not necessary to test the two general predictions of the frugivory network model. Natural arrowwood fruit densities ranged from 85 to 2,185 fruits m^{-2} (median 741 fruits m^{-2}) and arrowwood fruit mass (wet pulp plus seed) per unit area ranged from 12.4 to 177.6 g m^{-2} (median 63.6 g m^{-2}). Our manipulation of the subplot centers controlled adequately for initial crop size (mean ± SD: 221 ± 82 fruits) in paired subplots (paired $t_{15} = 0.92$, $P = 0.36$).

Monitoring fruit fate

Of the eight cymes remaining in the center of each subplot, we selected three at random and enclosed them in loose, fine (2.25-mm^2) nylon bags to prevent avian consumption. We used enclosed cymes to estimate natural fruit abscission in each subplot and the five remaining unenclosed cymes to assess the pattern of fruit removal by migratory songbirds. Fruits were counted every 3 days (median; range 2–6) from 16 September to 2 November ($n = 14$ counts), although monitoring did not begin on two southern plots until the third count period; the experiment encompassed the greater part of fall migratory songbird use of the island and the availability of edible arrowwood. We estimated the number of fruits consumed and abscised on each subplot in each count period according to the following rules: (1) if the abscission rate on the enclosed cymes equaled or exceeded the rate of fruit loss on unenclosed cymes, we attributed the change in fruit abundance on unenclosed cymes entirely to abscission; or (2) if abscission rate was lower than the rate of fruit loss on unenclosed cymes, we used the abscission rate from the enclosed cymes to estimate the number of fruits that abscised from the unenclosed cymes with the balance of missing fruits attributed to removal by migratory birds.

Patterns of frugivore activity

Manipulating or monitoring frugivore activity on arrowwood plots proved logistically impractical. We initially considered point counts to document patterns of frugivore activity at each plot, but the density of the maritime shrub community impaired our ability to visually detect birds, which are likewise less conspicuous vocally during fall migration. Thus we elected to use seasonal fluctuations and island-scale geographic variation in migrant abundance to index frugivore activity. First, westerly winds associated with passing fall cold fronts displace large numbers of migratory songbirds offshore (Baird and Nisbet 1960; Able 1977); this weather dependency typically results in widely fluctuating frugivore densities throughout the fall migration on Block Island. We derived seasonal patterns of migrant (and thus frugivore) abundance during our experiment from concurrent radar work on Block Island (Mizrahi et al. 2010; Svedlow et al. 2012); marine surveillance radar is a standard method for estimating temporal patterns of abundance for nocturnally migrating songbirds (e.g., Harmata et al. 1999). Second, frugivore density is not uniform within the island's shrub community, and there exists a well-documented pattern in migrant densities on Block Island: migrants occur in higher densities on the northern half of the island following arrival, where they prepare for reoriented flights to the mainland or subsequent migratory flights to the south (Baird and Nisbet 1960; Able 1977). In support of this general pattern, mist-netting capture rates in the maritime shrub community were considerably lower at southern locations (A. Smith, unpublished data; S. Comings, unpublished data). Indeed, the two migration banding operations on the island (Reinert et al. 2002; United States Fish & Wildlife Service, unpublished data) continue to exploit the phenomenon, as have multiple previous studies (Parrish 1997b; Smith et al. 2007; Smith and McWilliams 2010; Bolser et al. 2013). The extent of frugivory by migrants possibly increased as arthropod prey availability decreased throughout the fall (Parrish 2000; A. Smith, unpublished data); this suggests a seasonal increase in frugivore activity independent of changes in frugivore abundance. Importantly, such an increase likely did not vary geographically, nor did we expect other aspects of frugivore behavior that might influence foraging activity to vary geographically (e.g., foraging efficiency, fruit preferences, risk of predation). Thus, in our case, we expect that patterns of frugivore abundance represented a reliable proxy for frugivore activity.

Separating arrowwood species and geographic frugivore activity effects

The natural distribution of the two arrowwood species on Block Island potentially confounded or conflated any influence on fruit removal of geographic differences in frugivore activity in 2009. We conducted a second experiment to separate the effects of frugivore activity (as it related to geography) and arrowwood species on patterns of fruit removal, and thus inform inferences in the 2009 experiment. In autumn 2010 we monitored the fate of co-fruiting northern and southern arrowwood fruits at 12 locations (five northern, seven southern). At each location, we identified an arrowwood pair comprising single fruit-laden northern and southern arrowwood plants growing within 5 m of each other; the distance to the nearest neighboring pair averaged 376 and 583 m on northern and southern Block Island, respectively, with a minimum separation of 54 m. On each plant we removed all fruit except for eight representative cymes distributed evenly throughout the plant, occupying an area similar to 2009 (ca. 3 m^2; Fig. 2b; initial crop size mean ± SD, 173 ± 60 fruits; paired $t_9 = 1.23$, $P = 0.25$). We monitored and estimated fruit abscission and removal as described previously, counting fruits every 5 days (median; range 4–8) from 16 September to 7 November ($n = 10$ counts). Arrowwood pairs typically occurred in more diverse maritime shrub associations relative to the dense arrowwood-dominated stands used in 2009 (Fig. 2b). We used individuals growing in close proximity to control for neighborhood influences around arrowwood pairs, which we neither manipulated nor quantified.

Statistical analyses

Arrowwood removal from focal plants varied considerably over time and among plants, with many instances of no removal or extensive removal. We accounted for this overdispersion by modeling counts of fruits removed with the negative binomial distribution; however, the prediction of zero and near-zero removal remained inadequate, particularly in 2009 (see Online Resource 1). Failure to account for excess zeros results in biased parameter and variance estimates (see, e.g., Martin et al. 2005). We thus used zero-inflated negative binomial (ZINB) mixture models (Lambert 1992) to evaluate the influence of fruit neighborhood and the expected geographic effect of frugivore activity on fruit removal rates; such models have proven appropriate in plant-frugivore networks (Carlo and Morales 2008; Morales and Vázquez 2008). To generate the ZINB rate model, we offset counts of arrowwood removal by the number of fruits present at the beginning of a count period, minus the number of fruits estimated to have abscised in that count period. We fit the ZINB models using the glmmADMB package (Skaug et al. 2012) in R (R Development Core Team 2011). Examination of removal rates over time within experimental units suggested that random intercepts were justified among plots in 2009 and 2010; we also retained random intercepts for subplots (i.e., treatments within plots in 2009 and species within pairs in 2010) given their role in the experimental design.

Rather than assess every possible combination of models, we compared a suite of models that addressed specific hypothetical scenarios for arrowwood removal (Table 2, Online Resource 1). We judged the relative importance of competing models using sample size-corrected Akaike's information criterion (AIC_c) (Akaike 1974) and Akaike weights. If the model with the lowest AIC_c value had an Akaike weight <0.9, we constructed a 95 % confidence set of models with Akaike weights summing to ≥0.95 (Burnham and Anderson 2002). In the interest of parsimony, we excluded any model with a higher AIC_c value than a simpler, nested model and preferred the simpler of multiple, equally supported models (Burnham and Anderson 2002; Richards 2005).

Subsequent to the ZINB models, we used permutation tests to compare changes in arrowwood removal rates with seasonal patterns of migrant abundance inferred from concurrent marine radar (see above). We calculated, in each year, the average change in fruit removal rate for the count periods following the five nights of highest migratory activity. Our choice of five nights was somewhat arbitrary, but seemed reasonable based on the patterns of migratory activity (Figs. 1, 2, Online Resource 1). Using the count period subsequent to the measured migratory activity rather than the coinciding count period allowed us to accommodate an expected short (1–3 days) time lag between the arrival of migrants and detectable fruit removal [i.e., search and settling time (Alerstam and Lindström 1990)]. We compared this average change in fruit removal rates to 10,000 comparable changes calculated after permuting the nightly radar activity data (see Online Resource 1).

Finally, we considered post hoc whether the change in spatial context of focal arrowwood plants between years affected the probability of frugivores finding focal arrowwood plants; recall that in 2009 focal plants occurred in plots encompassing large, dense, arrowwood-dominated stands, while in 2010 they occurred in multi-species associations. To do so, we constructed logistic generalized linear mixed models (GLMMs) using the lme4 package (Bates et al. 2011) for each season that evaluated the occurrence of any fruit removal (i.e., we dichotomized zero and non-zero fruit removal rates) as a function of the same suite of hypothetical scenarios (Table 2, Online Resource 1).

Results

General patterns of arrowwood fruit loss

In 2009, we monitored the fate of 4,471 and 7,066 fruits on 96 enclosed and 160 unenclosed arrowwood cymes, respectively. Patterns of fruit loss from enclosed (abscission) and unenclosed (abscission and removal) cymes revealed highly episodic fruit removal and suggested that when removal episodes occur, rates of fruit removal are higher on focal plants in low-density arrowwood neighborhoods (Fig. 3a, c) than in natural high-density neighborhoods (Fig. 3b, d). In 2010, we monitored 3,094 and 4,651 fruits on 72 enclosed and 120 unenclosed arrowwood cymes, respectively. As in 2009, patterns of fruit loss revealed variable and episodic fruit removal and suggested that focal plants on northern arrowwood pairs (Fig. 4a, c) experienced more consistent fruit removal than those on southern arrowwood (Fig. 4b, d).

Arrowwood removal

In 2009, arrowwood removal rate varied irregularly during the season and was somewhat influenced by neighborhood fruit density (64 % of the ZINB confidence set; Table 1), with arrowwood fruits surrounded by low-density arrowwood neighborhoods sustaining increased removal at 1.5 times (95 % confidence interval 1.0–2.3) the rate of fruits surrounded by a high-density neighborhood (Fig. 5a). However, non-negligible support for a model without the neighborhood fruit density effect (36 % of the ZINB confidence set; Table 1) suggested that the decrease in fruit removal rate attributable to neighborhood fruit density was not especially strong (Table 1). A geographic effect (frugivore activity) was not indicated in either supported model (Table 1). In 2010, the rate of arrowwood fruit removal varied episodically over the course of the season, as in the previous year, and varied with geographic differences in frugivore activity (84 % of the ZINB confidence set; Table 1); arrowwood fruits on northern Block Island sustained removal rates 4.1 times higher (95 % confidence interval 1.2–14.4) than fruits on southern Block Island (Fig. 5b). Differences in removal rate related to arrowwood species were negligible; a reduced model without the arrowwood species effect was supported equivalently, thus the effect was superfluous (Table 1). In both years, a consistent relationship emerged between the seasonal fluctuations in fruit removal rate and seasonal changes in migratory bird activity measured via radar (Fig. 5). In general, fruit removal rates increased in

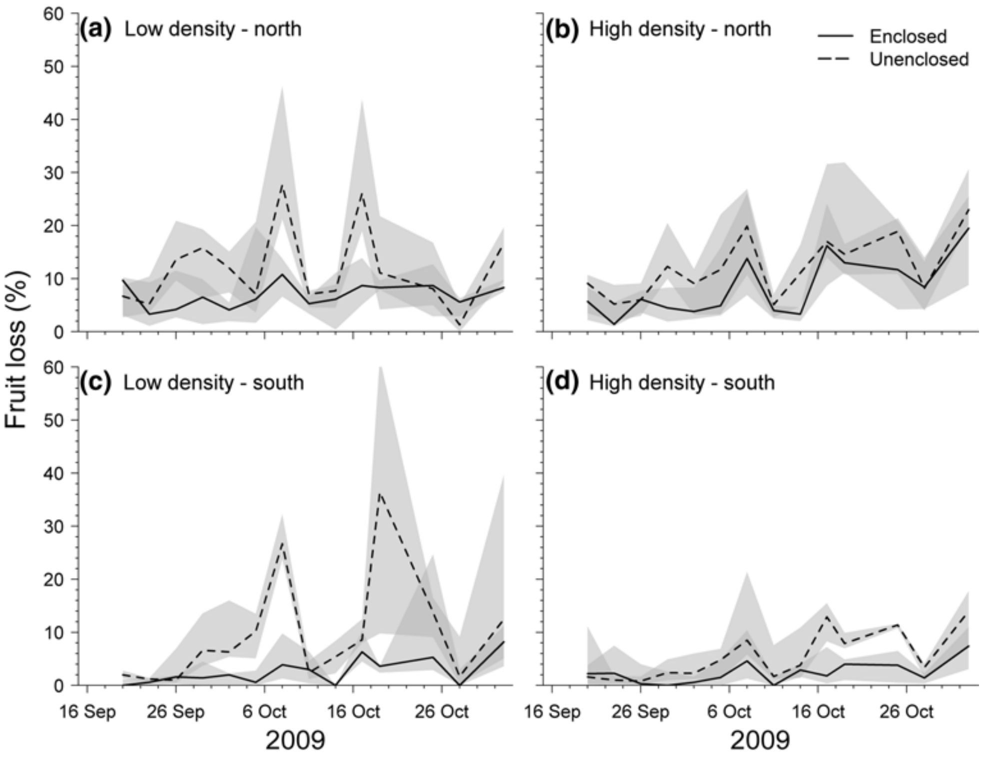

Fig. 3 Percentage fruit lost since the previous fruit count (interquartile range shown in *shading*) from enclosed (*solid line*) and unenclosed (*dashed line*) arrowwood infructescences in **a** low- and **b** high-density neighborhoods on northern Block Island and from **c** low- and **d** high-density neighborhoods on southern Block Island during autumn 2009

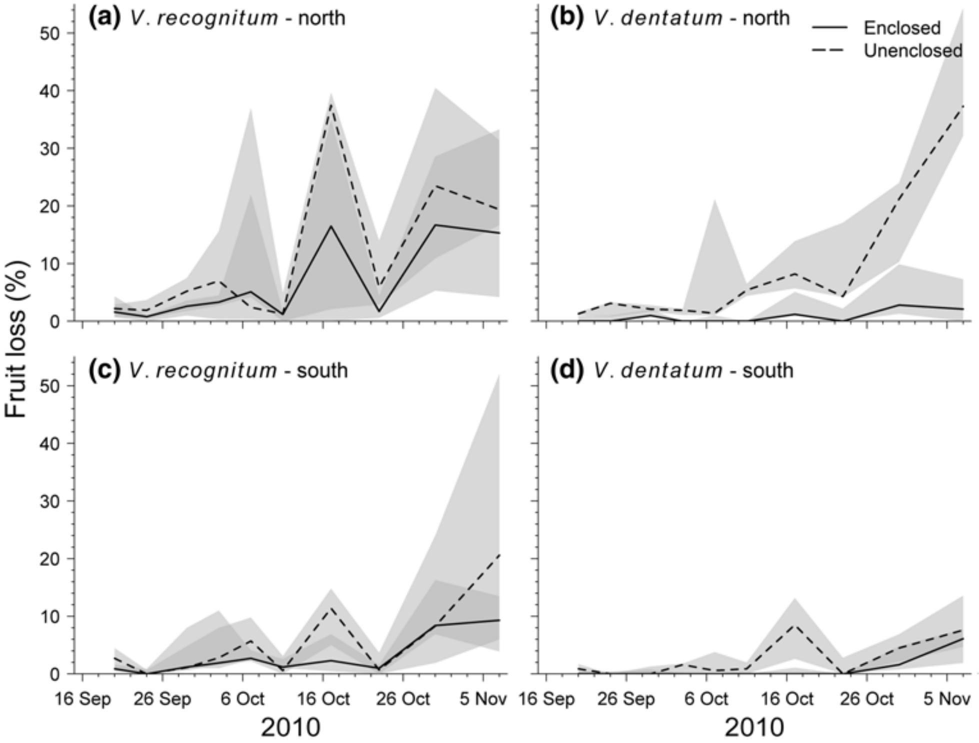

Fig. 4 Percentage fruit lost since the previous fruit count (interquartile range shown in *shading*) from enclosed (*solid line*) and unenclosed (*dashed line*) cymes of northern arrowwood (*V. recognitum*) on **a** northern and **b** southern Block Island and from southern arrowwood (*V. dentatum*) on **c** northern and **d** southern Block Island during autumn 2010

the count periods following the nights of highest migratory activity in 2009 (permutation test; $P = 0.078$) and 2010 (permutation test, $P = 0.007$). Specifically, the distinct bouts of increased migratory activity were usually followed by distinct and occasionally prolonged increases in rates of arrowwood removal (Fig. 5). This pattern is consistent with the predicted positive relationship between frugivore activity and rates of fruit removal.

The probability of any fruit removal occurring in a given time period varied with the spatial context of focal arrowwood plants between years. In 2009, two models received equal support: a constant probability throughout the season for all focal plants and a more complicated linear change in the probability of removal that varied geographically (Table 1). We favored the much simpler, intercept-only model that suggested a statistically constant probability of sustaining removal over time in 2009. In contrast, the probability of fruit removal varied irregularly within arrowwood pairs during the 2010 season (Table 1), and very closely matched the corresponding pattern of fruit removal rates (i.e., Fig. 5b).

Discussion

The ecological interactions between plants and their avian frugivores are dynamic and complex—avian frugivores respond to and subsequently alter the distribution and abundance of fruit in space and over time, while also engaging in activities unrelated to fruit removal (e.g., foraging on arthropods, vigilance). We found moderate evidence that fruit-laden neighborhoods depressed fruit removal rates from the focal plants they surrounded, which agrees with most field research to date but contrasts with general theoretical expectation that conspecific fruiting neighborhoods facilitate fruit removal rates from focal plants (Carlo et al. 2007; Carlo and Morales 2008). We propose a general solution to this apparent conflict: the spatial contexts that favor facilitation are uncommon relative to the high-abundance neighborhoods and highly aggregated landscapes that promote competition. Northern temperate systems that support seasonally abundant frugivores provided a prime example. In agreement with theoretical expectation, we found two independent lines of support for an increase in fruit removal rates with increased frugivore activity; however, we suggest that in one particular instance the landscape context of our neighborhoods influenced frugivore activity and thus the expected pattern of fruit removal. Placed in the context of other work, our results further underscore the importance of considering spatial context (i.e., fruit abundance and aggregation, including the presence and influence of frugivory hubs) as well as frugivore activity in plant-avian frugivore interactions.

Influence of neighborhood fruit density on rate of fruit removal

Most field studies of neighborhood effects on rates of fruit removal or visitation by avian frugivores have

Table 1 Results of 95 % confidence set of zero-inflated negative binomial (*ZINB*) mixture models of fruit removal patterns and logistic generalized linear mixed models (*GLMM*) evaluating the probability of incurring fruit removal on Block Island in 2009 and 2010

Candidate model[a]	k^b	AIC_c	Δ_i^c	w_i^d	$\sum w_i^e$
ZINB					
2009					
(5) TIMEF + TRT	15	2,145.6	0.0	0.64	0.64
(2) TIMEF	14		1.2	0.36	1.00
2010					
(4) TIMEF + TRT + GEOG	12	1,132.0	0.0	0.43	0.43
(6) TIMEF + GEOG	11		0.1	0.41	0.84
(2) TIMEF	10		2.2	0.14	0.99
Logistic GLMM					
2009					
(8) TIME ǀ GEOG	4	526.2	0.0	0.55	0.55
(1) INTERCEPT ONLY	1		0.4	0.45	1.00
2010					
(2) TIMEF	10	293.0	0.0	0.99	0.99

TRT denotes the effect of a neighborhood fruit density manipulation (2009) or arrowwood species (2010) on fruit removal; *TIMEF* denotes a categorical specification of time (i.e., count period); *GEOG* denotes the effect of geography on fruit removal. See Online Resource 1 and the text for details

[a] Number preceding model corresponds to model listing in Table 1 of Online Resource 1

[b] Number of fixed effect parameters estimated; the random effects structure did not vary among models

[c] Difference in AIC_c between model i and best model [lowest sample size-corrected Akaike's information criterion (AIC_c)]

[d] Akaike weights, analogous to the probability of model i being the best approximating model in the set (Burnham and Anderson 2002; but see Richards 2005; Link and Barker 2006)

[e] Cumulative sum of Akaike weights from the best model to model i

documented competition or no discernible effect of neighborhood fruit density (Moore and Willson 1982; Manasse and Howe 1983; Herrera 1984a; Denslow 1987; French et al. 1992; Gryj and Domínguez 1996; García et al. 2001; Saracco et al. 2004; Saracco et al. 2005; Carlo and Morales 2008; Blendinger et al. 2008; Blendinger and Villegas 2011). We likewise found a moderate competitive effect of increased neighborhood fruit density, although the spatial context possibly contributed to this effect. Focal plants in our high- and low-density neighborhoods were in close proximity (ca. 10 m apart) within uniformly dense arrowwood stands that likely concentrated frugivore activity. Whereas this design controlled effectively for non-uniformly distributed avian migrants and heterogeneity in the surrounding maritime shrub community, we recognize that such a placement possibly inflated frugivore visitation rates to low-density neighborhoods (relative to naturally low-density neighborhoods). We suggest this further illustrates the importance of spatial context when considering neighborhood influences on fruit removal (see below). We further note, however, that neutral neighborhood effects suggest some level of competition if facilitation is the expected outcome of plant-frugivore interactions as the alternative explanation, frugivore saturation (Fig. 1, line e), is likely uncommon and readily documented (e.g., all fruits consumed). In contrast, few studies have demonstrated that neighborhood fruit density facilitates rates of fruit removal or visitation by avian frugivores, and in most cases the facilitation was weak (Takahashi and Kamitania 2004; Pizo and Almeida-Neto 2009), inconsistent among sites or species (García et al. 2001; Blendinger et al. 2008), or restricted to marginally important heterospecific species (Saracco et al.

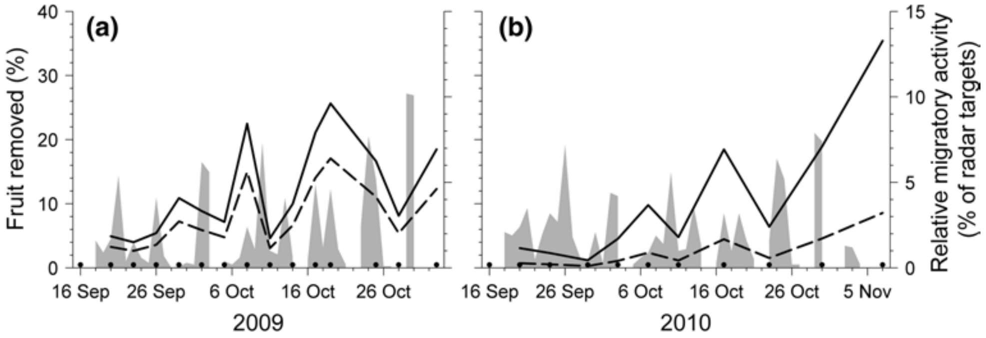

Fig. 5 Seasonal patterns in arrowwood fruit removal by avian frugivores (*lines*) and migrant activity based on concurrent marine radar monitoring (*gray shading*, see text) during fall migration on Block Island in **a** low-density (*solid line*) and high-density neighborhoods (*dashed line*) in 2009 and on **b** northern (*solid line*) and southern Block Island (*dashed line*) in 2010. Dates of fruit counts are indicated by *filled circles* along the abscissa. Gaps in the radar data indicate missing data; concurrent acoustic data suggested that no considerable migratory activity occurred on these dates (see Online Resource 1). Confidence intervals around removal patterns are omitted for clarity

2005). Fruit removal facilitated by interspecific neighborhood fruit abundance has been inferred in some host-parasite-frugivore interactions (e.g., van Ommeren and Whitham 2002; Carlo and Aukema 2005; but see Saracco et al. 2005), although to our knowledge patterns of fruit removal from infected plants as a function of their parasitic neighborhood has not been documented explicitly.

The simulations of Carlo and colleagues (Carlo et al. 2007; Carlo and Morales 2008) suggest that competition can emerge when two neighborhood conditions are met: conspecific fruit is abundant at the neighborhood spatial scale, and the neighborhood occurs in a highly aggregated fruiting landscape. Fruit densities in our study system far exceeded those at which competition became manifest in their simulations; for example, our densest 50 m^2 neighborhood alone contained more fruit than their entire simulated landscape (25 km^2), an area equivalent to all of Block Island. Arrowwood is also very patchily distributed and thus highly aggregated on Block Island (sensu Carlo and Morales 2008); likewise, most work documenting competition or neutral neighborhood effects involves species that are at least moderately aggregated on the landscape (i.e., Moore and Willson 1982; Manasse and Howe 1983; Herrera 1984b; Denslow 1987; Gryj and Domínguez 1996; Saracco et al. 2004; Carlo and Morales 2008; Blendinger et al. 2008); we were unable to evaluate the landscape distribution of focal species in several studies (French et al. 1992; García et al. 2001; Saracco et al. 2005; Blendinger and Villegas 2011). Furthermore, the clearest documented example of facilitation occurred in a highly homogeneous fruiting landscape. Sargent (1990) found that dense fruiting neighborhoods of northern arrowwood facilitated removal relative to low-density neighborhoods, but the experimental neighborhoods were carved out of an expansive arrowwood monoculture. Such a landscape with low plant and fruit aggregation strongly favors facilitation (Carlo and Morales 2008) and stands in stark contrast to the distribution of arrowwood on Block Island and fruits in most other research to date.

Although Carlo and colleagues (Carlo et al. 2007; Carlo and Morales 2008) recognized that landscape context influenced the effects of neighborhood fruit density, our review of previous studies and our experience with arrowwood on Block Island suggest potential mechanisms by which neighborhood fruit density and landscape context can interact to produce facilitation or competition. We propose that competition is the typical outcome of increased neighborhood fruit density in a landscape in which fruits are highly aggregated, but the reason for competition varies with landscape context. For example, in neighborhoods within frugivory hubs, concentrated frugivore activity within the hub decreases the residual quality of the neighborhood and thus limits the recruitment of additional frugivores, resulting quickly in competition for limited frugivores as neighborhood fruit densities increase. We suggest this reasonably describes the situation for arrowwood on Block Island and possibly other work (e.g., Manasse and Howe 1983; Denslow 1987; Gryj and Domínguez 1996; Carlo and Morales 2008), although it was typically difficult to infer the network context of focal plants (e.g., position relative to, and existence of, frugivory hubs). At the other extreme, isolated neighborhoods not associated with frugivory hubs, but occurring within a highly aggregated fruiting landscape, may also experience decreased removal rates as neighborhood fruit densities increase; however, in this case, we suggest the competition with neighboring plants for frugivores results from the difficulty of recruiting frugivores to the isolated neighborhoods. However, when fruits are not highly aggregated on the landscape (e.g., Sargent 1990; Takahashi and Kamitani 2004; Pizo and Almeida-Neto 2009), frugivores, like the fruits they seek, are relatively uniformly distributed and thus easily recruited to neighborhoods with higher fruit density. In these cases, we propose that easy frugivore recruitment and a higher residual quality in the neighborhood makes facilitation the more likely outcome of increased neighborhood fruit density.

Collectively, existing evaluations of neighborhood effects (1) support a prominent influence of the spatial distribution of fruit, on multiple scales, on the patterns of fruit removal, (2) rarely document facilitation in contrast to theoretical expectations, and (3) suggest that moderately and highly aggregated plant (and fruit) distributions are prevalent in plant communities. Thus, contemporary theoretical models (e.g., Morales and Carlo 2006; Carlo et al. 2007; Carlo and Morales 2008), while quite useful, may not adequately characterize most empirical work to date, particularly in temperate systems that support seasonally abundant frugivores. As such, models of plant-frugivore interactions will benefit from the exploration of alternative or additional model parameters (see below).

Influence of frugivore activity on rate of fruit removal

Simulations within spatially explicit networks clearly indicate that increased frugivore activity increases average fruit removal from individual plants (Carlo et al. 2007; Carlo and Morales 2008). We evaluated this predicted positive relationship in two ways: using temporal changes in frugivore (migrant) abundance during the migration season, and the well-documented differences in frugivore abundance associated with geography on Block Island. We interpreted geographic effects in 2009 without regard to arrowwood species because the 2010 experiment indicated frugivores did not strongly discriminate among fruits from the two arrowwood species.

Differences in frugivore activity due to patterns of migrant arrival

Migrant activity on Block Island fluctuated throughout the migration season, often dramatically (Fig. 5) (Mizrahi et al. 2010; Svedlow et al. 2012). However, fruit removal rates consistently increased in the days following the most substantial migratory movements over Block Island during 2009 and 2010 (Fig. 5), in accordance with the predicted positive relationship between frugivore activity and fruit removal rates (Carlo et al. 2007; Carlo and Morales 2008). A 1- to 3-day lag was often apparent between the presumed arrival of migrants and the concomitant removal of fruit, likely due to search and settling time (Alerstam and Lindström 1990).

Differences in frugivore abundance due to geography

We expected and documented higher fruit removal rates on northern Block Island in arrowwood pairs in 2010; however, this difference was not evident among arrowwood plots in 2009. Recall that experimental plots were selected to encompass uncommonly dense concentrations of arrowwood, whereas the arrowwood pairs occurred within more typical mixed-species maritime shrub stands. We thus considered whether this change in the spatial context of focal plants influenced the distribution of frugivores (logistic GLMMs; Table 1, Online Resource 1). Focal plants in dense arrowwood stands (2009) experienced a consistent probability of incurring fruit removal throughout the season while plants not associated with arrowwood concentrations (i.e., most 2010 focal pairs) sustained lower rates of removal in general and only experienced significant removal when frugivores were abundant (Fig. 5). This discrepancy suggests that the 2009 plots acted as frugivory hubs, concentrating frugivore activity at the plot (neighborhood) scale, effectively counteracting the prevailing differences in frugivore activity at a larger landscape scale.

Conclusion

Current individual-based frugivory models (Morales and Carlo 2006; Carlo et al. 2007; Carlo and Morales 2008; Morales and Vázquez 2008) establish a strong, though necessarily simplified foundation, but their foremost property is their flexibility. Generating predictions for plant-frugivore interactions in different ecosystem contexts can be accomplished with relative ease by modifying existing parameters of these models and, if necessary, incorporating additional parameters. For example, previous frugivory models possess a distinctly “tropical” inclination, but simple changes in the specification of existing parameters, such as modifying patterns of fruit regrowth (or ripening) and accommodating larger and more variable initial crop sizes and frugivore abundances, would increase the relevance of simulations to temperate systems like the maritime shrub community on Block Island. Likewise, these frugivory models can be customized to anticipate the dynamics of plant-frugivore interactions in particular ecological contexts. Songbird migration stopover provides an example relevant to the current study. The “temperate” frugivory model could be extended to provide simulated foragers with alternative foraging decisions that more adequately capture frugivore activity [e.g. varying abundances, phenologies, and preferences for multiple co-fruiting species and co-occurring arthropod resources; see, e.g., Carnicer et al. (2009)] under a particular maximization scheme (e.g., energy intake relative to energy expenditure). Certainly, achieving fully mechanistic models of avian dispersal will be challenging (Muller-Landau et al. 2008), but we argue that there is much to be gained despite this potential limitation. Seeking the general properties of plant-frugivore interactions will require the evaluation of many specific ecosystem and ecological contexts, but we expect individual-based frugivory models will play a key role in doing so.

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