
16 Plant–Frugivore Interactions as Spatially Explicit Networks: Integrating Frugivore Foraging with Fruiting Plant Spatial Patterns

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Introduction

Dispersal is essential for the persistence of populations in space and time (McArthur and Wilson, 1968; Levins, 1969). Theoretical and empirical studies suggest that seed dispersal is one of the major mechanisms that build and sustain diversity in plant communities (Nathan and Muller-Landau, 2000; Webb and Peart, 2001; Condit *et al.*, 2002). In many plant communities, frugivorous animals are believed to play the major role in structuring and maintaining diversity through their seed dispersal services (Schupp *et al.*, 2002; Terborgh *et al.*, 2002). The relevance of frugivores is implicit in the many adaptations for endozoochory (i.e. seed dispersal through guts) in nearly all plant taxa (van der Pijl, 1972), as well as in the high proportions of woody plant species that are dispersed by frugivores in many plant communities (Herrera, 2003). Therefore, in order to understand the ecology of many plant communities it is necessary to have a mechanistic understanding of frugivore–plant interactions and their relationship to plant population dynamics and diversity. However, we still know very little about how frugivores influence plant distribution, community structure and plant evolution (Wang and Smith, 2002).

Endozoochory is set apart from other dispersal modes, such as wind dispersal, by several important properties. First, frugivores create non-random seed shadows that show strong patterns of directionality towards specific habitats, cover types, species of plant, branches, topographic features and more (Janzen, 1970; Reid, 1991; Wenny, 2001; Schupp *et al.*, 2002; Kwit *et al.*, 2004a; Russo and Augspurger, 2004). Second, fruiting plants usually surpass frugivores in the numbers of individuals and/or species, creating asymmetries that could further limit seed dispersal services among plant species or individuals (Wheelwright, 1985; Jordano,

1987; Carlo *et al.*, 2003). This suggests that for frugivore-dispersed plants, frugivory, and thus dispersal, are highly contingent on context and location relative to other co-fruiting individuals or species (Saracco *et al.*, 2004; Carlo, 2005a). Furthermore, frugivores show preferences for particular species of fruiting plant and this can accentuate asymmetries in per capita seed dispersal of plants when frugivores are shared (Carlo *et al.*, 2003). Preferences may then promote more limitation in seed dispersal services among co-fruiting individuals or species. This results in multiple indirect plant–frugivore and plant–plant interactions that are highly variable in space and time because they take place between assemblages of unspecialized frugivores and multiple species of fruiting plant (Janzen, 1983; Jordano, 1987; Fleming *et al.*, 1993; Jordano *et al.*, 2003; Bascombe *et al.*, 2006). In ecological and evolutionary terms, such relationships are diffuse, because interactions between plants and frugivores generally lack strong specificity (Herrera, 1982; Janzen, 1983; Fleming *et al.*, 1993).

In this chapter, we attempt to fit the diffuse characteristics of frugivore–plant interactions into a framework that provides new ideas about frugivory and seed dispersal patterns, plant community associations and evolution. Specifically, we propose that frugivory and seed dispersal patterns should be examined in a spatially explicit manner that will help explain variability at the levels of both plant individuals and species. We argue that the framework can shed light on fruiting plant community structure, diversity and evolution.

A field without a conceptual framework

The realization that a majority of plant–frugivore relationships are diffuse and apparently non-equilibrium (Herrera, 1998) brought conceptual progress in the field of frugivory and seed dispersal to a halt (Howe, 1993; Levey and Benkman, 1999). This can be attributed to the influence of traditional ecological concepts centred on the individuality of species (Callaway, 1997; Bruno *et al.*, 2003; Lortie *et al.*, 2004), to the notion that omnivory destabilizes food webs (Pimm and Lawton, 1978; but see Agrawal, 2003), and on the principle of competitive exclusion championed in niche theory (Hutchinson, 1957). In accord with these views, the original conceptual framework of the frugivory and seed dispersal field, once known as ‘the paradigm’, proposed that there are two types of plant frugivore systems, specialized and generalized (McKey, 1975). The paradigm predicted that specific fruit traits (e.g. high nutrient content, seed/pulp ratio, water content), phenology patterns, quantity and quality of dispersal, and specificity of interactions with frugivores would determine whether plants followed generalized or specialized strategies (McKey, 1975; Howe, 1993). For example, species with lipid-rich fruits should show asynchronous fruiting patterns to sustain a handful of highly specialized species of frugivore, thus providing high-quality dispersal, while those with watery and sugary fruits (i.e. cheaper fruits to produce) should produce

superabundant and synchronous fruit crops in order to attract multiple unspecialized and opportunistic frugivores and omnivores that provide massive, although low-quality, dispersal on a per-seed basis (McKey, 1975; Howe, 1993).

However, as evidence mounted, the predictions of this paradigm found little support (Howe, 1993). For example, many fig trees show asynchronous phenology patterns and have large groups of frugivore consumers that include specialists and non-specialists as dispersers, while producing small, sugary fruits (Cruz, 1974; Terborgh, 1986; Kannan and James, 1999). Other species, such as *Schefflera morototoni* (Araliaceae), produce small, nutrient-rich fruits in superabundant and synchronous fruit displays that attract multiple non-specialized frugivores (Carlo *et al.*, 2003; Saracco *et al.*, 2005). In some cases, omnivores have been reported to behave, from a plant's perspective, as specialized frugivores (Carlo *et al.*, 2003). For example, *Phainopepla nitens* (Bombycillidae) can be considered a frugivore specializing on *Phoradendron californicum* (Viscaceae) during the winter in the Sonoran Desert. However, *P. nitens* is mostly an insectivore during the summer at high elevations, and *P. californicum* is also effectively dispersed by other species of bird in the desert (Larson, 1996; Chu and Walsberg, 1999). Hence, most (if not all) plant–frugivore systems involve plants sharing multiple frugivores, and frugivores visiting multiple plants and feeding on other organisms at different trophic levels as well.

The impacts of shared consumers on community structure have been poorly explored theoretically and empirically (Agrawal, 2003), particularly in the plant–frugivore literature. This is surprising because:

1. seed dispersal is central in theories of diversity and community ecology (Hubbell, 2001; Terborgh *et al.*, 2002; Wang and Smith, 2002)
2. plants that are dispersed by frugivores are prevalent in many communities (Herrera 2003)
3. almost all species of plant dispersed by frugivores share multiple frugivore seed dispersers (Jordano, 1987; Carlo *et al.*, 2003; Jordano *et al.*, 2003).

Understanding the distribution and abundance of species of fruiting plant, associations and communities may require a mechanistic approach that explicitly incorporates the importance of multiple fruit resources and the ubiquity of having shared and generalized plant–frugivore interactions.

Competition and facilitation in frugivore-dispersed plants: neighbourhood effects

García *et al.* (2001) titled a paper 'Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes'. Their title reveals not only a common finding in many frugivory and seed dispersal studies, it also represents the type of result that 'the paradigm'

could not handle conceptually and that we still lack adequate theory to describe. We have no theory to explain how variability in characteristics that exist beyond an individual plant (e.g. having co-fruiting intra- and heterospecific neighbours) affects frugivory and seed dispersal of plants.

A common source of variation in frugivory services that is beyond the level of the organism is the fruiting neighbourhood of a fruiting plant (Manasse and Howe, 1983; Herrera, 1984; Denslow, 1987; Sargent, 1990; Saracco *et al.*, 2005; Carlo, 2005a; Canham and Uriarte, 2006). Failing to account for intra- and heterospecific neighbourhood interactions may obscure key aspects of the effects of generalized frugivores on seed dispersal and the spatial patterning of plant communities (Carlo and Aukema, 2005). For example, Foster (1990) examined the contribution of 27 plant characteristics (e.g. seed/pulp ratio, nutrients, water content, crop size, height, etc) to the variation in rates of fruit removal among individuals of *Allophylus edulis* (Sapindaceae) in Paraguay. Of all the variables measured, Foster found only a few significant correlations (fruit crop size being most important; see also Davidar and Morton, 1986). Foster argued that interactions with influential heterospecific neighbours, in some cases, could override intraspecific trait variance in explaining seed removal rates. Explanations for results from both García *et al.* (2001) and Foster (1990) call for spatial and positional information of fruiting plant individuals in relation to others in order to make sense of observed patterns of fruit removal. A simple way to summarize and simplify spatial/positional information is to characterize the co-fruiting neighbourhood of a plant (Manasse and Howe, 1983; Sargent, 1990; Saracco *et al.*, 2005).

Neighbourhoods have long been suspected to be important in explaining frugivory patterns in co-fruiting plants through competition (Manasse and Howe, 1983) or facilitation (Herrera, 1984). However, studies often report conflicting results for the effects of both intra- and interspecific co-fruiting neighbours. Intraspecific neighbours have been reported to decrease fruit removal (Manasse and Howe, 1983) or to increase it (Sargent, 1990); and we know of only one study that reported no effects of intraspecific neighbour density on fruit removal rates (French *et al.*, 1992). Similarly, co-fruiting interspecifics have been noted to increase fruit removal (Herrera, 1984; Whelan *et al.*, 1998; van Ommersen and Whitham, 2002; Saracco *et al.*, 2005) as well as decrease it (Carlo *et al.*, 2003; Saracco *et al.*, 2005). Furthermore, in a field experiment, Carlo (2005a) found that seeds of *Solanum americanum* (Solanaceae) reached more sites and appeared in more faecal samples (i.e. dispersal units) when in a neighbourhood with *Cestrum diurnum* (Solanaceae) than in a neighbourhood composed only of other *S. americanum*. This was because mixed-species neighbourhoods were more attractive to frugivores than single-species neighbourhoods. A summary of studies that have looked at neighbourhood effects on frugivory and seed dispersal is presented in Table 16.1.

Competition and facilitation among fruiting plants that share seed-dispersal agents can be accentuated at the scale of plant neighbourhoods

Table 16.1. Studies that have looked at aspects of competition and/or facilitation among neighbouring plants for seed dispersal services by frugivores.

Source	Study species (Family)	Habitat/Climate	Effects of intraspecific neighbours	Effects of interspecific neighbours
Herrera and Jordano, 1981	<i>Prunus mahaleb</i> (Rosaceae)	Mediterranean scrubland	Competition	N/A
Moore and Wilson, 1982	<i>Lindera benzoin</i> (Lauraceae)			
Manasse and Howe, 1983	<i>Virola surinamensis</i> (Myristicaceae)	Tropical forest	Competition	N/A
Herrera, 1984	<i>Rosa canina</i> , <i>Crataegus monogyna</i> (Rosaceae)	Temperate	N/A	Facilitation
Denslow, 1987	<i>Sambucus pubens</i> (Caprifoliaceae)	Temperate	Competition	N/A
Sargent, 1990	<i>Viburnum dentatum</i> (Caprifoliaceae)	Temperate	Facilitation	N/A
French <i>et al.</i> , 1992	<i>Coprosma quadrifida</i> (Rubiaceae)	Subtropical montane wet sclerophyll forest	Neutral	N/A
Tewksbury and Nabhan, 2001	<i>Capsicum annum</i> (Solanaceae)	Sonoran Desert/temperate	N/A	Facilitation
Burns, 2002	Community meta-analysis	Temperate and tropical	N/A	Facilitation
van Ommeren and Whitham, 2002	<i>Phoradendron juniperinum</i> (Viscaceae) <i>Juniperus monosperma</i> (Cupressaceae)	Temperate evergreen forest	N/A	Facilitation
Aukema and Martínez del Rio, 2002	<i>Phoradendron californicum</i> (Viscaceae)	Sonoran Desert	Facilitation	N/A
Saracco <i>et al.</i> , 2004	<i>Schefflera morototoni</i> (Araliaceae)	Subtropical shaded coffee plantation	Facilitation	Facilitation
Saracco <i>et al.</i> , 2005	Bird-dispersed trees	Subtropical montane forest	Competition	Facilitation
Carlo, 2005	<i>Solanum americanum</i> , <i>Cestrum diurnum</i> (Solanaceae)	Tropical pasture	Neutral	Facilitation
Carlo and Aukema, 2005	<i>Phoradendron hexastichum</i> (Viscaceae) <i>Cecropia schreberiana</i> (Cecropiaceae)	Tropical moist forest	N/A	Facilitation

because the spatial patterning of fruit resources influences frugivore foraging decisions and movements (Levey *et al.*, 1984; Saracco *et al.*, 2004). Using simulation models developed by Morales and Carlo (2006), we show here that whether plants compete for or facilitate frugivory and seed dispersal services is contingent on two factors (Fig. 16.1):

1. the spatial patterning of the plant population
2. the availability of frugivores.

Thus, the disparate findings of the relatively few studies that have looked for or found neighbourhood effects (Table 16.1) might be understood when looking at the variance in both the spatial patterning of studied plant populations and the availability of frugivores. What is crucial is that fitness gradients may develop among plant individuals depending on their spatial context regarding co-fruiting intraspecific and interspecific individuals with which they share seed-dispersal agents.

On the other hand, frugivores may help maintain, strengthen, and propagate species associations by the co-dispersal of seeds from different species of plant from within neighbourhoods, and by directional seed dispersal patterns (Wenny, 2001; Clark *et al.*, 2004; Carlo and Aukema, 2005). Understanding interactions involving frugivores that show differential responses to species of plant and to the spatial patterning and abundance of fruit resources requires a conceptual framework that allows all such components (e.g. spatial pattern, frugivore behaviour and preferences) to interact and generate ecological patterns.

Plant–frugivore interactions as spatially explicit networks

Plant–frugivore relationships are characterized by indirect interactions, many of which are mediated by density of resources, pathogens, and herbivores (Janzen, 1970; Morales and Carlo, 2006), distance between sources (Levey *et al.*, 1984) and the properties of different species of plant, such as fruit nutritional value and size (Moermond and Denslow, 1985) and secondary compounds (Cipollini and Levey, 1997; Tewksbury and Nabhan, 2001). Frugivores physically link plant individuals and also affect how seeds are deposited in space (Herrera and Jordano, 1981), and thus generate the templates for plant recruitment (Schupp and Fuentes, 1995; Nathan and Muller-Landau, 2000). Plant–frugivore interactions can be modelled as a unique type of network: one that integrates plant–plant linkage through frugivore movements in a spatially explicit manner.

In many types of network, it is common for a few elements to drive most interactions, for example in such diverse systems as the Internet, Bose–Einstein condensates, biochemical pathways, social relationships, and trophic webs (Strogatz, 2001; Whitham *et al.*, 2003). Elements of a network that show high connectivity to other network elements are termed ‘hubs’. What is most important is that hubs facilitate connection among the elements of the network. In mutualistic networks of ecological interactions, hubs may

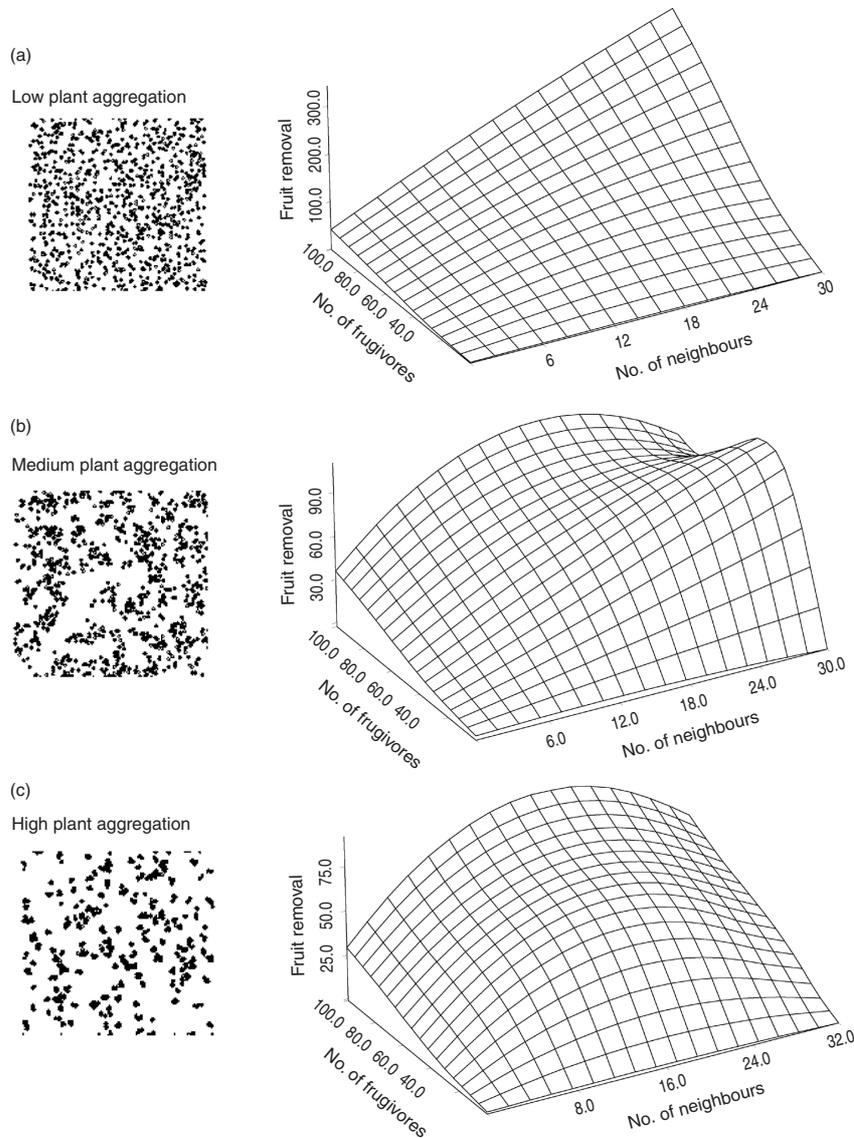


Fig. 16.1. Relationships between fruit removal (vertical axis), neighbourhood density, and frugivore abundance. Lines are from a quadratic fit to data smoothed as a response surface (using S-Plus 6.2). (a) Plants with a highly aggregated spatial pattern, (b) plants with medium spatial aggregation, (c) plants distributed at random. Results are from spatially explicit computer simulations developed by Morales and Carlo (2006, see also Carlo, 2005b). Simulated birds moved among plants, ate fruit, and dispersed seeds in a population of 1000 plants in 5×5 km landscapes using stochastic movement and foraging rules parameterized with field data (Carlo, 2005b). Three levels of frugivore abundance (1, 10 and 100 birds) were used. Simulated data were averaged across 30 replicate landscapes for each factor combination. The number of neighbours was counted within a 100-m radius around each plant and fruit removal values averaged across the 30 replicate landscapes.

promote the formation of hierarchical relationships among species of fruiting plants in a community (Bascompte *et al.*, 2003, 2006; Jordano *et al.*, 2003; Lázaro *et al.*, 2005). Hierarchical relationships between fruiting plants occur when certain species capture seed dispersal interactions more frequently and from more dispersers than other species.

Hierarchical network properties have already been described in plant–frugivore mutualistic networks (Terborgh, 1986; Jordano, 1987; Sallabanks, 1993; Bascompte *et al.*, 2003, 2006; Carlo *et al.*, 2003; Jordano *et al.*, 2003). Jordano *et al.* (2003) suggested that hierarchical network topologies could quite well describe many community patterns of frugivore–plant interactions worldwide. This idea implies that, in many communities, just a handful of plant and animal species will be responsible for a disproportionate share of the frugivory and seed dispersal interactions (Fig. 16.2). Still, the spatial component of plant–frugivore networks of ecological interactions has not been previously explored. The lack of a spatially explicit approach is remarkable, given that frugivory and seed dispersal patterns depend upon the ways in which frugivores move and interact with the spatial landscape structure of fruiting plant populations (Westcott and Graham, 2000; see Kwit *et al.*, Chapter 19, this volume; Holbrook and Loiselle, Chapter 13, this volume). Furthermore, the last

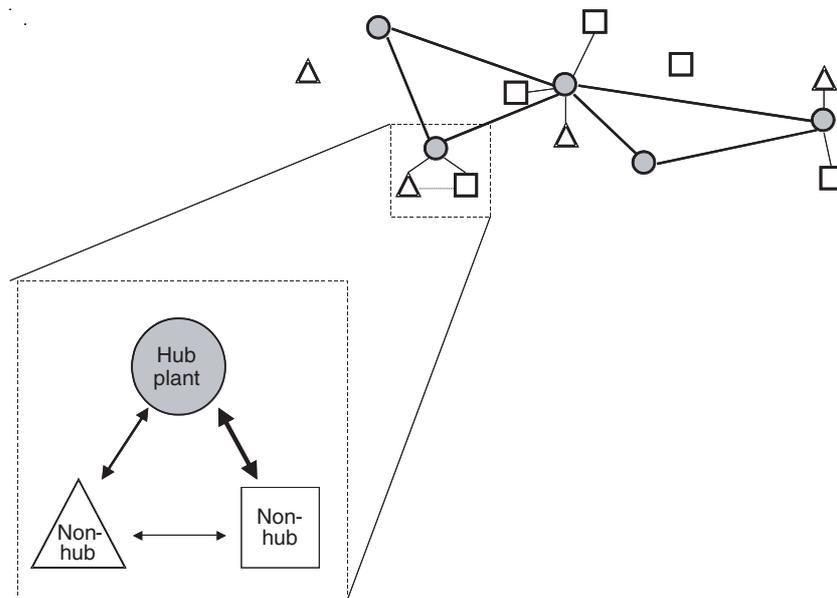


Fig. 16.2. Hypothetical representation of how hub plant species or neighbourhoods affect the flow of frugivore movements within a local plant community. Thickness of a line indicates the frequency of movement. Movement is most common between hubs (grey circles) and least common between non-hub species (triangles and squares). Inset shows that some non-hub species (squares) interact more strongly (heavier arrow) with hubs than others. The probability of movement from hub to non-hub plants decreases with distance.

decade has seen an emphasis on the importance of space in ecological and evolutionary processes (Tilman and Kareiva, 1997). It is time to explicitly incorporate space in the modelling of plant–frugivore interactions.

The spatial structure of landscapes influences movements of animals as different as beetles (Crist *et al.*, 1992; Morales and Ellner, 2002), birds (Levey *et al.*, 2005), and elk (Morales *et al.*, 2004). Frugivores are known to detect and track fruit abundance at small and large spatial and temporal scales (Levey, 1988; Rey, 1995; Kwit *et al.*, 2004b; Márquez *et al.*, 2004). Therefore it should be expected that fruit removal rates would be affected by both landscape patterns of resource distribution and the local neighbourhoods of plants. But irrespective of the exact mathematical function describing connectivity in plant–frugivore systems (i.e. power-law, truncated power-law, exponential; Jordano *et al.*, 2003), it is crucial that we develop a basic understanding of the role that well-connected (i.e. hub) species of plant play in communities. In this chapter we will explore the case of plant–frugivore networks that have hubs or hub-like elements, and the implications for plant population dynamics, community ecology, and diversity.

Hubs in plant–frugivore spatial networks

Plant–frugivore networks have a dual nature and can be viewed from the plants' perspectives or from the frugivores' perspectives (i.e. plants connecting frugivore consumers or frugivores connecting plants; Jordano *et al.*, 2003). Here we depict the network in the following way. We consider plants as the network elements to be connected by frugivores because plants are sessile elements and frugivores move among them, creating visitation patterns that are influenced by the explicit locations of plants. We define a frugivory hub as a plant individual, species or neighbourhood which has a higher probability of visitation than the rest of the elements forming the network. Thus, frugivory hubs capture a large share of frugivory and dispersal services in a population and/or community. We propose that hubs emerge both among individuals of a species in an intraspecific network, and among different co-fruiting species in an interspecific community network. The network concept has been applied at the interspecific level (Bascompte *et al.*, 2006), although not in a spatially explicit manner, but intraspecific networks have not been previously examined. In the real world, both interspecific and intraspecific networks are simultaneously in action and interacting with each other; such interactions have potentially important effects on community composition and structure.

Frugivory hubs within a single-species plant population

In a population of a fruiting plant species, particular individuals can receive disproportionate frugivory and seed dispersal services. We refer to these individuals as intraspecific hubs. An individual may become a hub because

of individual attributes (e.g. larger size) and/or spatial location (e.g. neighbourhood). Carlo (2005b) examined distributions of fruit removal (i.e. histograms for average fruit removal per plant individual) in bird-dispersed plant populations, using spatially explicit computer simulations of frugivory and seed dispersal (Fig. 16.3). He found that distributions were highly skewed when frugivore density was in the range of 0.01–0.001 frugivores per plant, regardless of the degree of spatial aggregation of the population (Fig. 16.3a,b). Only at high frugivore densities of 0.1 frugivores per plant were distributions unimodal, with most individuals having an intermediate number of fruits removed (Fig. 16.3c). Nevertheless, the distributions from the simulation model had much more variance compared with null models where birds chose fruiting plants at random (T.A. Carlo and J.M. Morales, 2006, unpublished results). This means that fruit removal services were monopolized, to a greater degree than expected by chance, by a handful of fruiting plants in the population (Carlo *et al.*, 2003; T.A. Carlo and J.M. Morales, 2006, unpublished results). At the same time, more plants than expected received little or no frugivory services, especially in aggregated landscapes (Fig. 16.3).

Neighbourhood density was generally positively correlated with frugivory (Fig. 16.1). Indeed, positive density dependence is probably the best documented pattern in the frugivory and seed dispersal literature, where positive relationships between crop size and visitation rates have been shown repeatedly (Davidar and Morton, 1986; Foster, 1990; Sargent, 1990; Sallabanks, 1993; Saracco *et al.*, 2005). Positive density dependence in fruit removal rates can be expressed at both individual (Davidar and Morton, 1986; Sallabanks, 1993) and neighbourhood scales (Aukema, 2004; Saracco *et al.*, 2004) because the spatial definition of a fruit 'patch' depends on the spatial perception of resources by frugivores. It is probably largely irrelevant for a frugivore if 500 fruits within a 4-m² area are all in one plant or found in five plants each with 100 fruits, or 50 smaller plants each with 10 fruits. Spatial autocorrelation in fruit removal services at small spatial scales (relative to the range of animal movements; see Aukema and Martínez del Río, 2002) is likely to be a general phenomenon (Kwit *et al.*, 2004b; Saracco *et al.*, 2004) and a contributing factor to hub formation. Hence, the emergence of hubs within a fruiting plant population is also dependent on the way in which individuals are distributed in space.

Evidence for the emergence of hubs in single-species plant networks

Hubs are not only visible in theoretical models but are also observable in nature. Evidence for hubs can be found by examining the frequency distribution and linkage of frugivore visits to plants or neighbourhoods of plants. For example, mistletoes are aggregated within the host trees they parasitize, so each host tree can be considered as a mistletoe neighbourhood with unique characteristics (location in space, mistletoe fruit crop, physical

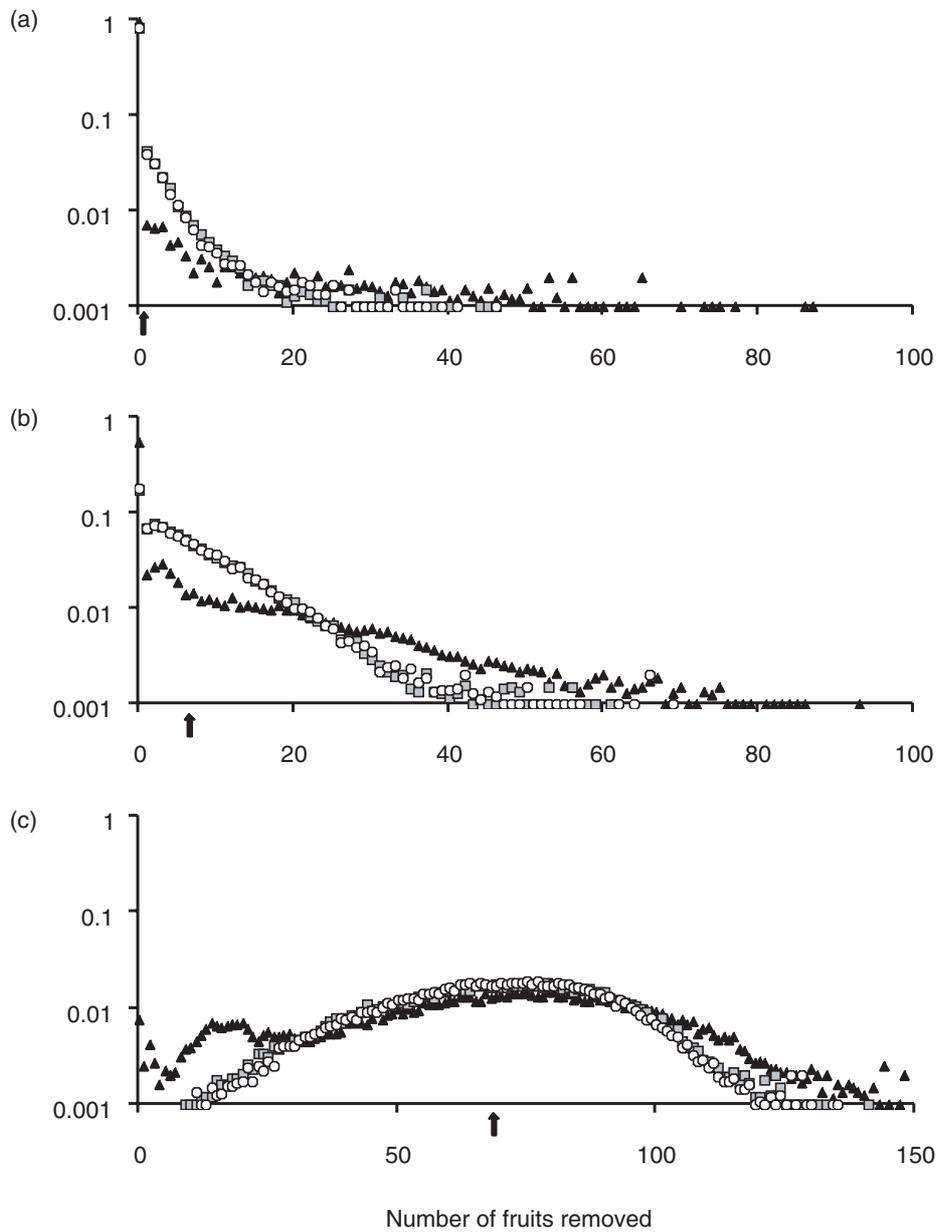


Fig. 16.3. Frequency distributions of fruit removal events by (a) 1 frugivore, (b) 10 frugivores, or (c) 100 frugivores in simulated plant populations with high landscape aggregation (black triangles), medium landscape aggregation (grey squares) or low landscape aggregation (white circles). The x axis is the number of fruits removed from a plant. The y axis is the average proportion (of 30 replicate runs) of individuals in the population (1000 plants) receiving a given amount of fruit removal. Black arrows indicate the mean values. Data were produced with spatially explicit computer simulations developed by Morales and Carlo (2006, see also Carlo, 2005b and legend of Fig. 16.1).

characteristics of the tree, etc). On a mapped 4-ha plot, J.E. Aukema (2001, unpublished results) observed phainopeplas (*P. nitens*, the primary dispersers of the mistletoe *P. californicum*) visiting a few trees very frequently, while failing to visit most trees (Fig. 16.4a). In addition, she found that phainopepla flights linked a handful of trees to a large number of other trees, while a majority of infected trees were linked to few, if any, other trees (Fig. 16.4b). Nine out of 250 mistletoe-infected trees were responsible for capturing 56% of observed visits, and acted as hubs linking visits to a large number of other mistletoe-infected trees. When looking at the characteristics of the mistletoe-infected trees that acted as frugivory hubs, Aukema (2001) found that the nine most-linked trees, on average, had denser mistletoe populations than other infected trees ($t = 2.19$, $P = 0.029$, $n = 260$). In addition to mistletoe resources, hub trees also had other physical and spatial features that were attractive to phainopeplas. Hub trees were significantly taller than other infected trees ($t = 2.85$, $P = 0.01$, $n = 260$), often had dead branches suitable for perching on (J.E. Aukema, 2006, unpublished results), and were located on drainages more frequently than would be expected by chance ($\chi^2 = 8.78$, $P = 0.011$, $n = 242$).

Further evidence for hubs within a species is found in studies such as that of Aldrich and Hamrick (1998) who, using molecular approaches, found that a few trees were producing the most seedlings in a fragmented landscape. Although there were many individuals present in the study area, they hypothesized that the reproductive dominance of the individuals was due to a privileged spatial position in pastures that allowed them to produce more fruit and to attract more frugivores. In the context of plant–frugivore networks, these individuals acted as hubs.

Frugivory hubs among plant species

Frugivores commonly show preferences for particular species among the available fruiting plants that they use (Levey *et al.*, 1984; Moermond and Denslow, 1985), which often results in a disproportionate use of a subset of fruiting species *versus* others in the field (Carlo *et al.*, 2003; Bascompte *et al.*, 2006). Therefore, interspecific hubs for frugivory can form when some species serve as magnets (*sensu* Johnson *et al.*, 2003) for mutualists. In other words, in an interspecific context, frugivory hubs are species that receive a disproportionate amount of attention from frugivores and are less dispersal-limited than the rest of the species in a given plant community.

While the emergence of hubs in intraspecific networks seems largely controlled by patterns of local density, relationships among interspecific hubs and other species are likely to be determined largely by species properties. For example, species of plant vary not only in aspects of the quality and quantity of their fruits (Moermond and Denslow, 1985), they also differ in the timing and length of fruiting. For example, Carlo *et al.* (2003) found that the most connected (*sensu* Jordano *et al.*, 2003) and preferred species across forested habitats in Puerto Rico had long fruiting

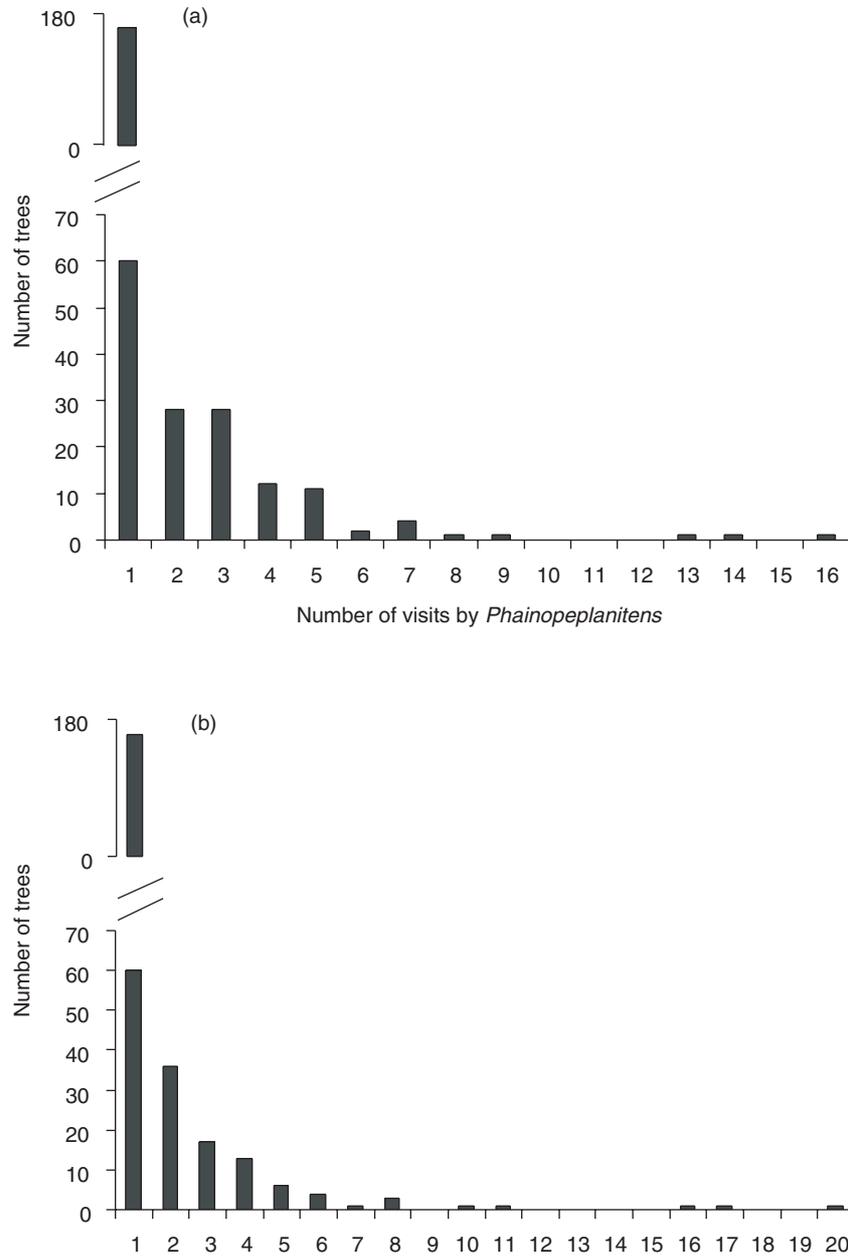


Fig. 16.4. On a 4-ha mapped plot in the Sonoran Desert, J.E. Aukema (2001, unpublished results; see also Aukema and Martínez del Río 2002) observed that *Phainopepla nitens*, a bird specializing on mistletoe (*Phoradendron californicum*) berries, visited a few mistletoe-infected mesquite trees (*Prosopis velutina*, Mimosaceae) frequently, but visited most trees very rarely (a). Similarly, only a few trees were linked to many other trees through direct tree-to-tree flights (b). Those trees that received many bird visits and were connected to many other trees through bird flights acted as intraspecific hubs for frugivory.

seasons and could re-fruit faster than less connected species. Therefore, for a species to become an interspecific hub of frugivory and seed dispersal, it appears that it might be necessary to be able to offer fruit for time periods that are longer than those of non-hub species, although the generality of this result still remains to be documented.

The most important effect of interspecific frugivory hubs is that hubs will affect the movement patterns of frugivores and, consequently, the flow of frugivory and seed dispersal services in a locality. Therefore, the proximity of fruiting plants to hub species may determine whether an individual plant experiences facilitation (i.e. by being close to the hub; see Fig. 16.2) or competition (i.e. by being further from hubs). In addition, species serving as hubs could create strong directional patterns of seed dispersal (Wenny, 2001), with seed rain of frugivore-dispersed species higher near hub species.

Evidence for the existence of frugivory hubs among plant species

We were not able to find a single study and know of no data set that could be used to directly examine spatially explicit hubs in interspecific plant–frugivore networks. Co-evolutionary plant–frugivore networks have been explored for interspecific communities, though not in a spatial context (Bascompte *et al.*, 2003, 2006; Jordano *et al.*, 2003). These networks have been found to be asymmetric, with some species of plant interacting more strongly than others with animal dispersers (Bascompte *et al.*, 2006). Similar to the intraspecific case, plants functioning as frugivory hubs in plant communities should show high connectivity and preferential use by the frugivore community. Using data from Carlo *et al.* (2003) we found that five out of 68 endozoochorous species captured the most interactions with frugivores (i.e. connectivity, Fig. 16.5a) in forests of north/central Puerto Rico. The pattern was similar for the distribution of fruit preferences (i.e. fruiting species that were used by frugivores more frequently than expected based on their relative abundance, Fig. 16.5b). *Cecropia schreberiana* (Cecropiaceae) was the species with the greatest number of recorded avian fruit consumers; the same species was preferred by the most species of bird (four) in the community, while most species of plant (75%) were not preferred. *Cecropia schreberiana* also fruits all year-round (Carlo *et al.*, 2003), and thus meets the expected conditions for a hub species in Puerto Rican forest communities.

Consequences of frugivory hubs for patterns of seed deposition

Because hubs could strongly affect the flow of frugivory events among plant individuals and species, they should play an important role in subsequent patterns of seed deposition. In general, the probability of

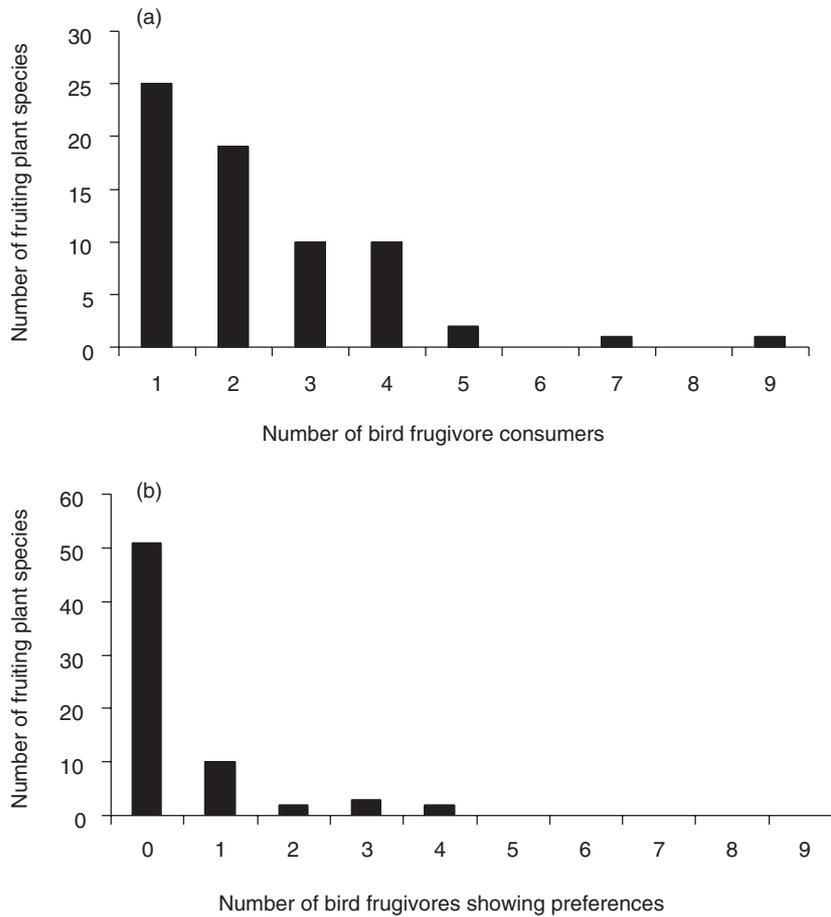


Fig. 16.5. Histograms showing avian fruit use and fruit preferences from Carlo *et al.* (2003) across five moist secondary forests and 8 months of observation in Puerto Rico. (a) The number of plants (*y* axis) in the plant community with the observed number of frugivorous bird consumers (*x* axis, maximum was 9). (b) The number of plant species that were preferred (i.e. observed use was greater than would be expected by the relative abundance of the species' fruits; see Carlo *et al.*, 2003), and how many species of bird preferred them. Note that a few plants captured most of the frugivory services and preferences in the communities.

frugivore movement would be greatest: (i) from one hub to another hub; (ii) from a hub to a non-hub plant; and (iii) from a non-hub to a hub; and would be least from one non-hub to another non-hub. The result is a series of 'avenues' of frequent movement accompanied by higher rates of frugivory and particular patterns of seed dispersal (e.g. directional, *sensu* Wenny, 2001) for the plants in or near such avenues (Herrera and Jordano, 1981). Specifically, we believe that at least two effects of hubs on seed fall patterns can be predicted.

1. Hubs create nested and directional patterns of seed deposition

Because frugivores visit hubs much more frequently, hubs then provide dispersal linkage for plants that are visited less frequently. This has at least two obvious implications. First, seeds from non-hub plants will have a disproportionate share of their seeds arriving under or near hubs. By the same token, seeds from hubs will be proportionally more widespread, reaching more locations than those of seeds from non-hubs. This should result in a nested deposition pattern (*sensu* Bascompte *et al.*, 2003) in which seeds (either intra- or interspecific) from most plants will be falling *within* the seed shadow of hubs. In the case of an interspecific hub, nested seed deposition patterns could then translate into nested patterns of plant species distributions like those described by Lázaro *et al.* (2005) in northern Europe. For the case of an intraspecific hub, spatial diversity of genotypes will be nested within the genotypes of hubs, with patches of high diversity (near hubs) and patches of low diversity elsewhere, where the genotypes of the hubs are overrepresented.

2. Hubs create seed dispersal limitation that is patchily distributed in space and time

Hub formation has an inescapable consequence: it alters the spatial distribution of dispersal services. This creates patches where non-hub plants are dispersal-limited and patches where hub plants are dispersal-rich. In the intraspecific case, plants that are far from hubs are expected to experience competition, whereas plants closer to hubs are expected to experience facilitation. The interspecific case is more complex because it involves overlapping spatial networks of several species at once. In this case, proximity to a hub species could result in either competition or facilitation. Hubs can cause competition for non-hub species that are nearby if the frugivores' preference for the fruits of the hub is so strong that they ignore the non-hub fruits nearby. For these non-hub species, the location of intraspecific hubs will not be spatially correlated with the hub species. Conversely, if frugivores are more generalized (which is the rule rather than the exception; see Bascompte *et al.*, 2006), proximity to hub species may facilitate both fruit removal and seed dispersal for non-hub species. In this case, the spatial position of intraspecific hubs is expected to be concordant with the position of the interspecific hubs. Interspecific facilitation will not only cause spatial association of hubs from different species, but will also lead to co-dispersal of seeds from hub and non-hub species.

Frugivore spatial networks: community ecology, evolution and conservation

The spatial network framework we have presented could be used to test diverse mechanistic hypotheses regarding plant community assembly, succession, invasions, range shifts under climatic change, and restoration practices. It also can provide a framework for developing new evolutionary hypotheses and experiments designed to explore in more detail the conditions that drive processes of natural selection in plant–frugivore systems.

The presence of interspecific hubs for frugivory and seed dispersal in plant communities can affect successional dynamics and influence their spatial patterning and diversity. Because hub species within plant communities are the broadest and strongest interactors with frugivore assemblages, they should not suffer from dispersal limitation. This allows them to reach more locations (including more long-distance dispersal) than ordinary frugivore-dispersed plants that (by definition) comprise the majority of the community. The dominance of hubs then serves to bring non-hub species to new locations by directed dispersal. In fact, some hub species may also be early successional and pioneer species, as is the case with *Cecropia schreberiana* and *Schefflera morototoni* in Puerto Rico. Thus, successional dynamics could be driven by the arrival of pioneer hub species (Vieira *et al.*, 1994). Alternatively, the establishment of pioneer species that do not interact with the frugivore community (e.g. *Spathodea campanulata*, see Lugo and Helmer, 2004) may retard the arrival and diversity build-up in, for example, secondary successional forests.

Conservation practices can also benefit from an understanding of frugivory networks and knowledge of the identity of hub species and the strength and frequency of linkages between species in regional communities. For example, exotic species that are animal-dispersed (such as the Russian olive, *Elaeagnus angustifolia*, Elaeagnaceae, in western North America) become elements of local frugivore networks. Invasive species can take advantage of the networks in order to spread. In some cases, exotic species could become hubs themselves in their new environments, which could actually have positive effects for native plants (through co-dispersal, directional dispersal and facilitation) and animals (by providing food resources). Knowing the topology of frugivory networks can also help restoration biologists to select which species to use in restoration projects. Planting hub species may accelerate the development of diverse plant and animal communities. In addition, climate change scenarios predict great shifts in the ranges of many species and widespread extinction if they are unable to respond to these changes and move into suitable areas (Thomas *et al.*, 2004). Maintaining plant–frugivore interactions will be critical to the persistence of thousands of plant and animal species. If hub species are able to, or are aided in, moving with the shifts in climate, other species may be able to hitch-hike through the dispersal network. Furthermore, because hub species are by definition

important to a diversity of frugivores, if hub species are able to move, they can supply resources for some other frugivores whose ranges are also shifting, as well as for frugivores in their new communities.

Hierarchical network structures can also affect processes of gene flow, spatial genetic structuring and natural selection. In theory, the interaction of frugivores with the spatial patterning of a plant population by itself generates asymmetries in the seed dispersal of individuals based on local neighbourhood density and location (Figs 16.1 and 16.3; Aldrich and Hamrick, 1998; Carlo, 2005b). In the absence of other factors influencing individual fitness, these asymmetries can then produce a type of genetic drift that can influence the genetic make-up of populations. For example, the spread and increase of particular alleles could be increased tremendously if they are found in individuals associated with hubs. Conversely, a potentially beneficial allele can be lost much faster than predicted by models that do not account for spatial interactions (e.g. the model of Levin and Kerster, 1975), given the large dispersal asymmetries produced by spatial positioning. Still, it remains a great challenge to understand the processes of natural selection taking place in the context of a spatial network. Evolution and co-evolution in a network context may depend on how much some species need the presence of others locally in order to receive sufficient seed dispersal services and maintain viable populations over time. Because plant–frugivore networks (including hub species) change regionally, the potential selective pressures of interspecific interactions within local networks can promote patterns of mosaic evolution (*sensu* Thompson, 1994).

In conclusion, theories that consider only competitive interactions fail to explain satisfactorily how multiple species coexist and why some plant communities are so diverse (Terborgh *et al.*, 2002; Lortie *et al.*, 2004). Because the dispersal of endozoochorous plants is contingent on the interaction of frugivores with the spatial distribution and diversity of fruiting plants, interactions in plant–frugivore networks can be important forces in the organization and diversity of communities where plant–frugivore mutualisms are common. Looking at them in spatially explicit ways could help explain patterns of ecological connectance that are just starting to be explored.

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References

- Agrawal, A.A. (2003) Why omnivory? *Ecology* 84, 2521.
- Aldrich, P.R. and Hamrick, J.L. (1998) Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. *Science* 281, 103–105.
- Aukema, J.E. (2001) Dispersal and spatial distribution of the desert mistletoe, *Phoradendron californicum*, at multiple scales: patterns, processes and mechanism. PhD dissertation, The University of Arizona, Tucson, AZ, USA.
- Aukema, J.E. (2004) Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* 27, 137–144.
- Aukema, J.E. and Martínez del Rio, C. (2002) Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* 83, 3489–3496.
- Bascompte, J., Jordano, P. and Olesen, J.M. (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Bascompte, J., Jordano, P., Melián, C.J. and Olesen, J.M. (2003) The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences of the USA* 100, 9383–9387.
- Bruno, J.F., Stachowicz, J.J. and Bertness, M.D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18, 119–125.
- Burns, K.C. (2002) Seed dispersal facilitation and geographic consistency in bird–fruit abundance patterns. *Global Ecology and Biogeography* 11, 253–259.
- Callaway, R.M. (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112, 143–149.
- Canham, C.D. and Uriarte, M. (2006) Analysis of neighbourhood dynamics of forest ecosystems using likelihood methods and modelling. *Ecological Applications* 16, 62–73
- Carlo, T.A. (2005a) Interspecific neighbours change seed dispersal pattern in an avian dispersed plant. *Ecology* 86, 2440–2449.
- Carlo, T.A. (2005b) Competition and facilitation in bird dispersed plants. PhD dissertation, University of Colorado, Boulder, CO, USA.
- Carlo, T.A., and Aukema, J.E. (2005) Female-directed dispersal and facilitation between a mistletoe and a dioecious host. *Ecology* 86, 3245–3251.
- Carlo, T.A., Collazo, J.A. and Groom, M.J. (2003) Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia* 134, 119–131.
- Chu, M. and Walsberg, G.E. (1999) Phainopepla (*Phainopepla nitens*). *Birds of North America* 415.
- Cipollini, M.L. and Levey, D.J. (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150, 346–372.
- Clark, C.J., Poulsen, J.R., Connor, E.F. and Parker, V.T. (2004) Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia* 139, 66–75.
- Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. and Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science* 295, 666–669.
- Crist, T.O., Guertin, D.S., Wiens, J.A. and Milne, B.T. (1992) Animal movements in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6, 536–544.
- Cruz, A. (1974) Feeding assemblages of Jamaican birds. *Condor* 76, 103–107.
- Davidar, P. and Morton, E.S. (1986) The relationship between fruit crop sizes and fruit removal rates by birds. *Ecology* 67, 262–265.
- Denslow, J.S. (1987) Fruit removal from aggregated and isolated bushes of red elderberry *Sambucus pubens*. *Canadian Journal of Botany* 65, 1229–1235.

- Fleming, T.H., Venable, D.L. and Herrera, L.G. (1993) Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. *Vegetatio* 108, 107–120.
- Foster, M. (1990) Factors influencing bird foraging preferences among intraspecific fruit trees. *Condor* 92, 844–854.
- French, K., O'Dowd, D.J. and Lill, A. (1992) Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. *Australian Journal of Ecology* 17, 35–42.
- García, D., Zamora, R., Gómez, J.M. and Hodin, J.H. (2001) Frugivory in *Juniperus communis* depends more on population characteristics than on individual attributes. *Journal of Ecology* 89, 639–647.
- Herrera, C.M. and Jordano, P. (1981) *Prunus mahaleb* and birds: the high efficiency seed dispersal system of a temperate tree. *Ecological Monographs* 51, 203–218.
- Herrera, C.M. (1982) Seasonal variation in the quality of fruits and diffuse coevolution plants and avian dispersers. *Ecology* 63, 773–785.
- Herrera, C.M. (1984) Seed dispersal and fitness determinants in wild rose: combined effects of hawthorn, birds, mice, and browsing ungulates. *Oecologia* 63, 386–393.
- Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* 68, 511–538.
- Herrera, C.M. (2003) Seed dispersal by vertebrates. In: Herrera, C.M. and Pellmyr, O. (eds) *Plant–Animal Interactions: An Evolutionary Approach*. Blackwell, Oxford, UK, pp. 185–208.
- Howe, H.F. (1993) Specialized and generalized dispersal systems: where does 'the paradigm' stand? *Vegetatio* 107/108, 3–13.
- Hubbell, S.P. (2001) *A Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22, 415–427.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 104, 501–528.
- Janzen, D.H. (1983) Dispersal of seeds by vertebrate guts. In: Futuyma, D.J. and Slatkin, M. (eds) *Coevolution*. Sinauer Associates, Sunderland, MA, USA, pp. 232–263.
- Johnson, S.D., Peter, C.I., Nilsson, L.E. and Agren, J. (2003) Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84, 2919–2927.
- Jordano, P. (1987) Patterns of mutualistic interactions in pollination and seed dispersal: dependence asymmetries, and coevolution. *American Naturalist* 129, 657–677.
- Jordano, P., Bascompte, J. and Olesen, J.M. (2003) Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* 6, 69–81.
- Kannan, R. and James, D.A. (1999) Fruiting phenology and the conservation of the great pied hornbill (*Buceros bicornis*) in the western Ghats of southern India. *Biotropica* 31, 167–177.
- Kwit, C., Levey, D.J. and Greenberg, C.H. (2004a) Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. *Oikos* 107, 303–308.
- Kwit, C., Levey, D.J., Greenberg, C.H., Pearson, S.F., McCarty, J.P., Sargent, S. and Mumme, R.L. (2004b) Fruit abundance and local distribution of wintering hermit thrushes (*Catharus guttatus*) and yellow-rumped warblers (*Dendroica coronata*) in South Carolina. *Auk* 121, 46–57.
- Larson, D.L. (1996) Seed dispersal by specialist versus generalist foragers: the plant's perspective. *Oikos* 76, 113–120.
- Lázaro, A., Mark, S. and Olesen, J.M. (2005) Bird-made fruit orchards in northern Europe: nestedness and network properties. *Oikos* 110, 321–329.

- Levey, D.J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58, 251–269
- Levey, D.J. and Benkman, C.W. (1999) Fruit–seed disperser interactions: timely insights from a long-term perspective. *Trends in Ecology and Evolution* 14, 41–42.
- Levey, D.J., Moermond, T.C. and Denslow, J.S. (1984) Fruit choice in neotropical birds: the effect of distance between fruits on choice patterns. *Ecology* 65, 844–850.
- Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. and Haddad, N.M. (2005) Effects of landscape corridors on seed dispersal by birds. *Science* 309, 146–148.
- Levin, D.A. and Kerster, H.W. (1975) The effect of gene dispersal on the dynamics and statics of gene substitution in plants. *Heredity* 35, 317–336.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15, 237–240.
- Lortie, C.J., Brooker, R.W., Choler, P., Michalet, R., Pugnaire, F.L. and Callaway, R. (2004) Rethinking plant community theory. *Oikos* 107, 433–438.
- Lugo, A.E. and Helmer, E.H. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management* 190, 145–161.
- Manasse, R.S. and Howe, H.F. (1983) Competition for dispersal agents among tropical trees: influences of neighbours. *Ecology* 59, 185–190.
- Márquez, A.L., Real, R. and Vargas, J.M. (2004) Dependence of broad-scale geographical variation in fleshy-fruited plant species richness on disperser bird species richness. *Global Ecology and Biogeography* 13, 295–304.
- McArthur, R.H. and Wilson, E.O. (1968) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA.
- McKey, D. (1975) The ecology of coevolved seed dispersal systems. In: Gilbert, L.E. and Raven, P.H. (eds) *Coevolution of Animals and Plants*. University of Texas Press, Austin, TX, USA, pp. 159–191.
- Moermond, T.C. and Denslow, J.S. (1985) Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs* 36, 865–897.
- Morales, J.M. and Carlo, T.A. (2006) The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* 86, 1489–1496.
- Morales, J.M. and Ellner, S.P. (2002) Scaling up movement in heterogeneous landscapes: the importance of behaviour. *Ecology* 83, 2240–2247.
- Morales, J.M., Haydon, D.T., Frair, J., Holsinger, K.E. and Fryxell, J.M. (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85, 2436–2445.
- Nathan, R. and Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15, 278–285.
- Pimm, S.L. and Lawton, J.H. (1978) On feeding on more than one trophic level. *Nature* 275, 542–544.
- Reid, N. (1991) Coevolution of mistletoes and frugivorous birds. *Australian Journal of Ecology* 16, 457–469.
- Rey, P. (1995) Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* 76, 1625–1635.
- Russo, S.E. and Augspurger, C.K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters* 7, 1058–1067.
- Sallabanks, R. (1993) Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74, 1326–1336.
- Saracco, J.F., Collazo, J.A. and Groom, M.J. (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139, 235–245.

- Saracco, J.F., Collazo, J.A., Groom, M. J. and Carlo, T.A. (2005) Crop size and fruit neighbourhood effects on visitation to fruiting trees. *Biotropica* 37, 80–86.
- Sargent, S. (1990) Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* 71, 1289–1298.
- Schupp, E.W. and Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *EcoScience* 2, 267–275.
- Schupp, E.W., Milleron, T. and Russo, S.E. (2002) Dissemination limitation and the origin of species-rich tropical forests. In: Levey D.J., Silva W.R. and Galetti M. (eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 19–43.
- Strogatz, S.H. (2001) Exploring complex networks. *Nature* 410, 268–276.
- Terborgh, J. (1986) Keystone plant resources in the tropical forest. In: Soulé, M.E. (ed.) *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, USA, pp. 33–44.
- Terborgh, J., Pitman, N., Silman, M.R., Schlichter, H. and Núñez V., P. (2002) Maintenance of tree diversity in tropical forests. In: Levey D.J., Silva W.R. and Galetti M. (eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK, pp. 1–18.
- Tewksbury, J.J. and Nabhan, G.P. (2001) Seed dispersal: directed deterrence by capsaicin in chillies. *Nature* 412, 403–404.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E. (2004) Extinction risk from climate change. *Nature* 427, 145–148.
- Thompson, J.N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago, IL, USA.
- Tilman, D. and Kareiva, P. (1997) *Spatial Ecology*. Princeton University Press, Princeton, NJ, USA.
- van der Pijl, L. (1972) *Principles of Dispersal in Higher Plants*. Springer, New York.
- van Ommeren, R.J. and Whitham, T.G. (2002) Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. *Oecologia* 130, 281–288.
- Vieira, I.G., Uhl, C. and Nepstad, D. (1994) The role of the shrub *Cordia multispicata* Cham. as a succession facilitator in an abandoned pasture in Paragominas, Amazonia. *Vegetatio* 115, 91–99.
- Wang, B.C. and Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17, 379–385.
- Webb, C.O. and Peart, D.R. (2001) High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecology Letters* 4, 491–499.
- Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3, 51–74.
- Westcott, D.A. and Graham, D.L. (2000) Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122, 249–257.
- Wheelwright, N.T. (1985) Competition for dispersers and the timing of flowering and fruiting in a guild of tropical trees. *Oikos* 44, 465–477.
- Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn, W.J. and Dilger, S. (1998) Are bird-consumed fruits complementary resources? *Oikos* 83, 195–205.
- Whitham, T.G., Young, W.P., Martinsen, G.D., Ghering, C.A., Schweitzer, J.A., Schuster, S.M., Wimp, G.M., Fischer, D.G., Bailey, J.K., Lindroth, R.L., Woolbright, S. and Kuske, C.R. (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84, 559–573.