



Review paper

Making dispersal syndromes and networks useful in tropical conservation and restoration



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ABSTRACT

Dispersal syndromes and networks must be used cautiously in conserving and restoring seed-dispersal processes. In many tropical forests most tree and shrub species require dispersal by animals for local persistence and for migration in response to environmental change. The most important errors to avoid in practical use of both dispersal syndromes (suites of fruit and seed characteristics that attract different dispersal agents) and network modules (groups of interacting dispersal agents and plants bearing fruits or seeds that they eat) are: (1) assuming that use of fruit resources by fruit-eating animals implies effective seed dispersal; (2) assuming that superficially similar fruits imply equally effective dispersal by similar animals, and (3) assuming that fruit resources at issue support animal populations. This essay explores strengths and weaknesses of uses of dispersal syndromes and disperser networks modules in conservation and restoration. Examples include some that are consistent with expectations from syndrome categorization and some that are not. An unappreciated weakness in using either dispersal syndromes or network modules is that contingent foraging by animals in highly disturbed habitats, now comprising 60%–70% of tropical land biomes, may not resemble foraging choices or consequences in protected closed forests, where most research on tropical seed dispersal is done. General prescriptions for the future include maintaining or creating habitat heterogeneity in largely deforested landscapes where remnant closed forests still exist, and active restoration in landscapes where little heterogeneity remains. In both cases, adaptations of multiple frame-work tree approaches have the best chance of preserving or enhancing populations of animal-dispersed trees and their seed vectors, and in opening migration paths in response to climate change.

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1. Introduction

Changes in land use and climate affect and will continue to affect interactions among species. The range of phenomena is potentially huge, including competition, predation, herbivory, pollination, and the balance of mutualistic and harmful microbes in soil, roots and above-ground tissues of plants (e.g. Blois et al., 2013; Brodie et al., 2014; Mangan et al., 2010; Valiente-Banuet et al., 2015). Alteration of any of these could be limiting for some plant and animal species, but the class of interactions most at risk that affects both plant persistence in place and migration in response to global change is seed dispersal (Corlett, 2009; Howe, 2014; Martínez-Garza and Howe, 2003; McConkey et al., 2012). Insufficient attention is given to tree persistence and migration in the 60%–70% of the area of tropical forest biomes that have been substantially altered by deforestation, habitat fragmentation, agriculture or bushmeat hunting within the last century (e.g. Effiom et al., 2013; McConkey and Drake, 2006; Moran et al., 2009). This is troubling because residual forests provide valuable functions that deserve attention (Turner and Corlett, 1996; Hernández-Ruedas et al., 2014). For instance, 50 km² of a 96% deforested Mexican landscape still hold more tree species than all of Europe (Arroyo-Rodríguez et al., 2009; Latham and Ricklefs, 1993). To preserve biodiversity in place and to facilitate tree migration, far more attention must be paid to conserving and restoring seed-dispersal processes in fragmented and otherwise disturbed landscapes than is now the rule.

A potential tool is to use fruit and seed characteristics to predict dispersal processes as tools for conservation and restoration of tropical biodiversity. Plants produce fruits and seeds that are clearly adapted by morphology and nutritional content for dispersal, and animals have morphological, physiological and behavioral adaptations for finding and eating fruits (Table 1). Van der Pijl (1982) documents broad suites of fruit or seed characters as “dispersal syndromes” reflecting agents most likely to disperse seeds. Potential relevance of dispersal syndromes is more important than ever with development of theory of mutualist networks (e.g. Bascompte and Jordano, 2014). Network frameworks promise to quantify interactions among mutualists within entire communities, both to understand the contemporary structure of interactions as indicated by which animals eat fruits and potentially disperse seeds, and by identifying “modules” of plant species served by predictable guilds of dispersal agents (Table 2). Understanding modular structure helps forecast changes in network structure from anthropogenic disturbances. Modules are not synonymous with dispersal syndromes, but both frameworks use suites of fruit and seed characteristics to predict use by different groups of animals. A difference is that dispersal syndromes are general properties thought to reflect evolutionary history, while modules are derived from empirical results that indicate that the indicated interactions exist somewhere some of the time. Legitimate questions are “How predictive are syndromes and networks in radically changing landscapes?” and “Are these networks of mutualists?”

Definitions offered here are simplified for discussion (Table 2). For instance, “narrow sense” effective dispersal is in principle possible to measure, but is not operational because it is not feasible to follow fates of thousands to millions of individual seeds from dispersal to reproduction for trees that require decades to mature (Schupp and Jordano, 2011). It is feasible to document rates of survival and mortality in demographic stages (seeds, seedlings, saplings, sub-adults, adults) for many plant species in different environments. Probabilities of survival vary with environment, but their estimation is possible, making the idea of effective dispersal instructive. In another example, actual definition of network modules employs an algorithm based on empirical determination of links (interactions) between fruit- or seed-eating animals and plants that they disperse (Bascompte and Jordano, 2014, pp. 151–152). This means that a prospective dispersal syndrome that predicts interactions is retrospectively reflected by empirical determination of network modules at a given time

Table 1

Non-exclusive list of animal, plant and external characteristics of factors that affect interactions among fruit- or seed-eating animals and plants.

Animal	Plant
Morphology	
Body size	Fruit size, structure and display
Gape	Seed size and number per fruit
Strong gizzard or crushing bill or teeth	Seed-coat hardness
Digestive track attributes	Fruit-crop size
Physiology	
Ability to digest pulp contents	Amount and type of pulp reward
Sensory capabilities	Color and scent lures
“Behavior”	
Foraging tactics	Fruiting phenology
Behavior after ingesting or carrying fruit	Ripening and dehiscence details
External	
Competing conspecifics	Competing conspecifics
Competing heterospecifics	Competing heterospecifics
Risk of predation on foragers	Risk of flower and seed predations
Weather	Weather

Table 2

Glossary of terms.

Connector species: Fruit- or seed-eating animals that occasionally disperse seeds of plant species in other than their cluster of plant species.

Dispersal syndrome: A suite of fruit or seed characteristics associated with a category of dispersal agent (e.g. floating for water, winged for wind, fleshy for bird or mammal).

Dispersal system: A plant species and the animals that more or less effectively disperse its seeds in a given environment at a given time.

Disperser redundancy: More than one dispersal agent effectively disperses a plant species.

Effective dispersal: (1) Narrow sense: Removal of a seed from a parent plant and deposition in a site where the seedling grows to maturity. (2) Operational sense: Removal of a seed from a parent plant and deposition where seedling establishment and survival are likely.

Interaction network: Links indicating direct positive or negative interactions among species, higher taxa, or other entities.

Mutualist network: An interaction network of species or higher taxa that benefit each other (e.g. at the individual level, consistently increase each other's fitnesses).

Network module: Heuristically, non-random clusters of links in animal and plant networks.

Modules of seed-dispersal networks include subsets of animal communities that consistently interact with each other more than with other such clusters. Modules usually reflect morphological and behavioral attributes of dispersal agents and seeds or fruits.

Seed dispersal: Horizontal movement of seeds away from parent plants.

Seed predation: Consumption that kills a seed.

and place, but not at another time and place. For instance, a large-bodied toucan may feed on large arillate fruits in one environment, consistent with a toucan syndrome or module (Donatti et al., 2011), but not in another where favored foods are absent (Section 6.1). In networks with few (<50) interacting species, network modularity may be more heuristic than reliable (below and Olesen et al., 2007). A simplistic representation of modularity used here emphasizes that predictions of fruit use by either dispersal syndromes or mutualist networks in conservation and restoration should employ reasonable expectations of *effective dispersal*. Many vertebrates that eat fruits or seeds do not disperse them to sites where seedling establishment and maturation are likely.

Reliability of the mutualistic nature of disperser syndromes or networks is important for conservation and restoration of dispersal processes in tropical landscapes. In many regions of the wet tropics, most to almost all species of woody plants require seed dispersal by animals to mediate both local persistence and long-distance migration in response to changes in climate and land use (Howe and Smallwood, 1982; Jordano, 1995). Distinguishing agents of “effective seed dispersal” from those that simply eat fruits or seeds requires determining which animals deliver seeds to sites suitable for seed germination, seedling establishment, and ultimately recruitment to reproductive status (Schupp, 1993; Schupp et al., 2010). Describing mutualistic networks is usually restricted in protected remnants.

A largely unexplored but critical question is whether effective dispersal processes documented in protected forests exist for tree species in millions of hectares of fragmented or otherwise highly disturbed tropical landscapes. If the answer is affirmative, then current disproportionate research focus on protected areas is justified (e.g. Martin et al., 2012). Lessons from protected forests can be applied directly to highly disturbed landscapes. If the answer is “no” or a qualified “yes” and “no”, it is imperative to discover how local persistence and species movement can be maintained or re-established in and across inhospitable agrarian landscapes using management of fruit resources and fruit-eating animals.

The purpose of this essay is to explore implications for conservation or restoration of seed dispersal processes in diverse, tropical, disturbed ecosystems. A challenge for conservation and restoration is to know whether solutions that facilitate seed dispersal are “one-off” examples with no general application, or whether generalizations apply across communities, ecosystems and even continents (Caughley, 1994). Ultimate goals should be to understand: (1) How predictive of effective dispersal are dispersal syndromes and seed-dispersal networks? (2) What fruit and seed characteristics of species

are most important for conservation and restoration in disturbed habitats? (3) How does a manager choose species to protect or establish that best maintains diversity or accelerates assisted succession (restoration)? Answering these requires understanding of the predictive quality of fruit characteristics of trees that are likely to attract particular or a wide array of dispersal agents, and the fates of seeds that they carry and distribute. A challenge is to understand where dispersal syndromes or dispersal modules do not work in highly disturbed landscapes as compared with historically “natural” landscapes.

A comprehensive review of dispersal phenomena is beyond the scope of this essay. Earlier reviews and anthologies offer historical context, much of which remains applicable (e.g. Estrada and Fleming, 1986; Fleming and Estrada, 1993; Howe and Smallwood, 1982; McKey, 1975; Murray, 1986). More recent anthologies, monographs and reviews develop a wide array of viewpoints reflecting a rapidly-expanding field (e.g. Côrtes and Uriarte, 2013; Dennis et al., 2007; Dew and Boubli, 2005; section introduced by Forget et al., 2011; Levey et al., 2002; Wang and Smith, 2002). Overviews reflecting this huge literature and decades of experience are offered by Herrera (2002), Schupp and colleagues (2010) and Fleming and Kress (2013). The study of seed dispersal by animals is now a large and growing sub-discipline within ecology reflected by several hundred publications annually. This essay will draw on experience and a more limited literature relevant to the implications of predictability in animal use of seeds and fruits for biodiversity conservation and restoration in disturbed tropical landscapes.

2. Effective seed dispersal

2.1. Dispersal and local persistence

The idea of effective seed dispersal has had a long history. Janzen (1970) and Connell (1971) hypothesize that disproportionate density- or proximity-related mortality of seeds and seedlings near parent trees both give an advantage to dispersed offspring and open space for seedlings of other species that arrive in much lower densities. Beyond the advantage of an “escape effect” of avoiding shared enemies among conspecifics, effective dispersal might involve colonization of open habitats not occupied by the species or special edaphic conditions that favor a particular species (Howe and Smallwood, 1982). Natural history sometimes allows these to be distinguished easily (e.g. Wenny and Levey, 1998), while in other cases the challenge of distinguishing these hypotheses is not trivial (Schupp et al., 2010). The point remains that effective dispersal reflects transitions to plant recruitment, not just animal foraging.

Advantages to local dispersal are evident in a variety of tropical and temperate tree species. In a broad study, degrees of density-dependent mortality among seeds captured in seed traps occur in all 53 tree species tested on Barro Colorado Island; adjacent seedling communities are more diverse than seed rain into traps (Harms et al., 2000). Quantitative studies of seedling mortality further demonstrate that conspecific neighbors have a much greater negative effect on seedlings and saplings than on heterospecifics for most of 180 tree species tested (Comita et al., 2010), a generalization likely applicable to poles and adult trees of many species in tropical and temperate latitudes (Johnson et al., 2014; Peters, 2003). Microsatellite markers in Central America even demonstrate disproportionately high mortality of seedlings near their parents, as compared to nearby less-related members of the same species in the mid-story tree *Simarouba amara* (Simaroubaceae) and the canopy palm *Iriartea deltoidea* (Hardesty et al., 2006; Sezen et al., 2009). Agents that cause density-dependent mortality may differ within and between life stages, years, weather conditions, and habitats (Fricke et al., 2014; Gilbert et al., 2001). A key point, refined by Schupp and colleagues (2010), is that effective dispersal involves requires both seed removal from the tree and delivery to an environment where germination, seedling establishment, and survival are likely to produce reproductive adults.

Janzen–Connell effects may or may not be general among related individuals. It now appears likely that negative effects of conspecific proximity occur in many or most tree species in some or even all demographic stages (Caughlin et al., 2015; Terborgh, 2013). Whether in plantings, habitat fragments or extensive forests, local dispersal is necessary for local persistence of most tree species. Migration requires it.

2.2. Dispersal as migration

A second issue insufficiently appreciated is that to insure preservation of much of tropical biodiversity, seed dispersal is required for plant migration across inhospitable landscapes as land-uses and climates change (Corlett, 2009, 2011a; Howe, 2014; McConkey et al., 2012). Many tree species maintain genetic diversity through long-distance pollination when pollinators cross agricultural landscapes to forage in flowering trees (e.g. Kramer et al., 2008). Seed dispersal across inhospitable landscapes also mediates gene flow, but more importantly moves plant populations. Without costly and often economically infeasible assistance from humans (Minteer and Collins, 2010), seed dispersal is the only way for plant species to move in response to environmental change. Because movements of dispersal agents and seeds reflect changes in vegetation during succession or restoration (e.g. Corlett, 2011b; de la Peña-Domene et al., 2014; Reid et al., 2014), a major component of conservation and restoration of tropical biodiversity requires using vegetation to harness movements of dispersal agents.

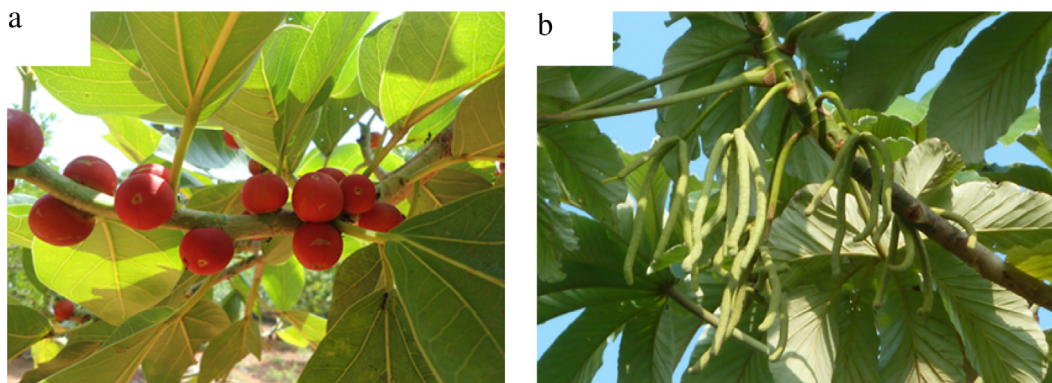


Fig. 1. Compound fruits with many small seeds sought by a wide variety of fruit-eating animals. (a) *Ficus benghalensis* (Moraceae) from Asia. Largely bird-dispersed, each fig contains > 100 seeds. (b) *Cecropia obtusifolia* (Cecropiaceae) from Mesoamerica. Dispersed by many birds and mammals, each spadix (finger-like projection) contains 2000–4500 seeds. Photo credits: (a) N. Adityamadhav; (b) H.F. Howe. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Syndromes and modules

3.1. Syndromes

Dispersal syndromes are uncontroversial at some levels and controversial at others. The distinction between biotically- and abiotically-dispersed fruits or seeds is uncontroversial. Wind-dispersed fruits or seeds are minute (e.g. orchids) or have morphological modifications that expand surface to mass ratios (e.g. Burrows, 1986; Augspurger, 1988). Dispersal distances and patterns are determined by seed weight, wing loading, wind speed, height from which seeds are released, and the likelihood of colliding with obstacles during descent. Other abiotic agents include flotation in water and gravity if seeds bounce or roll after dropping from a parent tree. Wind-dispersed seeds easily colonize disturbed habitats if they are small enough to be carried hundreds or even thousands of meters from source trees (e.g. Bacles et al., 2006). Seeds larger than a few milligrams with low wing loading are unlikely to colonize distant habitat patches if wind is the only possible vector (Corlett, 2009). Ballistic dispersal occurs in some taxa, but seeds normally fall in the immediate neighborhood of fruiting trees (Slocum, 2001). Abiotically-dispersed seeds may enter into interaction networks if animals eat and kill seeds without dispersing them. These are not mutualistic networks.

Fruits adapted for animal consumption usually produce fleshy edible rewards from maternal tissues around the seed(s) (Table 1; Figs. 1 and 2). Often the dispersal syndrome or empirically determined network module of vertebrate dispersers reflects fruit size, seed size, constituents of the reward, scent and color of the ripe fruit (Howe and Smallwood, 1982; Janson, 1983; Jordano, 1995; Wheelwright and Janson, 1985). Plants dispersed by fruit-eating birds are usually succulent and scentless, if dehiscent they often open during the day, and are often black, red, white, blue, or in mixed contrasting displays when ripe (Figs. 1(a), 2). Those dispersed by flying or arboreal mammals are often succulent, scented and dull in color. If dehiscent, many open at night. In Neotropical landscapes *Cecropia* (Cecropiaceae), figs and relatives, and several genera in the Lauraceae are nondescript and dispersed by both birds and mammals (Fig. 1(b); Wheelwright et al., 1984). Plants dispersed by adhesion to fur or feathers have hooks or barbs (burrs) derived from maternal tissues (Sorensen, 1986). Basic distinctions between biotically and abiotically dispersed seeds are uncontroversial; distinctions between bird- and mammal-dispersed fruits are often, but not always, possible from size, morphology, color and scent.

Ambiguity arises for hard nuts, and for large seeds encased within a fleshy or fibrous pulp for which there appear to be no contemporary dispersal agents. For instance, acorns produced fall under parent oaks, but pay a tax in seeds when dispersed a few meters by squirrels or hundreds to thousands of meters by jays or relatives (Pesendorfer et al., 2016; Vander Wall, 2010). Lost or forgotten seeds may germinate and result in seedling recruitment; biotic dispersal delineates a hoarding syndrome or network module (Section 6). Scatter-hoarding by rodents is common in the lowland tropics; re-caching incrementally moves seeds away from parents (e.g. Jansen et al., 2012; Klinger and Rejmánek, 2010). Long-distance scatter-hoarding by birds is probably common in mesic and dry tropical habitats (e.g. Cullieney et al., 2012), but is not as well-documented at low latitudes.

A caveat in application of syndromes and modules is that more than one dispersal process can operate simultaneously or sequentially for a given plant species. Trees dispersed by large herbivores (>40 kg) in Africa and Asia produce fruits that are large, dull, fibrous, and often indehiscent (Gautier-Hion et al., 1985). Still others, similar in structure and appearance to “megafaunal” fruits of the Paleotropics, occur in the Neotropics (Janzen and Martin, 1982). For instance, some Neotropical palms (e.g. *Attalea*) bear fruits with nuts encased in fibrous pulp. Many such fruits are likely botanical anachronisms left over from extinction of large mammalian dispersal agents that were abundant and diverse from the Miocene into the Pleistocene, but that disappeared during the Pleistocene and early Holocene (Guimarães et al., 2008). Now seeds of megafaunal fruits are often dispersed by rodents, livestock or humans. Over time, secondary dispersal agents became primary dispersal agents.

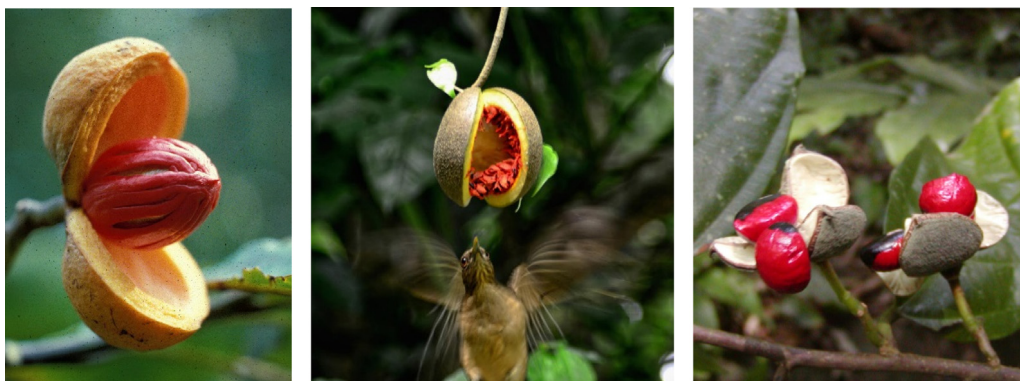


Fig. 2. Three bird-dispersed fruits. (a) *Virola surinamensis* (Myristicaceae) in Panama. Golf ball-sized capsules open in early morning; in most years open fruits are depleted or knocked down by toucans, guans, smaller birds or monkeys by mid-morning. (b) Partially depleted *Stemmadenia donnell-smithii* (Apocynaceae) fruit in Mexico. A variety of large and small birds eat the pulp and >100 small seeds embedded in it. Shown is a clay-colored robin (*Turdus grayi*) snatching pulp. Most seeds are taken in a day. (c) *Leptonychia usambarensis* (Malvaceae) in the Eastern Arc Mountains of Tanzania. Fruits of this mid-story endemic open upwards, as shown. Arillate seeds look appealing, but even in extensive forests, few birds visit each a tree in a day; uneaten seeds fall off the open capsule. Photo credits: (a) H.F. Howe, (b) J. Arnow, (c) N.J. Cordeiro. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Finally, dispersal syndromes may include more than fruit characteristics. Life history and plant-defense traits offer clues to historical adaptations of former ecological conditions, and perhaps insights into novel non-analog communities of the future (e.g. Williams and Jackson, 2007). For instance, the indehiscent pod of a temperate legume, *Gymnocladus dioicus*, resembles those eaten by African and Asian elephants, but has a pulp toxic to contemporary livestock (Zaya and Howe, 2009). *Gymnocladus* appears in Miocene deposits during rapid radiation of the American megafauna, but is now rare except in association with former Native American settlements or as a contemporary ornamental tree. African forests heavily damaged by elephants offer a clue (Owen-Smith, 1987). Dioecy, vigorous cloning, and shade intolerance of seedlings are inconsistent with a “naturally rare” species now growing in dense forests. *Gymnocladus* fruits probably are megafaunal relicts for which primary dispersal agents are long gone. The species probably also lacks a habitat where effective dispersal is likely. The latter was probably a megafaunal disclimax reduced to early and middle stages of perpetual succession by destruction from mammals much larger than contemporary cattle or horses.

In short, syndromes are heuristic guides to likely interactions of the past among plants and animals. An analogy in medicine would be “best available practices” for which the empirical justification ranges from anecdotal lore to quantitative validation, but still are useful most of the time. For instance, 50 years ago *Leptonychia usambarensis* in the Eastern Arc Mountains of Tanzania could easily be identified from fruit morphology and color as a bird-dispersed tree (Fig. 2(c)). Quantitative confirmation came much later from the Usambaras Mountains of the Eastern Arcs (Cordeiro et al., 2009). Dispersal syndromes implicitly assume that seed and fruit characteristics identifying the syndrome have evolved from differential selection by animals. Syndromes do not predict which fruit-eating animals eat a particular fruit and effectively disperse its seeds at different times and places.

3.2. Modules

Network modules also match characteristics of fruits and the animals that eat them, but differ in being empirically based, and embedded in interaction networks representing a community, a landscape or a region. For a given time and place, network modules are defined by observations of which animals eat which fruits of common trees and shrubs. Theoretically, they assume that interactions are mutualistic, although evidence indicating the degree of dependence of animals on plants and plants on effectively dispersal by animals is rarely offered.

As an example, Donatti and colleagues (2011) use a variety of methods to determine which fruits animals eat and disperse in the Pantanal of southern Brazil. An average of ~60 h of observation at each of 14 plant species records birds swallowing or carrying away fruits, 14,800 h of camera-trap records under fruiting individuals of 27 tree species document fruit use by ground-feeding vertebrates, counts of intact seeds from dissection of >700 vertebrate scats indicate potentially effective dispersal by mammals and reptiles, and gut contents of 80 individual frugivorous fish show which seeds are consumed and remain viable the digestive tract. Observations are from two sites totaling 18,500 ha. This seems a small sample of plants from a complex of habitats covering 100,000 km², but that is less concerning if, as is the case, a very small proportion of tree species cover most forested areas (Damasceno-Junior et al., 2005; Prance and Schaller, 1982; ter Steege et al., 2013). Broad outlines of the interaction network are probably correct; variations from place to place and time to time undoubtedly occur.

The more important concern is that a regional study over a vast area can only record part of the first component of effective dispersal (Schupp et al., 2010): use of a fruit species by animals identified within modules. The issue is that fruit consumption and seed arrival are usually poor predictors of seedling survival (Harms et al., 2000; Howe et al., 2010; Reid

and Holl, 2013; Rother et al., 2015; Schupp et al., 1989). Donatti and colleagues distinguish animals that carry seeds away from those that do not, but do not quantify the “quality component”, indicating where seeds germinate, seedlings survive, and recruitment occurs.

More detail is possible with more intensive observations of fewer tree species. In a study of use patterns of fruits of three tree species in the Atlantic Rainforest of Brazil, Rother and colleagues (2013, 2016) distinguish variance in seed removal attributable to number of visits per bird species from number of fruits manipulated by bird species for a palm and two trees (*Euterpe edulis*, *Sloanea guianensis*, *Virola bicuhyba*). This is an informative contribution to the quantitative and qualitative components of effective dispersal because it estimates relative contribution of bird species to seed removal. Removal studies are integrated with a demographic study of each species. Quantitative records for a palm (*Euterpe edulis*) recruitment in bamboo and non-bamboo habitats (Fig. 1 of Rother et al., 2013) allow a ranking of species as contributors to dispersal as compared with contribution to eventual recruitment to the seedling stage (Figs. 1 and 2 of Rother et al., 2016). All three plant species experienced heavy post-dispersal mortality, but enough data exists for *E. edulis* to conclude: (1) rank of bird species in seed removal imperfectly reflects rank of contribution to seedling survival (e.g. the toucanet *Selenidera maculirostris* contributes less to seedling recruitment than visits suggest), and (2) species dispersing seeds of this palm may perform complementary roles in recruitment, rather than represent redundant dispersal agents. That conclusion may be prescient.

3.3. Seed fate

Immediate fates of seeds consumed by animals are largely determined by treatment in the gut and behavior of the agent itself (Table 1; Côrtes and Uriarte, 2013; Traveset, 1998; Traveset et al., 2007). As for wind-dispersed seeds, size is important for animal-dispersed seeds. Large fruit-eating animals eat and disperse small as well as large seeds, while smaller animals are restricted to small-seeded species (Chen and Moles, 2015; Jordano, 1995; Martin, 1985; Wheelwright, 1985). Exceptions exist, but basic distinctions usually apply.

More controversial are conservation or restoration schemes that use dispersal syndromes or network modules to predict consequences of seed dispersal in altered landscapes. Accelerating changes in land use and climate require that conservation and restoration of ecological processes address the importance of, and where possible make use of, interactions among plants and animals in regions where a large proportion of tree and shrub flora require dispersal by animals (e.g. Corlett and Hau, 2000; de la Peña-Domene et al., 2014; Elliott et al., 2013; Foster, 2007; Martínez-Garza and Howe, 2003; McConkey et al., 2012; Wunderle, 1997). Ecological disruption brought about by environmental change now plays out against a backdrop of poorly understood or undocumented contingent interactions among species (Driscoll et al., 2014; Lawton, 1999). Moreover, interactions premised on understanding garnered in undisturbed forests may be inapplicable in regions increasingly altered by people.

Contingencies in space and time result in differences in strength and even sign of interactions in natural communities (Maron et al., 2014; Theimer, 2005). Interactions discussed by Maron and colleagues concern pollination and herbivory, but interactions between dispersal agents and fruiting plants are also conditional. For instance, in seed removal experiments, agoutis (*Dasyprocta leporina*) neither scatter-hoard nor eat a large proportion of palm (*Astrocaryum aculeatum*) seeds in continuous forests in the Brazilian Amazon (Jorge and Howe, 2009). They scatter-hoard the nuts in small forest fragments when alternative foods are available, but eat and kill the nuts in fragments when other foods are scarce.

Interaction differences lead to variability in plant species composition and animal ecosystem services in communities undergoing succession, particularly in species-rich communities (Mesquita et al., 2001; Norden et al., 2015). Variability does not mean that interactions are random; it does increase the likelihood that consequences of many interactions are indistinguishable from random (Howe, 2014). Dispersal syndromes that reflect shared evolutionary histories of plants with birds, bats, or larger mammals often predict common interactions in mature forests free of human disturbance. Less predictable interactions might occur in disturbed environments. Absence of knowledge has implications for determining how to conserve and restore species where dispersal syndromes are least likely to predict which animals effectively disperse what.

4. Fruit choice and external factors

Foraging is a contingent process. Experienced foragers choose a fruit or seed based on apparent nutritional value, accessibility, digestibility, what else is known to be available, and the risk of foraging in one place rather than another (e.g. Schoener, 1971). The challenge is that abstract value cannot be predicted in lieu of experience, which is incomplete. Such factors are at play in foraging behavior of wild animals in nature, including animals that eat fruit and disperse seeds; foragers alter food choices in a given place and time as experience is acquired (Table 1; Côrtes and Uriarte, 2013). Vertebrate morphologies and physiologies are less labile at the individual level than behaviors involving fruit choice and movements after eating fruits. From the plant perspective, digestive physiology may kill, impair or enhance seed survival, while recruitment of surviving seeds to seedlings and later stages depends on where and how viable seeds are deposited. The range of factors affecting fruit choice deserves attention if syndromes and network modules are to be used as conservation or restoration tools.

An inescapable reality is that foraging decisions in the field are often made on the basis of incomplete information. Relative influences of value and risk on fruit or seed choice for foraging animals are easily documented when food is of

exceptionally high quality to a forager (e.g. millet for small rodents). In such cases, the amount and accessibility of the highly preferred food can be manipulated at the same time as, for instance, exposure to different levels of risk (e.g. [Abu Baker and Brown, 2010](#); [Brown and Kotler, 2004](#)). In vivarium experiments where hunger levels of both gerbils (*Gerbillus andersoni*) and owl predators (*Tyto alba*) are controlled and millet is offered, the influences of risk to foraging rodents on seed consumption can be predicted with nearly axiomatic precision ([Berger-Tal et al., 2010](#)). Experimental studies of this genre are much less clear with seeds that have greater mechanical or chemical defenses, and therefore represent ambiguous or even interchangeable qualities from a forager's perspective. Experimental studies of this genre also rarely address how perceived risk influences seed dispersal, local plant recruitment or plant movement across landscapes. However, they do bring effects of fear on foraging into bold relief.

Risk aversion by birds and bats foraging for fruit in exposed tree crowns is an obvious contingency, but is difficult to demonstrate ([Howe, 1979](#); “external factors” in [Table 1](#)). For instance, extended observations of fruiting *Casearia coymbosa* H.B.K. (Flacourtiaceae) trees in Costa Rican rainforest indicate that small (<100 g) birds foraging for the fruits frequently dive *en masse* into the understory when a bird gives an alarm call, but much larger toucans (*Ramphastos sulfuratus* and *R. swainsonii*) do not, and sometimes tolerate a raptor of similar size in the same tree at the same time ([Howe, 1977](#)). Predation attempts by hawks of small birds occur, and partially eaten remains of small fruit-eating species under *C. corymbosa* indicate that feeding trees for frugivores are also feeding trees for predators. At an early successional ecotype of this tree in dry forest, nervous behavior of small foragers and predation attempts by resident forest falcons (*Micrastur* spp.) and migrant kestrels (*Falco sparverius*) of the predominate frugivore at the time, a migrant vireo (*Vireo flavoviridis*), also indicate foraging risk ([Howe and Vande Kerckhove, 1979](#)). Peripatetic foraging as a consequence of risk aversion is unlikely to result in long-distance seed dispersal, but it probably does result in effective local dispersal near (5–20 m) fruiting trees. If alternative fruits of comparable value and accessibility exist in less risky situations, frugivores will favor those over trees exposed to predators. These are among the external factors that alter foraging contingencies ([Table 1](#)), potentially obscuring relationships between fruit attributes and the quantity or quality of dispersal. Experimental evaluation of the consequences of ecology of fear by avian dispersal agents for tropical plant recruitment appears not have received much attention.

In a world of imperfect information, foraging choices are less predictable than in experimental designs because amount, reward, access, digestibility, distribution, competition and risk associated with different fruits are uncertain for foragers, fruit-bearing plants, and ecologists modeling behavior. While mutualist networks rely on direct observation and animal and plant characteristics, on first principles of foraging theory contingent fruit choices are likely to result in different effective dispersal agents of the same tree species in time and space. Beyond animals killing seeds, foraging choices may mediate or stymie plant recruitment. Information is least complete in disturbed tropical habitats, where choices are least likely to match expectations derived from results from habitats with intact floras and faunas.

5. Morphology and physiology of syndromes

5.1. Case studies consistent with dispersal syndromes

Unlike animals as foods, fruits are low in protein and vary widely in usable lipids, carbohydrates, and realized energy value. Variation in reward, presentation and “external factors” make predictions of animal use possible in some cases and not in others ([Table 1](#)). [McKey \(1975\)](#) first posited a continuum of reward and dispersal strategy, here termed the Resource-Fecundity-Dispersal Hypothesis. The hypothesis holds that small, abundant and individually inexpensive seeds match energetically inexpensive rewards of sugars and starches in fruit pulp. Such fruits draw a wide variety of opportunistic animals that eat the fruits and disperse the seeds ([Fig. 1](#)). This contrasts with protein- or lipid-rich fruits that appeal to a small core assemblage of specialists that seek them, and deplete fruits before less effective opportunists have a chance ([Fig. 2\(a\)](#)). The strong point of the hypothesis is that it emphasizes the potential for plants to manipulate allocation of resources to seeds and the rewards that mediate dispersal. A weak point is that it, like explicit foraging theory, assumes that easily-accessed energy is the appropriate currency for animal choices. Reward currencies may not be as straightforward.

Re-appraisal of familiar examples puts choices in fruit selection in context. For instance, percentage dry weight of protein in pulp of the monkey-dispersed tree *Tetragastris panamensis* (Burseraceae) in Panama is negligible (1%), with the reward comprised of sugars (94%) and lipids (4%) ([Howe, 1980](#)). Individual trees bear large fruit crops every few years, with numbers of fruits per tree ranging from <200 to nearly 100,000 (mean $\sim 23,000$) in years with large crops, with an average of 4 seeds per fruit. At least 26 birds and diurnal and nocturnal mammals forage for *T. panamensis* fruits. In Panama most seeds of this tree are dispersed by primates, especially howler monkeys (*Alouatta palliata*) that favor trees with large crops. It is plausible to assume that foragers at *T. panamensis* secure protein and other limiting nutrients elsewhere, making these fruits strictly complementary resources ([Whelan et al., 1998](#)). Two-hundred hours of observation, 1596 diurnal tree checks, and 300 nocturnal tree checks show that the number of species of fruit-eating animals at *T. panamensis* trees increases linearly with crop size. This is expected if the return to fruit-eating animals is easily accessed energy (18 kJ g^{-1}), with a pool of potential dispersal agents defined by the richness of the total assemblage of fruit-eating animals available. On Barro Colorado Island *T. panamensis* seed removal is far from complete (<30%). No visits to fruiting trees occur during some 10-hour watches. The tree is not fecund on the scale of pioneer *Cecropia obtusifolia* with potential seed production $> 10^6$ per year ([Alvarez-Buylla and Martinez-Ramos, 1992](#)), but *T. panamensis* is more fecund than many late-successional, animal-dispersed trees.

Other trees present quite different resources to animals. On Barro Colorado Island, arils of mostly bird-dispersed *Virola* (Myristicaceae) trees are individually much richer in protein and lipid, and are usually depleted within 2–4 h of first light. *Virola sebifera* is a mid-story tree with an annual crop size of 19 to ~3500 single-seeded fruits (mean ~ 1000), with a 0.7 g seed and small (0.23 g) but rich aril (Howe, 1981). Digestible parts of the aril by dry weight average 7% protein, 54% lipid, and 8% carbohydrate (29 kJ g⁻¹). The disperser assemblage is small despite a seed size easily consumed by birds of small (32 g; *Catharus ustulatus*) to moderate sizes (84–185 g; *Baryphthengus martii*, *Tityra semifasciata*, *Trogon massena*). Larger birds (230–640 g) remove most (66%) of the seeds that are taken, with one toucan (*Ramphastos swainsonii*) removing substantially more than a smaller congener (*R. sulfuratus*) or aracari (*Pteroglossus torquatus*). One hundred and fifty hours of observation show that the number of disperser species visiting trees increases with crop size, but plateaus at five, the maximum seen at any given tree.

The canopy congener *Virola surinamensis* had larger crops, ranging from 214–31,006 seeds per tree, with median crop sizes of 17–25 trees from 2082 in one year to 8579 in another (Fig. 2(a); see Howe, 1993). The 3.0 g seed and 1.7 g aril limited *T. semifasciata*, which picked at arils but could not swallow or carry seeds as it did from *V. sebifera*. By dry weight, digestible portions of the aril were ~3% protein, 63% lipid, and 9% usable carbohydrate (28 kJ g⁻¹), along with 2.4% tannins. Observations over 320 h showed that the larger tree also had a small dispersal assemblage dominated by the same toucan species as above, which removed 44% of the seeds that were taken by animals. The same trogon and motmot as above removed 24% of the seeds, but dropped most under or near fruiting trees where seed and seedling mortality were high. Infrequent visitors included larger guans (*Penelope purpurascens*; 2 kg) and spider monkeys (*Ateles geoffroyi*; 6–9 kg), which removed 9% and 3%, respectively. Preliminary estimates of dispersal effectiveness put toucan value to the tree at about 30× the value of smaller trogons and motmots (Howe and Miriti, 2004). Wider dispersal of seeds estimated with telemetry likely reflected greater toucan value to *V. surinamensis* (Kays et al., 2011). Species richness of dispersal agents did not increase with crop size of individual trees. Arils with >2% tannin content may have limited palatability to some fruit-eaters (e.g. howler monkeys and the author), and clusters of trees experienced depressed dispersal at peak season, suggesting disperser shortages (Manasse and Howe, 1983). *Virola sebifera* and *V. surinamensis* were preferred food resources for a small assemblage of fruit-eating animals. High preference was clear when toucans regularly arrived in crowns of fruiting trees just before dawn, and aggressively displaced other arriving foragers while they searched for and depleted open fruits.

5.2. Anomalies inconsistent with aspects of dispersal syndromes

Other examples fit the Resource-Fecundity-Dispersal Hypothesis less well. Some fruits offer rich arils for small seeds that are dispersed by many dispersal agents. *Stemmadenia donnell-smithii* (Apocynaceae) is a small pasture and forest tree in Mesoamerica (Coates-Estrada et al., 1993; McDiarmid et al., 1977). Bright orange-red arils accurately signal a bird-dispersed species (Fig. 2(b)). In western Costa Rica, compound fruits hold an average of ~130 seeds, each <0.1 g, embedded in a pulp that is 11% protein, 64% lipid and 17% usable carbohydrate (30 kJ g⁻¹). There and elsewhere the species has an extended fruiting season of at least 7–9 months that broadly overlaps with flower production on the same individual trees. Zero to 10 or more fruits open per day, and open capsules are quickly emptied by birds. McDiarmid and colleagues (1977) record 21 species of birds ranging in size from small warblers to large woodpeckers and jays eating the fruits. At Los Tuxtlas in southern Mexico, Coates-Estrada and colleagues (1993) report several more small to medium-sized resident and migrant birds eating pulp and removing seeds in dense forest; more casual observations by the author add more forest and edge species, including large oropendolas (*Psarocolius montezuma*; ~350 g) and toucans (*R. sulfuratus*; ~350 g). This is a generalist tree with high-value fruits.

Also at Los Tuxtlas, Coates-Estrada and Estrada (1988) show that the mid-story rainforest tree *Cymbopetalum baillionii* (Annonaceae) produces a rich aril exploited by many fruit-eating birds (also see Foster, 2007). Like *S. donnell-smithii*, *C. baillionii*, produces small crops of 44–173 (mean 101) fruits per tree per year, representing 792–3114 (mean 1966) seeds per year. Arils attached to <0.5 g seeds are 7% protein, 61% lipid and 24% usable carbohydrate (28 kJ g⁻¹) by dry weight. The authors report 24 species of fruit-eating birds feeding on arils, with larger jays and toucans responsible for most dispersal >30 m.

Stemmadenia and *Cymbopetalum* fit a bird-dispersed syndrome with bright red or orange displays and dehiscence during the day. Energetically expensive investment in pulp and protective husks for trees that produce few fruits and many small seeds is a stretch for the Resource-Fecundity-Dispersal Hypothesis as originally conceived, but is plausible for tree species colonizing or occupying edges, gaps or deforested areas where an unpredictable variety of dispersal agents forage.

Other bird-dispersed fruits are clear anomalies to the Resource-Fecundity-Dispersal Hypothesis. *Guarea glabra* (Meliaceae) produces substantial seeds (0.6–0.8 g) enveloped in very thin arils (0.3–0.5 mm thick) that are unlikely to be major sources of energy for many resident and migrant bird species that eat the ariloids and regurgitate or defecate the seeds intact (Howe and De Steven, 1979; Wenny, 1999). *Guarea glabra* rewards are even less obvious for spider monkeys (*Ateles geoffroyi*, 6–9 kg) that eat large quantities of fruits of this species in some Mexican forests (Chaves et al., 2012). The reward could be protein, as Prado (2013) suggests for a congener in Peru, or even trace nutrients unlikely to be found in fruits of other species.

Guarea fruits improbably attract much attention from frugivores, while others attract improbably little. In the Eastern Arc Mountains of Tanzania, the endemic midstory *Leptonychia usambarensis* (Sterculiaceae) is a low-fecundity tree with a seed >1 cm long partially covered with a red aril (Fig. 2(c)). Capsules open during daylight hours, but seeds may not be taken for

1–4 days, or at all (Cordeiro and Howe, 2003; Cordeiro et al., 2009). Five-hundred seventy-six hours of observation show that several birds eat the arilloids, but only two small bulbuls (*Andropadus milanjensis*, *A. masukuensis*) and a thrush (*Turdus roehli*) remove a substantial proportion of seeds, collectively taking a median of 10 seeds per 12-hour day per tree in continuous forest, and half that in forest fragments. Even in extensive rainforest, many seeds drop under fruiting trees and are eaten and killed by rodents and pigeons. The three primary dispersal agents are scarce or absent in forest fragments. In this instance, the tree produces a low-preference fruit taken by a small number of frugivores, slowly. *Leptonychia usambarensis* looks like the bird fruit it is, but it is anomalous for the Resource-Fecundity–Dispersal Hypothesis with a brilliant display, low fecundity, and very slow and apparently inefficient seed dispersal.

On a per-fruit basis, dispersal syndromes more or less fit, with need to tinker with definitions. The syndrome to which a fruit belongs refers to a guild of dispersal agents, sometimes matching related plant genera with related disperser genera, as happens with mistletoes and silky flycatchers in montane Colombia in comparison with montane Costa Rica (Restrepo et al., 2002). A widespread plant species often is dispersed by different taxa in different geographical locations. The brilliant red arils of *C. corymbosa* (Flacourtiaceae) are a case in point, with different and unrelated birds dispersing seeds in seasonal dry forest as compared with rainforest. For widespread species, such as *T. panamensis*, *V. sebifera* and *V. surinamensis* with populations of 5×10^8 to $>10^9$ in the Amazon Basin (ter Steege et al., 2013), bird species are necessarily different than in Central America because the key dispersal agents in Central America do not occur in South America. Relatives do. Arilloids of *Virola* species are eaten and seeds dispersed by toucans in Brazil (Galetti et al., 2000), Ecuador (Holbrook and Loiselle, 2007), French Guiana (Forget et al., 2000), and Panama (above and Kays et al., 2011). Toucans are often a consistent primary dispersal agent for the genus *Virola*.

In undisturbed rainforest in Peru a primate (*Ateles paniscus*) plays the dominant role in dispersal of *V. calophylla* (Russo, 2003; Russo et al., 2006). In Manu National Park, 647 h of observation show that two toucans and four araçari species, along with 10 other bird species, eat *V. calophylla* arilloids and disperse the seeds, but the monkey is responsible for 83% of seeds removed from the trees. This is a small dispersal assemblage for a forest with six primate species and many fruit-eating birds, but it is twice the assemblage size in Panama. The dominant role of a spider monkey probably reflects a reality that even in undisturbed nature, local conditions determine the outcome of conditional foraging decisions. *Virola calophylla* is widespread, estimated to have $>10^9$ individuals across the Amazon (ter Steege et al., 2013). Primates remove most seeds for some other species of *Virola* in parts of the Amazon Basin (*V. flexuosa*, *V. peruviana*), but *V. calophylla* is almost entirely dispersed by birds at some sites in the western Amazon, despite the fact that the most important consumers of other fruits in the forest are primates (Stevenson et al., 2015). This continues to be an excellent example of the local nature contingent foraging and of “dispersal systems” (Table 2), even of some large-seeded species.

Other factors that affect contingent choices include orders-of-magnitude differences in fruit quantity within and between species, within and between years, and substantial differences in abundance of competitors that limit frugivore choices. Uniquely rich rewards, analogous to millet seeds in gerbil experiments (Berger-Tal et al., 2010), are most likely to secure predictable use by fruit-eating animals. On first principles of foraging theory, it is not surprising that a few dedicated large birds closely track fruit production in large-seeded species such as *Virola surinamensis*, nor is it surprising from the plant perspective that of 108 species for which seed traps collected samples over 15 years on Barro Colorado Island, *V. surinamensis* ranks second in predictability of seed fall (inverse of coefficient of variation of seed number in seed traps; Wright et al., 2005). This is probably close to the extreme of a continuum in which rich rewards for carrying large seeds lead to consistent, widespread local dispersal (Kays et al., 2011; McKey, 1975). Fruit production of most tree species varies much more, and consequently presents quite different scenarios of fruit choice to animals. Wright and colleagues (2005) show that *V. sebifera* is in the top 25% of crop predictability, *T. panamensis* is in the bottom 33%.

5.3. Reward puzzles

Preoccupation with energetics in foraging theory, and morphological attributes of fruits and fruit-eating animals, obscure the fact that animals vary enormously in abilities to assimilate constituents of different foods. This limits the utility of some fruits for potential dispersal agents, and limits the value of gross energetic content as a proxy currency for understanding dispersal processes. It also means that dispersal syndromes, and perhaps dispersal modules with insufficient sampling, may not be predictive from size, morphology and color.

Physiology affects fruit use in non-obvious ways. Reward differences exist among sugars and other nutrients in fruits, with consequences for fruit choice and seed dispersal (Levey and Martínez del Río, 2001). For instance, some omnivorous fruit-eating birds, including European starlings (*Sturnus vulgaris*), lack sucrase and therefore cannot digest sucrose well (Karasov and Levey, 1990; Martínez del Río and Stevens, 1989). Among several North American birds, cedar waxwings (*Bombycilla cedrorum*), which subsist entirely on fruits during some seasons of the year, can digest monosaccharides and disaccharides including sucrose, although sucrose digestion is less efficient than that of fructose or glucose (Martínez del Río et al., 1989). Immense variation in sugar components exist among fruits of tropical plants, with only fruits eaten by Old World bats consistently high in sucrose (Baker et al., 1998). It is interesting that invasive species in Australia have more sugar-rich fruits than native species, and that the sugars are overwhelmingly fructose and glucose that are easily digested by many birds (Gosper and Vivian-Smith, 2010). If a dispersal syndrome were to be posited for invasive animal-dispersed trees and shrubs, the character suite would surely include easily assimilated glucose and fructose in fruit pulp.

Nutrient-processing capacities of tropical fruit-eating animals are not well known; a few well-studied examples and a much wider literature from temperate birds illustrate the breadth of phenomena likely to exist. Fruit-eating animals also have different abilities to digest lipids and proteins from fruits. Levey and Martinez del Rio (2001) distinguish fruit-eaters that consume sugar-rich fruits and pass them through the gut quickly from those that prefer lipid-rich fruits and retain pulp longer. Temperate waxwings, for instance, can eat lipid-rich fruits exclusively, but their digestion of lipids is less efficient than that of thrushes, and the waxwings prefer sugar-rich fruits (Witmer and Van Soest, 1998). Small (≤ 20 g) Neotropical tanagers discriminate fine differences in nutrient content (Schaefer et al., 2003a). In cage trials, *Chlorophanes spiza*, *Cyanerpes nitidus*, *Dacnis cayana*, *Tachyphonus cristatus* prefer sugar-rich mixtures; three can distinguish 1% differences in sugar content and two can discriminate 2% differences in lipid content of foods. Schaefer and colleagues find that these birds do not make fine discriminations between glucose and sucrose and even treat lipid and sugar more or less interchangeably at low sugar concentrations, but prefer high sugar content in isocaloric trials. The birds also discriminate different proteins in captivity. In the wild many more choices are available in some seasons and sites, fewer in others.

Energy might appear to be roughly sufficient as a proxy for fruit value, but it is not (Izhaki and Safriel, 1989). Drawing from the temperate literature, Izhaki and Safriel report that six partially frugivorous songbirds lose weight when fed diets of fruits of only one of six plants. It is not surprising that birds fare worse on buckthorn (*Rhamnus palaestinus*) with low protein content (2.7%), and better on gardrobe (*Osyris alba*) with higher protein content (6.4%). It is surprising that the blackcap (*Sylvia atricapilla*) does far worse on pistachio (*Pistacia palaestina*) with a high protein content (7.1%) than on buckthorn (Table 2 of Izhaki and Safriel, 1989). Notably, buckthorn and gardrobe have similar energy contents (15.2 vs. 15.5 KJ g⁻¹). Izhaki and Safriel suggest that secondary plant metabolites in ripe fruits interfere with protein digestion, inserting another contingent variable into predictability of seed-dispersal syndromes.

5.4. Deceitful dispersal

Animal and plant mutualisms rarely if ever represent a 100% confluence of fitness interests of each mutualist (Bronstein, 1994). Among obviously deceptive apparent mutualisms are thousands of plant species that offer no reward, but trick insects into bringing or carrying away pollen with visual or olfactory cues (Renner, 2006). Apparent non-symbiotic mutualisms can, and frequently do, represent interactions in which foraging errors drive the system. Plants deceive would-be mutualist partners successfully and repeatedly.

Some seed-dispersal systems also rely on foraging errors. Ridley (1930) and Van der Pijl (1982) reported that some legume genera, most notably *Erythrina* and *Ormosia*, produce dehiscent pods that expose showy black, orange, red, yellow or multi-colored seeds that have no aril, pulp or other reward. The seeds look like berries or drupes, but are not. It is difficult to demonstrate that they function as mimetic berries. Captive birds usually refuse to eat these seeds, and large numbers of seeds under fruiting adults imply poor dispersal (Foster, 2008). The possibility exists that some seed-coat colors are exaptations, or even aposematic (Galetti, 2002). Galetti reports that naïve toucans and captive guans eat some seeds, but that control seeds not ingested by birds germinate much faster than those regurgitated or defecated.

Rare field observations have been enlightening. Foster and Delay (1998) watched individual *Ormosia* trees of three species in southern Mexico and Peru. The most complete observations were in Mexico at an *O. isthamensis* tree that was visited 25 times by foragers over 36 h. Twelve species of birds removed a total of 39 seeds from pods and carried 19 away from the tree. Three seeds were eaten and probably killed by parrots. Two potentially naïve bird species were North American migrants (*Empidonax minimus*, *Vireo olivaceus*), but a resident tanager (*Eucometis penicillata*) carried 14 seeds > 10 m from the tree. Other visitors carried a few or pecked at red seed coats as if they were arils.

Seed handling in animal guts differs in effects on seed viability; different animal species often have different effects on viability of seeds of the same plant species (Traveset, 1998; Traveset et al., 2007). Following earlier observations, Foster (2008) reasons that small arboreal foragers, like tanagers, might have a different effect on *Ormosia* seeds than large ground-foraging guans (*Penelope*, *Pepile*) and tinamous (*Tinamou*) with strong gizzards. Scarified seeds that simulated handling by large birds did germinate more quickly than un-scarified seeds that simulate handling by small arboreal birds. Fewer seedlings from scarified seeds survive, however, because rapid germination subjects them to much higher mortality during a transition from dry to wet season. More seedlings from untreated seeds (simulating small-bird removal) that germinated during the wet season survived. Foster notes that dispersal is slow, but a low incidence coupled with high survival could be effective. For *Ormosia*, deception works.

Low rates of dispersal of berry mimics that offer no reward are comparable to removal of some fruits with rewards. In Foster and Delay's (1998) observations, no foraging visits were seen at one *O. isthamensis* in Mexico over 8.5 h, nor at an *O. bopienis* in Peru over 26 h. At least 6 birds foraged in a badly obscured *O. macrocalyx* over 23 h. Twenty-five visitors to a large *O. isthamensis* over 36 h removed 19 seeds at a rate of 2.0 h⁻¹. Some visitation rates for tropical trees from references cited earlier are greater, including *Guarea glabra* (e.g. 60 h @ 5.2 visits h⁻¹ and 8.0 seeds removed h⁻¹), while seed removal from others can be frenetic during short periods that fruits are available (e.g. *Stemmadenia donnell-smithii*, *Virola sebifera*, *V. surinamensis*). This is to be expected in comparisons of mimetic seeds to fleshy fruits.

Observations of higher visitation and removal of mimetic seeds than fleshy fruits were not expected. Visitation of foraging frugivores at rewardless *O. isthamensis* was greater than foraging of fruit-eating birds at low-priority *Leptonychia usambarensis* trees with arillate seeds in continuous forest in Tanzania (192 h @ 0.6 visits h⁻¹ with 1.0 seeds removed h⁻¹), and much higher than rates at *L. usambarensis* in forest fragments (120 h @ 0.2 visits h⁻¹ with 0.3 seeds removed h⁻¹). Some

temperate summer and fall-fruiting trees are depleted quickly (e.g. *Prunus mahaleb* in Europe, [Jordano and Schupp, 2000](#); several genera in North America, [Thompson and Willson, 1979](#)). But fruits of other familiar genera persist on plants for weeks or months over winter (*Crataegus monogyna*, *Rosa canina*, [Herrera, 1984](#); *Cornus Drummondii*, [Willson and Whelan, 1993](#)). Removal rates are probably episodic, but averaged over weeks to months, hourly removal rates are negligible compared to rewardless *O. ithamensis* in the one well-watched tree of the genus ([Foster and Delay, 1998](#)). Models for mimetic seeds are probably low-preference fleshy fruits that are also taken at very low rates. In the tropics, these are virtually unstudied.

5.5. Handling and dispersal

Plants are under selection on life histories to trade off few to many seeds (potential offspring) that are small to large (dispersal and potential competitive ability). The ability of fruit-eating animals to handle packaging and presentation of seeds in fruit could be a strong selective factor in itself ([Levey and Martinez del Rio, 2001](#)). Seeds are often ballast for a fruit-eating animal that must process but cannot digest them. Many birds strip off arils and regurgitate seeds before digesting the pulp. One might think that the premium would be on small seeds that pass easily through the gut, but it is not. Cedar waxwings (*B. cedrorum*) handle artificial fruits with surrogate seeds differently if they contain four small plastic beads or one large bead of equal volume ([Levey and Grajal, 1991](#)). Retention times of artificial pulp do not differ, but large seeds pass through the gut much more quickly than small seeds, allowing more pulp to be eaten. In these preference trials, all waxwings favor fruits with large seeds over small seeds. Processing pulp with small seeds is less efficient from the bird perspective than dumping the ballast quickly.

Tropical plant species face different challenges from seed handling, with a premium on rapid handling in some cases and retention for greater dispersal distances in others. Selective forces vary in time and space. For instance, *Virola surinamensis* and *V. calophylla* have single-seeded fruits in which the ratio of aril to seed mass varies from tree to tree ([Howe and Vande Kerckhove, 1980](#); [Russo, 2003](#)). In both Panama and Peru, birds that disperse seeds favor trees with larger aril to seed ratios over those with smaller ratios. In Panama that is important because birds are the primary dispersal agents. In Peru it does not matter because monkeys, the primary dispersal agents, are indifferent to aril to seed ratios. Instead primates favor trees with large rather than small crops. In another twist, [Murray et al. \(1994\)](#) report that a tropical solitaire (*Myadestes melanops*) handles artificial fruits with natural seeds (*Witheringia solanacea*) differently if extract from the fruit pulp is added to synthetic “pulp”. Seeds in synthetic fruits with extract are voided more quickly than synthetic fruits without extract, suggesting laxative properties of the natural fruits. The premium is on dispersal a few to a few tens of meters from fruiting shrubs, not long-distance dispersal, because there is a strong negative correlation between germination rate and seed-retention time in the gut.

Alternatively, for plants with seeds resistant to or benefitting from digestive processes, the premium may be on distance, and therefore longer retention times. In a study comprising 1440 h of woolly monkey (*Lagothrix lagothricha*) “follows” in Tinigua National Park, Colombia, [Stevenson \(2011\)](#) finds that it takes far longer for pulp of some species to detach from seeds than others, with a “detachment index” (time/g) ranging from 23.5 (*Eugenia nesiotica*, seed width 13.5 mm) to 24,870.0 (*Ficus nymphaeifolia*, seed width 1 mm). Three orders of magnitude difference in the index over 21 fruiting species suggest an adaptive advantage for some trees in prolonging seed retention through small seeds embedded in pulp, strong attachment, irregular seed surface and/or a thin pulp layer. Genera with high indices often have hundreds to thousands of seeds per fruit (e.g. *Cecropia*, *Coussapoa*, *Ficus*), with notable exceptions (*Pouteria*, *Prunus*). The extent to which seed retention enhances or impedes effective dispersal appears to vary greatly from plant to plant and dispersal agent to dispersal agent.

Rewards vary for other reasons. Fruit pulp varies widely in mineral content; plants sequestering scarce minerals in fruits could influence foraging and therefore dispersal ([Herrera, 1987](#); [Levey and Martinez del Rio, 2001](#); [Izhaki, 2002](#)). For instance, [Foster \(2014\)](#) notes that fruit-eating birds need calcium for egg shells and bones in developing young. Most birds acquire calcium by eating snails, woodlice and millipedes. Fruit-eating birds also do that, but among the fruits of many species available to them, some offer much more calcium than others (Table 1 of [Foster, 2014](#)). In units of mg of calcium in the pulp of a given fruit that a bird would consume, amounts range from <0.01 mg (*Pera benensis*) to 4.15 mg (*Ficus killipii*). In light of needs of many birds for high sugar content in fruits and some for minerals that are otherwise hard to get, it is not surprising that [Gosper and Vivian-Smith \(2010\)](#) find that invasive plants in Australia have elevated concentrations of calcium, phosphorous and/or sodium in fruit pulp, as compared with native species. Together with easily-digested fructose and glucose and needed calcium, invasives cater to broad disperser assemblages in new habitats.

Finally, fruits may have physiological handling costs. Fruits generally have far lower concentrations of secondary metabolites in ripe pulp than in leaves, unripe pulp, husks, or seeds, but potential toxins or deterrents occur ([Cipollini et al., 2002](#); [Cipollini and Levey, 1997](#); [Schaefer et al., 2003b](#)). Multiple adaptive roles exist for some secondary metabolites. For instance, emodin, one of 170 anthraquinones known in plants, occurs in at least 17 plant families in all tissues ([Izhaki, 2002](#); [Levey et al., 2007](#)). Emodin declines in fruits as they ripen, but remnants in ripe pulp deter some vertebrates. By contrast capsaicinoids, produced by some wild chilies as they ripen, have no deterrent effect on birds. They have multiple defensive roles. A natural polymorphism in capsaicin results in highly-pungent or not-pungent peppers in *Capsicum chacoense* in Bolivia ([Tewksbury et al., 2008](#)). Capsaicin protects ripening chilies against a fungal pathogen (*Fusarium*), the greatest source of pre-dispersal seed mortality, and deters hemipteran herbivores that give *Fusarium* access to seeds. Capsaicin also deters rodents ([Levey et al., 2006](#)). In field studies, fruits of two species of *Capsicum* are removed by birds during the day, but not

at night when rodents are active. Capsaicin in fleshy fruit defends seeds from pathogens, herbivores and rodents, but does not affect primary dispersal by birds.

5.6. Fruit processing, conditional foraging and conservation

The critical point for conservation in experiments of [Schaefer and colleagues \(2003a\)](#) with tropical tanagers mentioned earlier is not that the birds can digest sugars, lipids and proteins, it is that they actively discriminate among them, and that bird species differ in discriminations of apparently similar fruits. Sometimes the interaction of nutritional needs and secondary compounds is not obvious. Cedar waxwings (*B. cedrorum*) eat fruits throughout the year and depend entirely on fruits in fall, winter and early spring. [Witmer \(2001\)](#) reports that the birds eat few fruits of *Viburnum opulus* in fall or winter when other fruits are in short supply. They do eat the fruits in the spring when nearby cottonwood catkins (*Populus deltoides*) offer supplemental protein. Chlorogenic acid in the *V. opulus* interferes with digestion; the birds need extra protein to offset the acid and get a reward from the fruit. In cases like this, conservation or restoration of forests using fruit-eating animals would require multiple and complementary sources of fruits.

Other interaction puzzles belie easy categorization of dispersal syndromes. For instance, cedar waxwings do not eat fruits of two common nightshades in eastern North America, *Solanum americanum* and *S. carolinense*, both of which contain the glycoalkaloid α -solanomarginine. [Levey and Cipollini \(1998\)](#) find that waxwings fed artificial fruits with or without α -solanomarginine (0.1%–0.3%) eat the controls but reject all levels of α -solanomarginine, including treatments with extra nutrients in the mix. Results with this obligate frugivore are consistent with earlier experiments with omnivorous robins (*Turdus migratorius*) and opossums (*Didelphis marsupialis*). Both consume control artificial fruits but refuse artificial diets with α -solanomarginine. Something disperses seeds in these showy fruits of abundant species. The usual suspects do not.

5.7. Synopsis of choice

The point of the foregoing discussion is that contingent fruit choices might affect forest enrichment or restoration. Fruiting phenologies of potentially competing plants constantly change what is available, what is superabundant, what is valuable, and what is scarce from a forager's perspective. Reliance on morphological characters without direct observation would be folly, and even substantial observation in a limited time frame or area may miss substantial variation in dispersal and its consequences. Add to those caveats the fact that vast majority of tropical tree species are rare ([Hubbell, 2013](#); [ter Steege et al., 2013](#)) and many probably have inherently low dispersal rates (e.g. [Cordeiro et al., 2009](#)), it follows that use of dispersal syndromes or network modules beyond local scales must be done with care.

6. Community contexts

6.1. Frugivore-plant networks

A signature advance in the study of seed dispersal is development of network theory for dispersal mutualisms ([Bascompte and Jordano, 2007, 2014](#)). The promise is that by empirically documenting interactions among plants and dispersal agents throughout a community, networks allow predictions of how changes among some plants and animals affect interactions among others in a forest or landscape ([Figs. 3, 4](#)). The implication is that mutualist networks will predict how communities change if different sets of dispersal agents or plants are added or lost. A promise for the future is that network “architecture of biodiversity” offers a conceptual basis for selection of trees and dispersal agents with characteristics that are likely to be most useful in conserving or restoring forest biodiversity, particularly in latitudes where most trees that provide the physical structure of communities depend on dispersal by animals.

Network theory is well-developed in studies of transportation, communication and neurology, making it a convenient framework for studies of ecological communities ([Bascompte and Jordano, 2014](#)). Given contingencies in fruit choice and seed disposition, the risk in applying the theory to communities is: (1) empirical parameterization is strictly applicable to one time and place, (2) parameterization may be incomplete, especially if mutualism is assumed without knowing whether animals involved provide effective seed dispersal, nor whether the plants involved are important resources for the animals, and (3) too few species interact to reliably predict network structure. Interaction networks are interesting whether or not the animals and plants depend heavily on each other; they are of limited utility for conservation or restoration unless dependencies are verified.

Simplified hypothetical scenarios illustrate challenges in interpretation of disperser networks ([Fig. 3](#)). As is often the case, some large-seeded trees are dispersed by large birds (A1) and some smaller-seeded species (e.g. P1) are dispersed by both large and small birds (A1, A2). Birds eat fruits of and effectively disperse seeds of some fruits (P2) primarily dispersed by bats (A3), and bats eat and disperse some seeds eaten by small birds. In this hypothetical scenario three rodents scatter-hoard nuts adapted for animal dispersal; one large rodent (A4, e.g. agouti (*Dasyprocta*) in the Neotropics, pouched rat (*Cricetomys*) in Africa) also secondarily disperse palm seeds (P3) adapted for dispersal by large mammals (A5, A6). Large rodents potentially become primary dispersal agents if large mammals disappear (e.g. [Jansen et al., 2012](#)). Actual representations often indicate

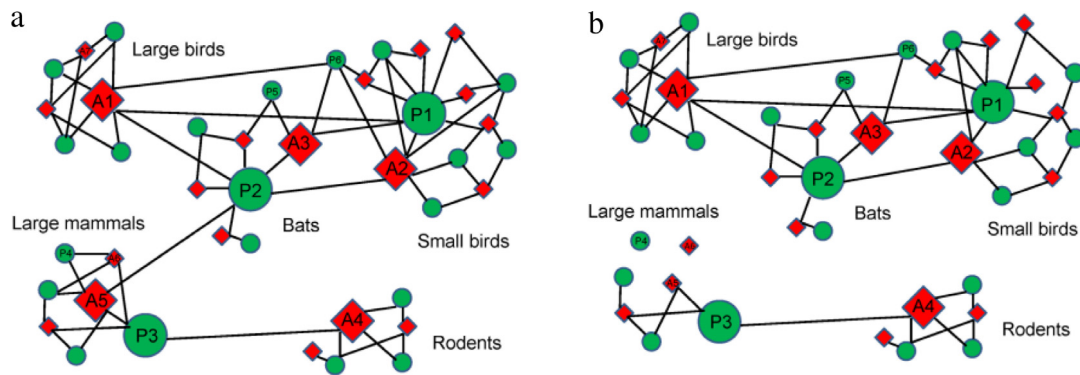


Fig. 3. Hypothetical apparent and functional networks of animal (red) and plant (green) dispersal modules: (a) Apparent network in forest based on observed use of plant species by indicated animals; (b) Functional network in which a large mammal species (A5) eats fruits of a bat hub tree (P2) but leaves seeds where seedlings cannot survive. In a network defined by contribution of animals to plant recruitment and plants to animal sustenance, one tree species (P4) and a large mammal (A6) do not interact with each other or other species in the large-mammal module as mutualists. A large scatter-hoarding rodent, thought to be a secondary dispersal agent of the megafaunal hub tree (P3), functions as its primary dispersal agent. Potentially important plant (hub) or animal (connector) species are represented by large symbols. In nature, tropical networks would include many more species, many more interactions among species, and more modules (e.g. arboreal mammals, fish). Connection lengths and points of insertion are arbitrary. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

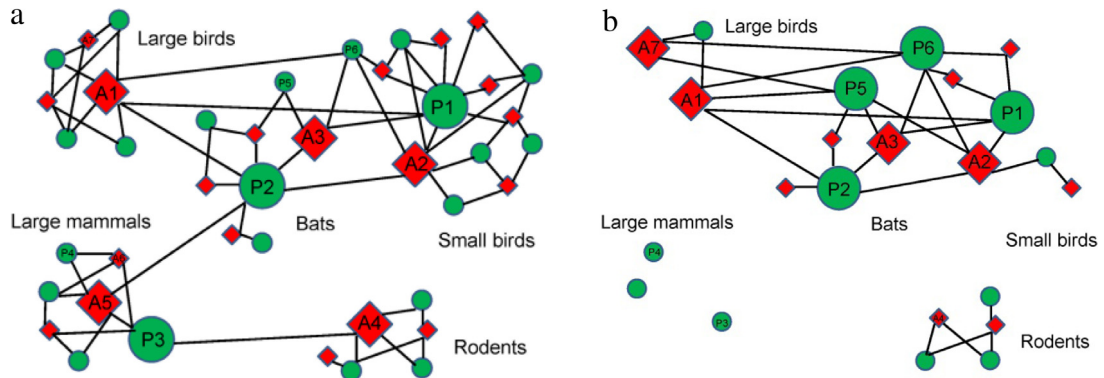


Fig. 4. Hypothetical functional mutualist networks of animal (red) and plant (green) dispersal modules defined by effective animal dispersal of seeds and effective plant sustenance of fruit-eating animals in (a) lightly hunted and (b) heavily hunted, selectively logged and fragmented forest. In the disturbed landscape, large mammals and large rodents are absent or so rare as to be ecologically extinct. Three of four apparent large-bird feeding trees are no longer shown because they are no longer important food resources; one of three large birds is also absent. Small-bird hub (P1) and bat hub (P2) trees retain their dependence on effective dispersal by birds and bats, but observation of seedling demography indicate that additional bat (P5) and small-bird (P6) trees also depend on large birds much more than use might suggest, and are therefore hub trees in the highly disturbed landscape. Symbols and qualifications are as before (Fig. 3). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

amount of use by scaled line thickness. Note that heavy use does not necessarily mean effective dispersal. For instance, a large mammal (A5) might eat many bat fruits, but digest seeds or leave them in huge concentrations where few survive.

In a qualified scenario of the same forest defined by dispersal potential from the plant perspective (Fig. 3(b)), interactions within and between bird and bat modules do not change. However, the large mammal connector (A5) eats fruits dispersed by bats (P2) but deposits seeds where survival is extremely unlikely. Defined by plant recruitment, the large mammal and bat modules are not connected; A5 performs dispersal functions only within the large-mammal module. Moreover, one tree in the large-mammal module is not effectively dispersed by any animals shown (P4), and one large mammal present in the forest is so rare as to be “ecologically extinct” (McConkey and Drake, 2006). Large mammal and rodent modules remain connected.

In hunted, logged and fragmented landscapes contingencies change (Fig. 4). Large mammals are gone, as are some trees. Large rodents (A4) are reduced in numbers and do not cross open pasture or cropland; rodent and large-mammal modules are no longer connected. Isolated trees adapted for large-mammal dispersal no longer recruit. Losses of animal and plant species re-shape the network. Remaining large birds (A1, A7) depend heavily on bat fruits (P1, P5), as do small birds (A2). The modules blur. Large birds (A1, A7), bats (A4) and small (A6) birds use a bat plant (P5) and small-bird plant (P6) so much that they become hubs. The ultimate structure does not indicate whether hubs depend on large and small birds and bats, or *vice versa*.

These scenarios are fanciful, but plausible in light of existing evidence. An infinite variety of such scenarios are plausible in light of existing evidence; literature on relevant natural history is often woefully incomplete. In many parts of the tropics,

little is known about what fruit-eating animals eat, much less how important they are for different plant species (e.g. Seltzer et al., 2013). That animals do not always eat what is expected from morphology and other display properties is not new (Herrera, 1985), nor is the expectation that networks change as a result of disturbance by humans (e.g. Guimarães et al., 2008). In one hypothetical scenario above (Fig. 3), the assumption that large mammals contribute to persistence or migration of some tree species cannot be assumed from what they eat. Real networks are far more complex (e.g. da Silva et al., 2015; Donatti et al., 2011; Mello et al., 2011; Pires et al., 2014), potentially admitting more contingency shifts due to differences in competition among dispersal agents or plants, in fruiting phenologies, in choice of foods by animals, and in factors affecting plant recruitment.

Finally, the number of links between species in different trophic levels matters. Network modularity calculated from tabulated interactions in communications or neuronal networks may be based on thousands to millions of links. In an analysis discussion of modularity in pollinator networks, Olesen and colleagues (2007) find that networks with >150 interacting plant and pollinator species always show modularity, while networks with <50 interacting species never do. Some quantitative limitations in networks of small or intermediate size can be overcome with simulation (Donatti et al., 2011), but reliability is greater with a vast number of empirically determined links than with a few. The number of interactions between dispersers and fruit trees in a mature forest may exceed 150, but probably will not in some highly-disturbed landscapes. Impermissible interactions still will not occur (small birds dispersing large seeds; tapirs dispersing seeds that they always digest), but clear network modularity may not either. In species-poor logged, fragmented or intensively hunted forests, heuristic network analysis and predictions based on dispersal syndromes merge. What remains most important is the degree of effective dispersal of seeds of each species of plant by each species of animal, and the extent to which animals rely on fruit resources produced by different plants.

6.2. Real and apparent mutualisms

Fruit-eating animals often rely heavily on fruits without effectively dispersing seeds, no matter how many fruits they eat. Beyond outright deception (Section 5.4), a challenge is to distinguish effective from apparent dispersal. Implicit in this discussion is that interaction networks of trees and fruit-eating animals often do not depict interactions among mutualists, and may change in unexpected ways. If a function of conservation and restoration is to provide resources for birds and mammals that disperse seeds of other species throughout an annual cycle, even nutritious fruits of rare trees miss the goal. Unless they happen to be available when other fruits are not, most low-priority fruits also fall short, as might some high-preference fruits that contain only sugars, or “the wrong” sugars (Section 5.3). Observations that distinguish ineffective fruit resources for animal sustenance or ineffective dispersal from the plant perspective are the exception.

A first step is to determine what animals eat. For instance, fruit consumption in the hyperdiverse Pantanal in southern Brazil shows a network of modules characterized by fruit and seed traits in common and potential dispersal agents (Donatti et al., 2011). Mammal and bird modules may be linked by connector species (e.g. toucans) that eat fruits from large mammal, large bird and small bird modules. That the animals indicated eat fruits of the plants indicated is not in question. The open questions are the degree to which fruit or seed use by each animal species is a useful indicator of plant benefit, and whether the plants support animal populations. In short, to what degree is this an interaction network including mutualists, antagonists and neutral interactions, as compared to a mutualist network?

The initial challenge for filling in the “quality” component of effective dispersal (Schupp et al., 2010) is to see whether ingested seeds survive, the second is to determine where fruit-eating animals leave seeds that germinate and produce seedlings able to recruit. Seed survival in the gut can be negligible. For instance, Campos-Arceiz et al. (2012) find that far fewer seeds survive passage through Asian tapirs (*Tapirus indicus*) than ecologically extinct Asian elephants (*Elephas maximus*) or rhinos (*Dicerorhinus sumatrensis*, *Rhinoceros sondaicus*). Compared to elephants and rhinos, tapirs are marginal dispersers of small-seeded trees and are predators of larger seeds.

The next step is to determine where different dispersal agents leave seeds. Crude early approximations simply distinguish dispersal agents that leave seeds near fruiting trees, where seed and seedling mortality is severe, from animal movements to areas with less mortality (e.g. animal dispersal of *Virola*, Howe et al., 1985). More comprehensive efforts follow the animals to determine where seeds land, seedlings emerge, and mortality occurs (e.g. birds, two tree species and a palm, Rother et al., 2016; primates and *Virola*, Russo et al., 2006). The best evaluation is from integrated studies of animal movement and seed and seedling mortality where genetic contribution of different parent plants can be established (e.g. birds and temperate *Prunus*, Jordano et al., 2007). The concern is that network analyses rarely distinguish real from apparent mutualism, much less the relative importance of different animals on seed and later seedling survival, or fruit-resource use on animal survival. Only rarely can subtle differences in seedling mortality be attributed to different dispersal agents (e.g. Brodie et al., 2009a; McConkey and Brockelman, 2011; Rother et al., 2016). Efforts with this level of discrimination are prohibitive for community-wide studies. However, at least crude estimates of relative effect of animals on plant recruitment are usually feasible. These should be part of community analyses that are intended to be foundational for conservation or restoration efforts.

6.3. Real and apparent disperser redundancy

Tropical tree species illustrate the full range of apparent dependencies on different dispersal agents. Small to medium-sized seeds are often accessible to a wide range of fruit-eating animals, and are most likely to have genuinely redundant dispersal assemblages in regions. *Cecropia* and *Stemmadenia* examples discussed earlier appear to have redundant disperser assemblages; wherever they are studied, a variety of avian – and in the case of *Cecropia* mammalian – taxa eat the fruits and disperse viable seeds. It may also be true of some, like *Casearia* discussed earlier (Section 4), that depend on one or a few dispersers at a particular place and time, but other disperser species at other places or times. Redundancy probably occurs among figs and other plants that are eaten by a variety Neotropical bats (Bonaccorso, 1979; Muscarella and Fleming, 2007). If differences in effective dispersal of extremely fecund pioneer trees exist, they are difficult to document because virtually all seeds and seedlings die.

Redundancy cannot be assumed; small-seeded species may also have restricted effective seed dispersal. Loiselle and Blake (2002) explore the hypothetical consequences of local extinction of four fruit-eating birds for dispersal of four understory shrubs of the Melastomaceae in rainforest in eastern Costa Rica—all species with minute seeds. Fecal samples of seeds suggest that one manakin, *Pipra mentalis*, is an important dispersal agent that faces little risk of extinction in the foreseeable future because it is abundant. Loss of a rare tanager (*Chlorothraupis carmioli*) now in decline might have an important effect. Another manakin (*Corapipo leucorrhoa*) is an elevational migrant that might be threatened by loss of connectivity with higher elevations. Its diet overlaps greatly with *P. mentalis*, but in the presence of the latter, shrubs would continue to be dispersed. A North American migrant thrush (*Hylocichla mustelina*) is in general decline, but is not as important for dispersal of these shrubs. This is a small assemblage for shrubs and trees producing berries with minute (<0.5 mg) seeds. The existential risk remains that if disease decimated *P. mentalis*, remaining birds might be unable to provide equivalent seed and seedling distributions, resulting in severe effects on recruitment of this guild focal shrubs.

Broader community analyses likewise predict substantially different consequences for seed dispersal by 42 bird species in fragmented rainforest landscapes in subtropical Australia (Moran and Catterall, 2014; Moran et al., 2004, 2009). Lacking direct information of effects of dispersal agents on plant recruitment, the authors ordinated bird species by handling behavior (crush or disperse seeds), gape width (small, medium, large), level of frugivory (minor, mixed, major), and habitat (extensive, remnant, regrowth). Most large birds likely to disperse a large volume and variety of plants are less common in regrowth than remnants or forest. A result is that in regrowth, dispersal potential of many plant taxa is restricted to a few available agents. For large-seeded plant species, dispersal into and around regrowth and small remnants is restricted to one large bird common in secondary vegetation (figbird, *Sphecotheres viridis*). In general, Moran and Catterall (2014) suggest that maintenance of dispersal processes is likely to diminish in fragments more than 200 m from extensive rainforest cover.

Loss of functional roles of dispersal agents is much more likely with large seeds dispersed by larger animals. A growing number of studies show that elimination of large fruit-eating primates by hunting leads to recruitment failure for large-seeded species that normally depend on primates for seed dispersal (e.g. Balcomb and Chapman, 2003; Effiom et al., 2013; Hawes and Peres, 2014; Nuñez-Iturri et al., 2008; Terborgh et al., 2008; Vanthomme et al., 2010). Key dispersal agents need not be extirpated for pervasive negative effects on dispersal of large-seeded species. On the Pacific islands of Tonga, for example, McConkey and Drake (2006) find that dispersal function of a large flying fox (*Pteropus tonganus*) for 14 species of large-seeded tropical trees is lost long before the bat is rare. When bats are abundant enough to fight in fruiting trees, seeds are often carried far from their sources. When bats are less common, most seeds are dropped under the parental crowns.

Other examples of disperser inadequacy are difficult to detect, but are nonetheless real. In central Thailand the tree *Choerospondias axillaris* (Anacardiaceae) attracts three mid-size mammals that consistently eat fruits and carry away seeds: a gibbon (*Hyllobates lar*), sambar deer (*Rusa unicolor*), and muntjac deer (*Muntiacus muntjak*). Brodie and colleagues (2009a, b) find that all three animals remove substantial numbers of fruits, but only the muntjac consistently leaves them in forest light gaps where seedlings have a small but measurable chance of survival. In this case clues to real redundancy of the dispersal assemblage are subtle. Large birds and other large mammals may disperse some *C. axillaris* seeds (Kitamura et al., 2002, 2007), but the key point is that classification of effective dispersal based on fruit use that would place gibbons and both deer in the same category within a network “module” would be incorrect. This tree feeds all three animals (to an unknown degree), but only muntjacs mediate tree recruitment. Brodie and colleagues argue that overhunting key dispersal agents creates an extinction debt in dependent trees. Few studies are comprehensive enough to reveal subtle differences in ultimate dispersal effectiveness to accurately predict tree-extinction debts.

Another set of examples from the Paleotropics illustrates both the clarity and ambiguity of “use data” as proxies for mutualist effects. Hornbills (Bucerotidae) are important agents of dispersal of large seeds across tropical Africa and Asia (Datta and Rawat, 2003; Holbrook et al., 2002; Kinnaird and O'Brien, 2007; Kitamura, 2011). In foothills of the East Indian Himalaya, three hornbills (*Aceros undulates*, *Anthraceroceros albirostris*, *Buceros bicornis*) are important dispersal agents for many large-seeded trees (Sethi and Howe, 2009, 2012). In the case of *Chisocheton paniculatus* (Meliaceae), hornbills are the critical dispersal agents; where hunting decimates hornbills, seedling recruitment beyond the crown is far lower than in less-disturbed forests. For *C. paniculatus*, fruit use is an accurate proxy for dispersal. In contrast, *Dysoxylum binectariferum* (Meliaceae) and *Polyalthia simiarum* (Annonaceae) are not as dispersal-limited when hornbills are decimated. Seedling and juvenile tree recruitment are lower in hunted areas, but substantial recruitment occurs beyond crowns of trees. Dispersal agents of *D. binectariferum* and *P. simiarum* in hunted forests is probably by imperial mountain pigeons (*Ducula badia*), a frugivore that tolerates some human disturbance. Similar disparities in response to disturbance occur in other tree species

dispersed by hornbills in northeastern India (Naniwadekar et al., 2015). For some, loss of hornbills prevents seedling recruitment. For others, it does not.

7. Conservation and restoration of dispersal processes

7.1. Generalists preserve specialists

A major insight is that all networks are asymmetrical. The property is general whether the networks are of neurons, traffic, communications, or animal and plant interactions (Bascompte and Jordano, 2007, 2014). Some fruit-eating animals disperse seeds of many trees and shrubs, others disperse few. Likewise, some tree species support far more species of frugivores than others (hubs and connectors in Figs. 3 and 4). Networks might illustrate how community architecture retains biodiversity (Bascompte et al., 2006). Preservation of or planting trees that appeal to many birds and mammals may help maintain both effective dispersal agents of the target trees and other fruit-eating animals, some of which effectively disperse other tree and shrub species. A useful generalization from modular structure is that generalist foragers and plants provide important resources for specialists (Tylianakis et al., 2010). Ideally, generalist fruits and generalist fruit-eaters buffer ecological communities against catastrophic change.

With notable exceptions (Elliott et al., 2013; Lamb et al., 2005; Parrotta et al., 1997), many conservation and restoration programs give only lip service to seed dispersal and dispersal limitation (McConkey et al., 2012). In conservation and restoration of highly disturbed but diverse tropical landscapes, conceptual frameworks and empirical studies are scarce. This impoverished literature is especially troublesome because in logged, burned, and fragmented landscapes, animal and plant interdependence is likely to be both critical for regeneration and idiosyncratic. A few examples show how this might work in disturbed habitats.

Dispersal assemblages in disturbed habitats may differ markedly from those in less-disturbed closed forest. For instance, on Barro Colorado Island in Panama, birds and bats partition fig resources as one might expect from dispersal syndromes (Kalko et al., 1996). Green or yellowish figs of medium to large size of free-standing species are dispersed by bats, while small blue, black or red figs of stranglers are dispersed by birds. Other species of fruit-eating animals undoubtedly eat the fruits, which in large reproductive trees appear to be superabundant, but syndromes are predictive. In a diverse tropical forest with many fruit resources available to many fruit-eating animals, foragers specialize “because they can”. Predictable food sources accessible to animals of different sizes and physiological constraints favor specialization, even on sometimes superabundant fruits. Optimization does not require scarcity.

Predictable specialization may not occur to the same degree in disturbed habitats where animals have fewer choices. On Barro Colorado Island, for instance, the green 1.8 cm wide figs of freestanding *Ficus yoponensis* are generally regarded as mammal fruits that are also eaten by birds (Bonaccorso, 1979; Kalko et al., 1996). Phylogenetic analyses are consistent with the view that evolutionary history of mammalian dispersal is involved in what until recently have been vast continuous-forests (Lomáscolo et al., 2008). In southern Mexico, isolated *F. yoponensis* trees are visited by bats in pastures, but as many as 47 species of fruit-eating birds also forage in the trees (Guevara and Laborde, 1993). Fruit traps monitored under trees day and night find that 433 of 564 (77%) seeds of strangler figs are, as would be predicted by dispersal modes, caught by traps open during the day, indicating dispersal by birds. Fifty-nine of 70 (84%) seeds of free-standing figs are caught at night, indicating dispersal by bats (Galindo-Gonzalez et al., 2000). Four points are relevant: (a) 23% of the seeds of “bird-dispersed” strangler figs are deposited by bats at night, (b) 77% of strangler seeds left during the day by birds are dropped under focal free-standing “bat figs”, and (c) birds leave 16% of the seeds of free-standing figs under focal free-standing figs during the day. Seed deposition day and night elsewhere in southern Mexico also indicates substantial deposition of bird–fig seeds by bats and bat–fig seeds by birds (Medellin and Gaona, 1999). In Mesoamerican agricultural landscapes, breakdown of specificity brings with it uncertainty of what could work in conservation and restoration of connectivity.

Other tree species supply general resources. Few if any fruit-eating birds and mammals specialize on *Cecropia* spadices (Fig. 1), but many fruit-eating vertebrates eat them. In extensive forest at Los Tuxtlas, Estrada et al. (1984) report 47 species of likely dispersers eating spadices of *Cecropia obtusifolia*, including a reptile (*Iguana iguana*), 13 mammals, and 33 birds over fruiting seasons lasting 7–12 months. Germination does not occur in spadices that fall off the tree, and is low (0.5%) if any pulp is attached to seeds. Germination rates of seeds passed through digestive tracts range from 58% (howler monkey, *Alouatta palliata*) to 86% (migrant wood thrush, *Hylocichla mustelina*). Absence of specialization might seem puzzling because almost 10% of the pulp is protein, 7% lipid and 40% soluble carbohydrate. However, the pulp is also 38% fiber and contains a large volume of seeds that are not digested, and are slowly processed by foragers (Section 5.5).

Some figs and relatives that are eaten by a wide variety of animals are candidates for “keystone species” in tropical forests because long or multiple fruiting seasons provide resources when fruits of other species are scarce (Diaz-Martin et al., 2014; Shanahan et al., 2001; Terborgh, 1986). For the same reason, figs are valuable as isolated food sources for frugivores in agricultural landscapes because they mediate movement of seeds of tree species across matrices between forest remnants (e.g. Cottee-Jones et al., 2015; Guevara and Laborde, 1993; Laborde et al., 2008). Trees providing fruits eaten by many animals appear to be ideal nodes in plant and frugivore networks for supporting specialist and generalist foragers that might serve as effective dispersal agents of many other tree species at other times of the year.

7.2. Creating generalized dispersal portfolios

No single species or genus is sufficient for supporting large frugivore assemblages in conservation and restoration plans, nor is any single animal sufficient for dispersal services. A single fruit resource is vulnerable to disease or other enemies, or simply may be unavailable at some times of the year or in some years (e.g. following El Niño events, Wright et al., 1999). Even figs may only support small frugivores. In more than 2000 h of observation of trees used by woolly monkeys (*Lagothrix lagothricha*) in extensive forest in Colombia, for instance, Stevenson (2005) reports fruit production over three annual cycles. Fruiting phenologies vary greatly from year to year, a finding consistent with evidence elsewhere (e.g. Muller-Landau et al., 2008; Wright et al., 2005). One finding is that intensities and durations of fruit scarcity differ from year to year; another is that different tree species provide resource bridges between periods of high fruit diversity and abundance. Stevenson notes that figs as individual species do not produce enough fruits to maintain populations of large (5–10 kg), fruit-eating primates. Most striking in Stevenson's study, fig-fruit production appears to be low during some months of dearth (Stevenson's Fig. 1). More than originally envisioned (e.g. Howe, 1977; Terborgh, 1986), the identity and productivity of tree species that provide critical resources to frugivores during scarcity vary in time and space.

Efforts to conserve or restore dispersal processes must conserve or plant generalist “nodes” to support frugivores; multiple nodes are less likely than one to leave long periods without fruit resources. In an experimental restoration now entering its 10th year in southern Mexico, fruit production diversifies as different species of planted and recruited animal-dispersed trees reach reproductive age (de la Peña-Domene et al., 2013; Martínez-Garza et al., 2013). Pioneer *Cecropia obtusifolia* trees produce some fruits throughout the year and superabundant resources for several months (Figs. 1(b) and 5). Other species beginning to bear fruit (*Ficus yoponensis*; *Inga sinacae*, *Stemmadenia donnell-smithii*, *Tabernaemontana alba*) will become consistent food resources as they mature. Several well-established planted or recruited tree species are likely to produce fruits for at least 50–100 years (Martínez-Ramos, 1985). The expectation is that eventually a varied assortment of 10–30 or more tree and shrub species will provide a variety of diets to obligate and opportunistic fruit-eating animals most of the year, and something all of the year.

Birds are ecosystem engineers in small and large ways (Jones et al., 1994; Wenny et al., 2011). In the experiment mentioned above, early fruit resources dominated by *C. obtusifolia* have led to substantial colonization by ~50 shrub and tree species from the surrounding landscape that were not planted in the original design (Fig. 6). The vast majority of these recruits are bird-dispersed. Some colonizing species have seeds large enough to require transport by large birds (e.g. trees: *Cupania glabra*, *Nectandra ambigua*, *Ocotea uxpanapana*; likely daily dispersers: *Cyanocorax morio*, *Psarocolius montezuma*, *Ramphastos sulfuratus*). For the first 10 years of the Los Tuxtlas restoration experiment, birds are the overwhelmingly dominant agents of seed dispersal for tree and shrub species that displace homogeneous pasture, thereby creating physical environments that accelerate succession.

8. Synthesis

8.1. Action under uncertainty

Conservation and restoration of tropical biodiversity must increasingly recognize and integrate the role of animals in maintaining or re-establishing plant diversity in highly disturbed landscapes (Corlett, 2011a,b; Howe, 2014; McConkey et al., 2012). Changes in abiotic factors will likely yield reasonable predictions for interactions of some animal and plant species (Maron et al., 2014). Biotic factors present more contingencies derived from differences among numbers and effectiveness of dispersal agents, among fruit resources of trees that vary in fecundity, age and growth conditions, and even effects of non-mutualists (e.g. destructive livestock). None of these are well understood in agricultural landscapes. Very few tropical locations have the depth of empirical knowledge from intensive studies of seed dispersal and its consequences that could predict successional pathways of even a small set of plants and frugivores (e.g. Rother et al., 2013, 2016). Nowhere is it clear how dispersal and recruitment will shift for whole communities adjusting to changes in land use or climate.

The first challenge is to retain or create habitat heterogeneity in agricultural landscapes. Agricultural mosaics in localized areas in southern Mexico remain surprisingly diverse in vegetation of both large and small forest remnants (Arroyo-Rodríguez et al., 2009, 2013) and in animal use of these and isolated fruiting trees and living fences (Estrada et al., 1993; Galindo-Gonzalez et al., 2000; Guevara and Laborde, 1993). Where habitat heterogeneity persists, small-seeded species and some common fruit-eating animals also persist. Heterogeneous matrices between forest remnants include living fence rows, forested habitat patches in topographies that are difficult to farm, isolated shade trees, forested ridges that preserve watersheds, multiple-use woodland patches, and mixed cropping systems (Laborde et al., 2008; Melo et al., 2013; Perfecto and Vandermeer, 2010; Toledo et al., 2003). Heterogeneous agricultural landscapes also accelerate forest regrowth if land is abandoned (Chazdon, 2014; Reis et al., 2010; Rey Benayas et al., 2008; Zahawi et al., 2013). With planning, enough heterogeneity may be conserved or re-established to allow persistence and movement of many tree and shrub species.

Maintaining heterogeneity that includes larger animal-dispersed seeds is a more vexing challenge. Many birds and mammals capable of dispersing large seeds do not tolerate intensive hunting (e.g. Bodmer et al., 1997; Effiom et al., 2013; Moran et al., 2009; Nuñez-Iturri et al., 2008; Peres and Palacios, 2007). Even if not exterminated, hunting may reduce animal species below the point at which they are effective dispersal agents.

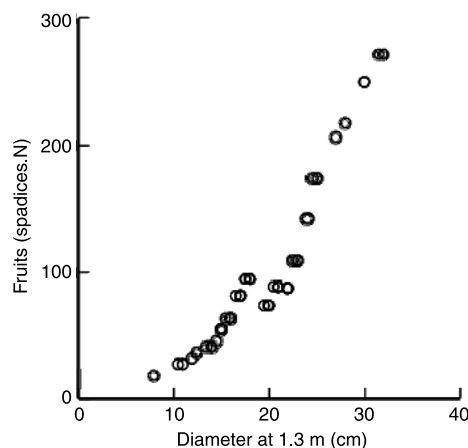


Fig. 5. Estimated fruit production of *Cecropia obtusifolia* either planted or recruited into 14 30x30 m fenced plots in cattle pasture in 2015. Diameter at breast height (dbh) of trees is used to predict individual and then total fruit production consistent with allometries reported by [Alvarez-Buylla and Martínez-Ramos \(1992\)](#) from Los Tuxtlas. Each spadix, which is what birds or mammals eat, holds thousands of seeds; annual seed production is estimated to be >1,250,000 for the largest female trees. The discontinuity at ~20 cm dbh is an adjustment of the calculation of seeds per spadix for smaller versus larger adults.

Failure on the plant side of community function in conservation or restoration also might occur. One failure would be if showy but low-preference fruits, such as *Leptonychia usambarensis* in east Africa ([Cordeiro et al., 2009](#)), are expected to be key hubs in partially conserved or restored dispersal networks. The experiment has not been done, but patches or plantings featuring such species would be expected to accumulate fewer recruits of animal-dispersed trees than similar sites with patches or plantings of trees with broadly palatable fruits. Figs and other generalist taxa with high content of soluble carbohydrates will likely be the most useful in helping maintain and attract fruit-eating animals and the seeds that they carry.

A second failure would be if focal species for restoration are dominated by taxa with short seasons or low fruit production. Conserved or restored habitat patches with fruit some of the year might draw animals and the seeds that they carry when fruits are abundant, but they will not attract or sustain local fruit-eating animals in times of scarcity or promote seed movement throughout an annual cycle. Active assistance through planting figs or other generalist fruiting trees that have long or multiple annual fruiting seasons within remnants – or planting entire stands – increases the influx of dispersal agents and the seeds that they carry (e.g. [de la Peña-Domene et al., 2014](#); [Elliott et al., 2013](#); [Howe, 1984](#)). Understanding effects of different fruiting species on tree biodiversity and disperser maintenance remains spotty. The safest route may be to plant species with multiple fruiting season per year or long fruiting seasons, and let other species accumulate as dispersal agents bring in seeds.

Inevitably, conservation and restoration proceeds with uncertainty regarding frugivore diets and consequences for dispersal in changing tree communities. Competition for space and dispersal agents within dynamic plant assemblages, unpredictable network structure with diminished numbers of possible interactions, and changes in land management and climate are all likely to influence landscape diversity. In lieu of extensive knowledge of relevant landscapes, the rational course is to acknowledge uncertainty and build taxonomic and quantitative redundancy of food resources into existing remnants, create forest islands and corridors with trees that produce food resources, and avoid expectations from literal interpretations of inter-dependence on studies from protected forests with intact floras and faunas.

8.2. When passive restoration is clearly inadequate

Across the tropics, active restoration of connectivity is becoming critical. West of the Los Tuxtlas Biosphere Reserve and east along the Gulf Coast, forest patches vanish. There and in many landscapes across the tropics, a “world without seed dispersers” is reality ([Farwig and Berens, 2012](#)). Overcoming dispersal limitation is a critical factor in maintenance of plant and animal diversity, and in restoring diversity to barren landscapes ([Elliott et al., 2013](#); [Wijdevan and Kuzee, 2000](#)). Some fallow land may be so close to extensive forests that active restoration as an end in itself is unjustified ([Holl and Aide, 2011](#)). As a means of providing connectivity for dispersal agents and the plants that they disperse, most landscapes deserve attention.

Deciding which plants and animals are most likely to preserve biodiversity by facilitating dispersal into or migrating through agricultural landscapes is important. Plant traits offer predictions about which later-successional trees will grow in early-successional habitats. For instance, in southern Veracruz, intraspecific variation in the ratio of leaf mass/leaf area (SLM) predicts up to 88% of basal growth and 64% of seedling survival of mid-story rainforest trees ([Martínez-Garza et al., 2005](#)). Where community, government, NGO or private resources are available, a “framework tree” process like that practiced in Thailand selects candidate tree species using criteria of growth rate, survival probability and fruit palatability to a variety

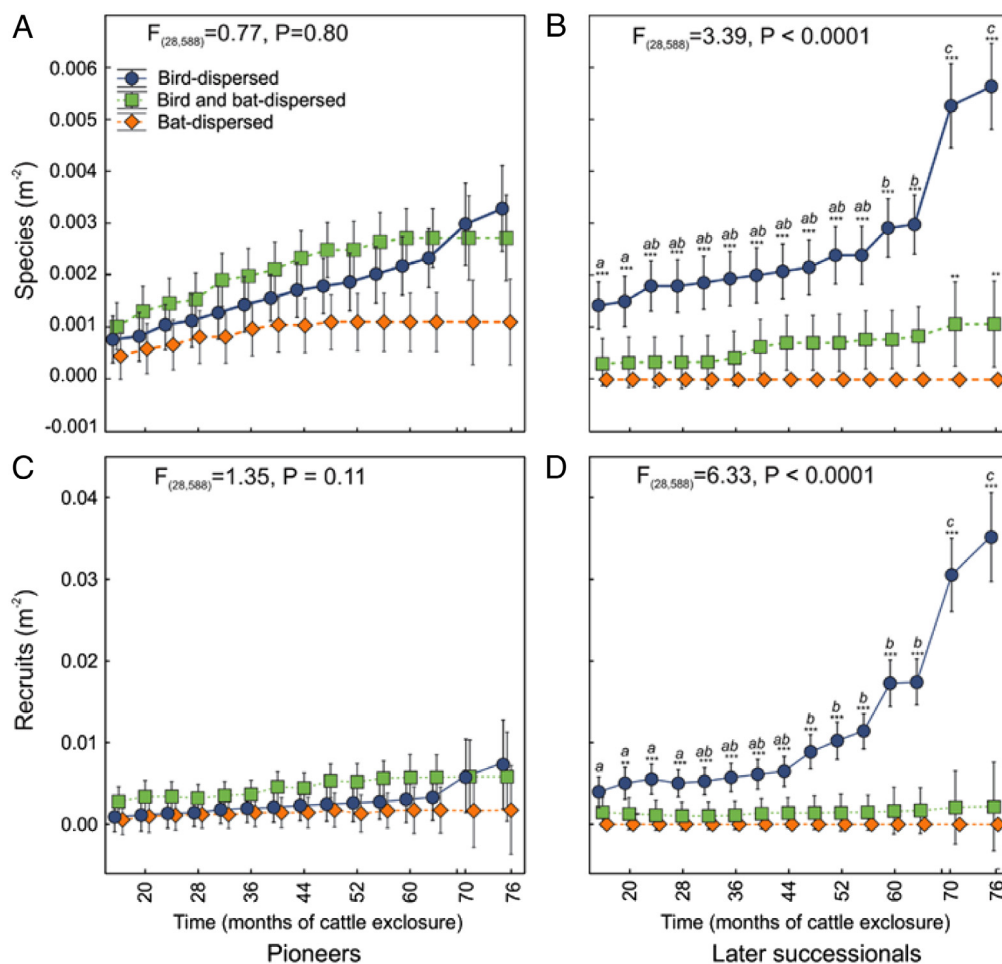


Fig. 6. Recruited species and individuals by dispersal group over time in 8 fenced 30 × 30 m plots planted with 12 species of animal-dispersed trees, 8 plots planted with wind-dispersed trees, and 8 plots fenced but without plantings to simulate natural succession. Shown are (A) pioneer species, (B) later-successional species, (C) pioneer individuals, (D) later successional individuals. Blue circles indicate primarily bird-dispersed, green squares both bird- and bat-dispersed, and rust diamonds primarily bat-dispersed species. Asterisks indicate differences between dispersal categories in the same time period. ANOVA statistics indicate disperser category by time interactions. Letters show differences for bird-dispersed later-successional trees from onetime period to the next using Bonferroni-corrected post-hoc tests ($P < 0.05$). Shown are means and 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Source: From de la Peña-Domene et al. (2014).

of animals (Corlett and Hau, 2000; Elliott et al., 2013). To meet full potential, this approach requires facilities for growing seedlings and personnel to select framework trees, raise and planting the seedlings, and monitor results. Much can be saved or restored with fewer resources.

Asymmetric properties of dispersal networks provide clues to useful approaches, including planting species with generally palatable fruits that attract a variety of dispersal agents. Elliott and colleagues (2013) recommend 20–30 species of fruiting trees. That is an excellent program, provided that initial plantings include rapidly growing trees with generalized dispersal by a variety of birds and mammals that cross inhospitable landscapes. Attention should also be paid to seedling requirements. The Los Tuxtlas experiment would be improved by establishing rapidly growing shade trees in both planting treatments. There the best would be wind-dispersed *Heliocarpus appendiculatus* (Tiliaceae; see Martínez-Garza et al., 2013), which casts even shade sufficient to suppress grasses within four years. Most other planted species cast shade too dense for seedling growth, have such open canopies that thick grasses and ferns impair tree-seedling establishment, or grow slowly. Assuming that no “perfect” planting scheme can replace historical forests or predict features of future non-analog communities (Williams and Jackson, 2007), stepping-stone plots, or segments planted with different mixed species assemblages within corridors between remnants, make a restoration program itself an experiment with treatment effects (Howe and Martínez-Garza, 2014). Multiple treatments build species and structural diversity into the planting process. A variety of patch types are likely to respond to changes in land use and climate better than any single planting scheme.

8.3. Realistic expectations

Expectations must be realistic. It is optimistic to predict that most tropical tree species will migrate across agricultural landscapes, even if stepping-stone forest patches or ribbons of forest connect restorations and remnants (Corlett and Wescott, 2013). Migrations of some tree species require centuries, not years. Meta-analyses using samples of 7–48 tropical tree species begin to sort out the importance of disturbance for effective seed dispersal (Markl et al., 2012), but it would be optimistic to predict from a few dozen species what occurs among 40,000–53,000 tropical tree species in natural landscapes (Slik et al., 2015), much less highly disturbed landscapes. Dispersal success will probably occur in descending order of seed mobility, from small (<0.1 g) wind-dispersed seeds, to small and medium-sized (<1 g) animal-dispersed seeds, to larger animal-dispersed seeds (>1 g), to large (>1 g) wind or ballistically-dispersed seeds.

Failures of unassisted migration will be severe. In southeast Asia, dominant components of forest biota are large-seeded abiotically-dispersed species in the Dipterocarpaceae that are unlikely to fall >100 m from fruiting trees (Corlett, 2009). Elsewhere, if connectivity is from stepping stones of remnant or restored forest patches or agriculturally heterogeneous landscapes of mixed crops (e.g. de la Pena et al., 2013; Perfecto and Vandermeer, 2010), large-seeded palms and other trees dispersed by rodents that shun open spaces are unlikely to move. These effects may be minimized by biodiversity-friendly landscapes in which habitat remnants are connected by riparian tree communities, second growth or tree plantations that permit understory colonization, or by protecting immediate watersheds with ribbons of forest along ridgelines (e.g. Lamb et al., 2005; Melo et al., 2013). The reality remains that many tropical trees and the biota associated with them will not migrate without human assistance. Others, with protected or managed disperser communities, will move.

8.4. Surrogates

Where native dispersal agents are ecologically extinct and re-introduction is infeasible, it may be necessary to encourage surrogate dispersal agents that coexist with people. In Africa and Asia, for instance, most species of cercopithecine monkeys disperse species of large-seeded trees in habitats where apes have been exterminated (Albert et al., 2014; Gross-Camp and Kaplan, 2011). They are not as effective as ecologically or actually extinct apes, but some coexist with agriculture and do move seeds away from fruiting trees to forest patches. Elephants are ecologically extinct in many parts of Asia, but livestock might substitute for dispersal of some of the flora. Cattle (*Bos primigenius*) and water buffalo (*Bubalus bubalus*) digest more seeds than elephants, but overall effectively disperse at least three species of large-seeded trees (*Artocarpus chaplasha*, *Careya arborea*, *Dillenia indica*) in India in regions where elephants are ecologically extinct (Sekar and Sukumar, 2013; Sekar et al., 2015). Janzen and Martin (1982) argue that livestock eat and disperse seeds of many Neotropical tree species once dispersed by now extinct mega-herbivores. Cattle and horses may be ineffective compared with more diverse or much larger mega-herbivores that once occurred in the Americas (Zaya and Howe, 2009), but they do effectively disperse some species. On a smaller scale, Pejchar (2015) reports that fruit-eating birds introduced to Hawaii now provide dispersal for some native plants, but not as well as the nearly extinct native frugivore avifauna. If the alternative is no dispersal of tropical plants, protection of, introduction of, or even strategic use of surrogate dispersal agents has potential. At present, that potential has not been thoroughly explored.

8.5. Conclusions

Caveats and qualifications aside, syndromes and networks have important roles to play. Syndromes remain the best explanation for the immense variety of form and function in fruits, and syndromes have practical uses. For instance, a inventory of literature on use of fruits by vertebrates indicate that some fruits thought to be restricted to birds and bats are not so limited, but most assignments to syndromes of species recruiting in the Los Tuxtlas experiment do fit expected syndromes (Appendix S1, Table S1 of de la Peña-Domene et al., 2014). In this case categories of dispersal agents (birds, bats, both) can be assigned to recruiting seedlings in a restoration on the basis of the species' fruits, without much more expensive, and error-prone, sampling of bird and bat behavior and seed fall throughout a 12-month year.

Basic natural history also makes networks useful. For instance, Dáttilo and colleagues (2015) distinguish effective beetle pollinators (Nitidulidae) of the abundant mid-story palm *Astrocaryum mexicanum* from ineffective pollinators of many flower-visiting taxa in the Los Tuxtlas landscape. Ineffective pollinators vary with forest-fragment size, but effective pollinators do not. Core networks of effective pollinators persist within and between forest fragments, ensuring successful seed set and genetic mixing. Likewise, Stevenson and colleagues (2015) distinguish between seed predators and seed dispersers in fruit removal by diurnal birds and mammals at 73 canopy tree species in Colombian rainforest. This study estimates fruit biomass of tree species consumed per day, and provides a “keystone index” reflecting production during times of relative fruit scarcity. Some keystone trees are productive but have few consumers (e.g. the palm *Oenocarpus batua* with 6), while others are less productive but have many (e.g. the fig *Ficus sphenophylla* with 43). Network representation of overall fruit consumption shows primates vastly more important than other dispersal agents, with two heavy-bodied species (*Ateles belzebuth*, *Lagothrix lagothricha*) far more important than others. Sampling nocturnal animals and seedling recruitment are beyond the scope of this study, but it certainly opens productive paths for conservation and restoration.

What kinds of lessons can be gleaned from reappraisal of dispersal syndromes and networks for conservation and restoration? The pieces exist for a comprehensive approach in highly disturbed landscapes. I am unaware of a study of

core dispersal agents comparable to core pollinators in the *Astrocaryum mexicanum* study (Dáttilo et al., 2015). What can one take from a cutting-edge study of community-wide frugivory in oldgrowth rainforest for restoration of fragmented habitat (Stevenson et al., 2015)? One lesson for that region, if hunting can be controlled, is that restored corridors are necessary for linking remnants rather than stepping-stone patches because many large primates do not cross inhospitable pasture or croplands. Where hunting cannot be controlled, some tree species heavily used by large primates will need assisted dispersal by people. If stepping-stone patches are used, a breakdown of fruit-crop consumption offers clues (Table 2; Stevenson et al., 2015). In the Neotropics, framework trees (*sensu* Elliott et al., 2013) would best be those attracting many dispersal agents rather than few. Generalist fruits with high concentrations of easily-digested soluble carbohydrates of rapidly-growing species, like *Cecropia*, *Coussapoa* and *Ficus*, should figure prominently. At least some of these should reflect high “keystone” indices, with fruit production in times of scarcity (Table 4 of Stevenson et al., 2015). It is difficult to streamline demographic studies, but understanding recruitment dynamics of particular species of interest (Rother et al., 2013, 2016), and of community-wide recruitment dynamics (de la Peña-Domene et al., 2013; de la Peña-Domene et al., 2014), may further refine choices.

Realistic objectives are important. The path forward will not preserve all tropical species in fragmented and degraded habitats, but intelligent management may allow persistence in place or migration of many species in the face of climate change. Protection or introduction of dispersal agents or surrogates will be necessary. Dispersal syndromes and perhaps network modules can identify generalist magnet trees of interest to many fruit-eating animals that carry seeds across agricultural landscapes.

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References

- Abu Baker, M., Brown, J.S., 2010. Islands of fear: Effects of wooded patches on habitat suitability of the striped mouse in a South African grassland. *Funct. Ecol.* 24, 1313–1322.
- Albert, A., McConkey, K., Savini, T., Huynen, M.-C., 2014. The value of disturbance-tolerant cercopithecine monkeys as seed dispersers in degraded habitats. *Biol. Cons.* 170, 300–310.
- Alvarez-Buylla, E.R., Martinez-Ramos, M., 1992. Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree—an evaluation of the climax-pioneer paradigm for tropical rain forests. *J. Ecol.* 80, 275–290.
- Arroyo-Rodríguez, V., Pineda, E., Escobar, F., Benítez-Malvido, J., 2009. Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. *Conserv. Biol.* 23, 729–739.
- Arroyo-Rodríguez, V., Rös, M., Escobar, F., Melo, F.P.L., Santos, B.A., Tabarelli, M., Chazdon, R., 2013. Plant β -diversity in fragmented rain forests: Testing floristic homogenization and differentiation hypotheses. *J. Ecol.* 101, 1449–1458.
- Augsburger, C.K., 1988. Mass allocation, moisture content, and dispersal capacity of wind-dispersed tropical diaspores. *New Phytol.* 108, 357–368.
- Bacles, C.F.E., Lowe, A.J., Ennos, R.A., 2006. Effective seed dispersal across a fragmented landscape. *Science* 311, pp. 628–628.
- Baker, H.G., Baker, I., Hodges, S.A., 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica* 30, 559–586.
- Balcomb, S.R., Chapman, C.A., 2003. Bridging the gap: Influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecol. Monogr.* 73, 625–642.
- Bascompte, J., Jordano, P., 2007. Plant–animal mutualistic networks: The architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593.
- Bascompte, J., Jordano, P., 2014. *Mutualistic Networks*. Princeton Univ. Press, Princeton, USA.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.
- Berger-Tal, O., Mukherjee, S., Kotler, B.P., Brown, J.S., 2010. Complex state-dependent games between owls and gerbils. *Ecol. Lett.* 13, 302–310.
- Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. *Science* 341, 499–503.
- Bodmer, R.E., Eisenberg, J.F., Redford, K.H., 1997. Hunting and the likelihood of extinction of Amazonian mammals. *Conserv. Biol.* 11, 460–466.
- Bonaccorso, F.J., 1979. Foraging and Reproductive Ecology in a Panamanian Bat community. In: *Bull. Florida State Museum, Biol. Sci.*, vol. 4, pp. 359–408.
- Brodie, J.F., Aslan, C.E., Rogers, H.S., Redford, K.H., Maron, J.L., Bronstein, J.L., Groves, C.R., 2014. Secondary extinctions of biodiversity. *Trends Ecol. Evol.* 29, 664–672.
- Brodie, J.H., Helmy, O.E., Brockelman, W.Y., Maron, J.L., 2009a. Functional differences within a guild of tropical mammalian frugivores. *Ecology* 90, 688–698.
- Brodie, J.H., Helmy, O.E., Brockelman, W.Y., Maron, J.L., 2009b. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecol. Appl.* 19, 854–863.
- Bronstein, J.L., 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* 9, 214–217.
- Brown, J.S., Kotler, B.P., 2004. Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* 7, 999–1014.
- Burrows, F.M., 1986. The aerial motion of seeds, fruits, spores and pollen. In: Murray, D.R. (Ed.), *Seed Dispersal*. Academic Press, Sidney, Australia, pp. 1–47.
- Campos-Arceiz, A., Traeholt, C., Jaffar, R., Santamaria, L., Corlett, R.T., 2012. Asian tapirs are no elephants when it comes to seed dispersal. *Biotropica* 44, 220–227.
- Caughley, G., 1994. *Directions in conservation biology*. J. Anim. Ecol. 63, 215–244.
- Caughlin, T.T., Ferguson, J.M., Lichstein, J.W., Zuidema, P.A., Bunyavechewin, S., Levey, D.J., 2015. Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. *Proc. R. Soc. B* 282, 20142095. <http://dx.doi.org/10.1098/rspb.2014.2095>.
- Chaves, O.M., Stoner, K.E., Arroyo-Rodríguez, V., 2012. Differences in diet between spider monkey groups living in forest fragments and continuous forest in Mexico. *Biotropica* 44, 105–113.
- Chazdon, R.L., 2014. *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. Univ. Chicago Press, Chicago.
- Chen, S.C., Moles, A.T., 2015. A mammoth mouthful? A test of the idea that larger animals ingest larger seeds. *Glob. Ecol. Biogeogr.* 24, 1269–1280.
- Cipollini, M.L., Bohs, L.A., Mink, K., Paulk, E., Böhning-Gaese, K., 2002. Secondary metabolites of ripe fleshy fruits: ecology and phylogeny in the genus *Solanum*. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, New York, pp. 111–128.

- Cipollini, M.L., Levey, D.J., 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. *Am. Nat.* 150, 346–372.
- Coates-Estrada, R., Estrada, A., 1988. Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. *J. Trop. Ecol.* 4, 157–172.
- Coates-Estrada, R., Estrada, A., Meritt, D., 1993. Foraging by parrots *Amazonia autumnalis* on fruits of *Stemmadenia donnell-smithii* Apocynaceae. in the tropical rain forests of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 9, 121–124.
- Comita, L.S., Muller-Landau, H.C., Aguilar, S., Hubbell, S.P., 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329, 330–332.
- Connell, J.H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees. In: Boer, P.J., Gradwell, G. (Eds.), *Dynamics of Populations*. PUDOC, Wageningen, The Netherlands, pp. 298–312.
- Cordeiro, N., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci. USA* 100, 14052–14056.
- Cordeiro, N.J., Ndangalasi, H.J., McEntee, J.P., Howe, H.F., 2009. Dispersal limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90, 1030–1041.
- Corlett, R.T., 2009. Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica* 41, 592–598.
- Corlett, R.T., 2011a. Impacts of warming on tropical lowland rainforests. *Trends Ecol. Evol.* 26, 606–613.
- Corlett, R.T., 2011b. How to be a frugivore (in a changing world). *Acta Oecol.* 37, 674–681.
- Corlett, R.T., Hau, B.C.H., 2000. Seed dispersal and forest restoration. In: Elliott, S., Kirby, J., Blakesley, D., Hardwick, K., Woods, K., Anusarnsunthorn, V. (Eds.), *Forest Restoration for Wildlife Conservation*. International Tropical Timber Organization and Forest Restoration Research, Chiang Mai University, Thailand, pp. 317–325.
- Corlett, R.T., Wescott, D.A., 2013. Will plant movements keep up with climate change? *Trends Ecol. Evol.* 28, 482–488.
- Córtés, M.C., Uriarte, M., 2013. Integrating frugivory and animal movement: A review of the evidence and implications for scaling seed dispersal. *Biol. Rev.* 88, 255–272.
- Cottee-Jones, H.E.W., Matthews, T.J., Bregman, T.P., Barua, M., Tamuly, J., Whittaker, R.J., 2015. Are protected areas required to maintain functional diversity in human-modified landscapes? *PLoS One* 10 (5), e0123952. <http://dx.doi.org/10.1371/journal.pone.0123952>.
- Damasceno-Junior, G.A., Semir, J., Dos Santos, F.A.M., Leitao-Filho, H.F., 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguaí, Pantanal, Brazil. *Flora* 200, 119–135.
- da Silva, F.R., Montoya, D., Furtado, R., Memmott, J., Marco, A., Pizo, M.A., Ricardo, R., Rodrigues, R.R., 2015. The restoration of tropical seed dispersal networks. *Restoration Ecol.* 23, 852–860.
- Datta, A., Rawat, G.S., 2003. Foraging patterns of sympatric hornbills during the nonbreeding season in Arunachal Pradesh, northeast India. *Biotropica* 35, 208–218.
- Dáttilo, W., Aguirre, A., Quesada, M., Dirzo, R., 2015. Tropical forest fragmentation affects floral visitors but not the structure of individual-based palm-pollinator networks. *PLoS One* 10 (3), e0121275. <http://dx.doi.org/10.1371/journal.pone.0121275>.
- de la Peña-Domene, M., Martínez-Garza, C., Howe, H.F., 2013. Early recruitment dynamics in tropical restoration. *Ecol. Appl.* 23, 1124–1134.
- de la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S., Rivas-Alonso, E., Howe, H.F., 2014. Roles of birds and bats in early tropical-forest restoration. *PLoS One* 98, e104656. <http://dx.doi.org/10.1371/journal.pone.0104656>.
- Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), 2007. *Seed Dispersal: Theory and its Application in a Changing World*. CAB International, Cambridge, Massachusetts.
- Dew, J.L., Boubli, J.P. (Eds.), 2005. *Tropical Fruits and Frugivores*. Springer, Dordrecht.
- Diaz-Martin, Z., Swamy, V., Terborgh, J., Alvarez-Loayza, P., Cornejo, F., 2014. Identifying keystone plant resources in an Amazonian forest using a long-term fruit-fall record. *J. Trop. Ecol.* 30, 291–301.
- Donatti, C.I., Guimarães, P.R., Galetti, M., Pizo, M.A., Marquitti, F.M.D., Dirzo, R., 2011. Analysis of a hyper-diverse seed dispersal network: Modularity and underlying mechanisms. *Ecol. Lett.* 14, 773–781.
- Driscoll, D.A., Banks, S.C., Barton, P.S., Ikin, K., Lentini, P., Lindenmayer, D.B., Smith, A.L., Berry, L.E., Burns, E.L., Edworthy, A., et al., 2014. The trajectory of dispersal research in conservation biology. *Systematic Review*. *PLoS One* 94, e95053. <http://dx.doi.org/10.1371/journal.pone.0095053>.
- Effiom, E.O., Nuñez-Iturri, G., Smith, H.G., Ottosson, U., Olsson, O., 2013. Bushmeat hunting changes regeneration of African rainforests. *Proc. R. Soc. B* 280, 20130246. <http://dx.doi.org/10.1098/rspb.2013.0246>.
- Elliott, S., Blakesley, D., Hardwick, K., 2013. *Restoring Tropical Forests: A Practical Guide*. Kew Publishing, Kew.
- Estrada, A., Coates-Estrada, R., Meritt Jr., D., Montiel, S., Curiel, D., 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. *Vegetatio* 107/108, 245–257.
- Estrada, A., Coates-Estrada, R., Vazquez-Yanes, C., 1984. Observations on fruiting and dispersers of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. *Biotropica* 16, 315–318.
- Estrada, A., Fleming, T.H. (Eds.), 1986. *Frugivores and Seed Dispersal*. Dr. W. Junk Publ., Dordrecht, The Netherlands.
- Farwig, N., Berens, D.G., 2012. Imagine a world without seed dispersers: A review of threats, consequences and future directions. *Basic Appl. Ecol.* 13, 109–115.
- Fleming, T.H., Estrada, A. (Eds.), 1993. *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects*. Kluwer Academic Publ., Dordrecht, The Netherlands.
- Fleming, T.H., Kress, W.J., 2013. *The Ornaments of Life: Coevolution and Conservation in the Tropics*. University of Chicago Press, Chicago.
- Forget, P.-M., Jordano, P., Lambert, J.E., Böhning-Gaese, K., Traveset, A., Wright, S.J., 2011. Frugivores and seed dispersal (1985–2010); the 'seeds' dispersed, established and matured. *Acta Oecol.* 37, 517–520.
- Forget, P.-M., Milleron, T., Freer, R., Henry, O., Dubost, G., 2000. Effects of dispersal pattern and mammalian herbivores on seedling recruitment for *Virola michelii* (Myristicaceae) in French Guiana. *Biotropica* 32, 452–462.
- Foster, M.S., 2007. The potential of fruit trees to enhance converted habitats for migrating birds in southern Mexico. *Bird Conserv. Int.* 17, 45–61.
- Foster, M.S., 2008. Potential effects of arboreal and terrestrial avian dispersers on seed dormancy, seed germination and seedling establishment in *Ormosia* (Papilionoideae) species in Peru. *J. Trop. Ecol.* 24, 619–627.
- Foster, M.S., 2014. Can fruit pulp meet the calcium needs of tropical frugivorous passerines during reproduction? *J. Trop. Ecol.* 30, 79–88.
- Foster, M.S., Delay, L.S., 1998. Dispersal of mimetic seeds of three species of *Ormosia* (Leguminosae). *J. Trop. Ecol.* 14, 389–411.
- Fricke, E.C., Tewksbury, J., Rogers, H.S., 2014. Multiple natural enemies cause distance-dependent mortality at the seed-to-seedling transition. *Ecol. Lett.* 17, 593–598.
- Galetti, M., 2002. Seed dispersal of mimetic fruits: Parasitism, mutualism, aposematism or exaptation? In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI, New York, NY, pp. 177–191.
- Galetti, M., Laps, R., Pizo, M.A., 2000. Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica* 32, 842–850.
- Galindo-Gonzalez, J., Guevara, S., Sosa, V.J., 2000. Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conserv. Biol.* 14, 1693–1703.
- Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., et al., 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65, 324–337.
- Gosper, C.R., Vivian-Smith, G., 2010. Fruit traits of vertebrate-dispersed alien plants: smaller seeds and more pulp sugar than indigenous species. *Biol. Invasions* 12, 2153–2163.
- Gross-Camp, N.D., Kaplin, B.A., 2011. Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecol.* 37, 578–586.
- Guevara, S., Laborde, J., 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* 107/108, 319–338.

- Guimarães Jr., P.R., Galetti, M., Jordano, P., 2008. Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLoS One* 3 (3), e1745. <http://dx.doi.org/10.1371/journal.pone.0001745>.
- Hardesty, B.D., Hubbell, S.P., Bermingham, E., 2006. Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecol. Lett.* 9, 516–525.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A., Herre, E.A., 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404, 493–495.
- Hawes, J.E., Peres, C.A., 2014. Ecological correlates of trophic status and frugivory in neotropical primates. *Oikos* 123, 365–377.
- Hernández-Ruedas, M.A., Arroyo-Rodríguez, V., Meave, J.A., Martínez-Ramos, M., Ibarra-Manríquez, G., Martínez, E.M., Jamangapé, G., Melo, F.P.L., Santos, B.A., 2014. Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS One* 9, e9893.
- 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., 1985. Determinants of plant-animal coevolution: The case of mutualistic dispersal of seeds by vertebrates. *Oikos* 44, 132–141.
- Herrera, C.M., 1987. Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. *Ecol. Monogr.* 57, 305–331.
- Herrera, C.M., 2002. Seed dispersal by vertebrates. In: Herrera, C.M., Pellmyr, O. (Eds.), *Plant-Animal Interactions: An Evolutionary Approach*. Blackwell, Science, New York, pp. 185–208.
- Holbrook, K.M., Loiselle, B.A., 2007. Using toucan-generated dispersal models to estimate seed dispersal in Amazonian Ecuador. In: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), *Seed Dispersal: Theory and its Application in a Changing World*. CAB International, Cambridge, Massachusetts, pp. 300–321.
- Holbrook, K.M., Smith, T.B., Hardesty, B.D., 2002. Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25, 745–749.
- Holl, K.D., Aide, T.M., 2011. When and where to actively restore ecosystems? *Forest Ecol. Manag.* 261, 1558–1563.
- Howe, H.F., 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58, 539–550.
- Howe, H.F., 1979. Fear and frugivory. *Am. Nat.* 114, 925–931.
- Howe, H.F., 1980. Monkey dispersal and waste of a Neotropical fruit. *Ecology* 61, 944–959.
- Howe, H.F., 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. *Auk* 98, 88–98.
- Howe, H.F., 1984. Implications of seed dispersal by animals for management of tropical reserves. *Biol. Cons.* 30, 261–281.
- Howe, H.F., 1993. Annual variation in a neotropical seed-dispersal system. *Vegetatio* 107/108, 149–162.
- Howe, H.F., 2014. Diversity storage: Implications for conservation and restoration. *Glob. Ecol. Conserv.* 2, 349–358. <http://dx.doi.org/10.1016/j.gecco.2014.10.004>.
- Howe, H.F., De Steven, D., 1979. Fruit production, migrant bird visitation, and seed dispersal of *Guarea glabra* in Panama. *Oecologia* 39, 185–196.
- Howe, H.F., Martínez-Garza, C., 2014. Restoration as experiment. *Bot. Sci.* 92, 1–10.
- Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. *Bioscience* 54, 651–660.
- Howe, H.F., Schupp, E., Westley, L.C., 1985. Early consequences of seed dispersal in a neotropical tree (*Virola surinamensis*). *Ecology* 66, 781–791.
- Howe, H.F., Smallwood, J., 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228.
- Howe, H.F., Vande Kerckhove, G.A., 1979. Fecundity and dispersal of a tropical tree. *Ecology* 60, 180–189.
- Howe, H.F., Vande Kerckhove, G.A., 1980. Nutmeg dispersal by tropical birds. *Science* 210, 925–927.
- Hubbell, S.P., 2013. Tropical rain forest conservation and the twin challenges of diversity and rarity. *Ecol. Evol.* 3, 3263–3274.
- Izhaki, I., 2002. The role of fruit traits in determining fruit removal in East Mediterranean ecosystems. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, New York, pp. 161–175.
- Izhaki, I., Safriel, U.N., 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54, 23–32.
- Jansen, P.A., Hirsch, B.T., Emsens, W.-J., Zamora-Gutierrez, V., Wikelski, M., Kays, R., 2012. Thieving rodents as substitute dispersers of megafaunal seeds. *Proc. Natl. Acad. Sci. USA* 109, 12610–12615.
- Janson, C.H., 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219, 187–189.
- Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528.
- Janzen, D.H., Martin, P., 1982. Neotropical anachronisms: What the gomphotheres ate. *Science* 215, 19–27.
- Johnson, D.L., Bourg, N.A., Howe, R., McShea, W.J., Wolf, A., Clay, K., 2014. Conspecific negative density-dependent mortality and the structure of temperate forests. *Ecology* 95, 2493–2503.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Jordano, P., 1995. Angiosperm fleshy fruits and seed dispersers: A comparative analysis of adaptation and constraints in plant-animal interactions. *Am. Nat.* 145, 163–191.
- Jordano, P., Garcia, C., Godoy, J.A., García-Castano, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. USA* 104, 3278–3282.
- Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecol. Monogr.* 70, 591–615.
- Jorge, M.L.S.P., Howe, H.F., 2009. Can forest fragmentation disrupt a conditional mutualism? A case from Central Amazon. *Oecologia* 161, 709–718.
- Kalko, E.K.V., Herre, E.A., Handley Jr., C.O., 1996. Relation of fig fruit characteristics to fruit-eating bats in the new and old world tropics. *J. Biogeogr.* 23, 565–576.
- Karasov, W.H., Levey, D.J., 1990. Digestive trade-offs and adaptations of frugivorous birds. *Physiol. Zool.* 63, 1248–1270.
- Kays, R., Jansen, P.A., Knecht, M.E.H., Vohwinkel, R., Wikelski, M., 2011. The effect of feeding time on dispersal of *Virola* seeds by toucans determined from GPS tracking and accelerometers. *Acta Oecol.* 37, 625–631.
- Kinnaird, M.F., O'Brien, T.G., 2007. *The Ecology and Conservation of Asian Hornbills: Farmers of the Forest*. Univ. Chicago Press, Chicago, USA.
- Kitamura, S., 2011. Frugivory and seed dispersal by hornbills (Bucerotidae) in tropical forests. *Acta Oecol.* 37, 531–541.
- Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., Noma, N., 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133, 559–572.
- Kitamura, S., Yumoto, T., Poonswad, P., Wohandee, P., 2007. Frugivory and seed dispersal by Asian elephants, *Elephas maximus*, in a moist evergreen forest of Thailand. *J. Trop. Ecol.* 23, 373–376.
- Klinger, R., Rejmánek, M., 2010. A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia* 162, 951–963.
- Kramer, A.T., Ison, J., Ashley, M., Howe, H.F., 2008. The paradox of forest fragmentation genetics. *Conserv. Biol.* 22, 878–885.
- Laborde, J., Guevara, S., Sanchez-Rios, G., 2008. Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. *Écoscience* 15, 6–16.
- Lamb, D., Erskine, P.D., Parrotta, J., 2005. Restoration of degraded tropical forest landscapes. *Science* 310, 1628–1632.
- Latham, R.E., Ricklefs, R.E., 1993. Continental comparisons of temperate-zone tree species diversity. In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 294–314.
- Lawton, J.H., 1999. Are there general laws in ecology? *Oikos* 84, 177–192.
- Levey, D.J., Cipollini, M.L., 1998. A glycoalkaloid in ripe fruit deters consumption by Cedar Waxwings. *Auk* 115, 359–367.
- Levey, D.J., Grajal, A., 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. *Am. Nat.* 138, 171–189.
- Levey, D.J., Martinez del Rio, C., 2001. It takes guts (and more) to eat fruit: Lessons from avian nutritional ecology. *Auk* 118, 819–831.
- Levey, D.J., Silva, W.R., Galetti, M. (Eds.), 2002. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, New York.
- Levey, D.J., Tewksbury, J.J., Cipollini, M.L., Carlo, T.A., 2006. A field test of the directed deterrence hypothesis in two species of wild chili. *Oecologia* 50, 61–68.

- Levey, D.J., Tewksbury, J.J., Izhaki, E., Tsahar, E., Haak, D.C., 2007. Evolutionary ecology of secondary compounds in ripe fruits: Case studies with capsaicin and emodin. In: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), *Seed Dispersal: Theory and its Application in a Changing World*. CAB International, Cambridge, Massachusetts, pp. 37–58.
- Loiselle, B.A., Blake, J.G., 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, New York, pp. 397–406.
- Lomáscolo, S.B., Speranza, P., Kimball, R.T., 2008. Correlated evolution of fig size and color supports the dispersal syndromes hypothesis. *Oecologia* 156, 783–796.
- Manasse, R.S., Howe, H.F., 1983. Competition for dispersal agents among tropical trees Influences of neighbors. *Oecologia* 59, 185–190.
- Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I., Bever, J.D., 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* 466, 752–755.
- Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Böhning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.* 26, 1072–1081.
- Maron, J.L., Baer, K.C., Angert, A.L., 2014. Disentangling the drivers of context-dependent plant–animal interactions. *J. Ecol.* 102, 1485–1496.
- Martin, T.E., 1985. Resource selection by tropical frugivorous birds: Integrating multiple interactions. *Oecologia* 66, 563–573.
- Martin, L.J., Blosssey, B., Ellis, E., 2012. Mapping where ecologists work: Biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.* 10, 195–201.
- Martínez del Río, C., Karasov, W.H., Levey, D.J., 1989. Physiological basis and ecological consequences of sugar preferences in cedar waxwings. *Auk* 106, 64–71.
- Martínez del Río, C., Stevens, B.R., 1989. Physiological constraint on feeding behavior: Intestinal membrane disaccharidases of the starling. *Science* 243, 794–796.
- Martínez-Garza, C., Bongers, F., Poorter, L., 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecol. Manag.* 303, 35–45.
- Martínez-Garza, C., Howe, H.F., 2003. Restoring tropical diversity: Beating the time tax on species loss. *J. Appl. Ecol.* 40, 423–429.
- Martínez-Garza, C., Peña, V., Ricker, M., Campos, A., Howe, H.F., 2005. Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional mid-canopy trees in early-successional environments. *Forest Ecol. Manag.* 217, 365–379.
- Martínez-Ramos, M., 1985. Claros, ciclos vitales de los arboles tropicales y regeneración natural de las selvas altas perennifolias. In: Gómez-Pompa, A., Del-Amo, S. (Eds.), *Investigaciones sobre la regeneración de selvas altas en Veracruz, México*. pp. 191–240. Ciudad México, Alhambra Mexicana S.A. de C.V.
- McConkey, K.R., Brockelman, W.Y., 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. *Ecology* 92, 1492–1502.
- McConkey, K.R., Drake, D.R., 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87, 271–276.
- McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., Santamaría, L., 2012. Seed dispersal in changing landscapes. *Biol. Cons.* 146, 1–13.
- McDiarmid, R.W., Ricklefs, R.E., Foster, M.S., 1977. Dispersal of *Stemmadenia donnell-smithii* Apocynaceae by birds. *Biotropica* 9, 9–25.
- McKey, D., 1975. The ecology of coevolved seed dispersal systems. In: Gilbert, L.E., Raven, P.H. (Eds.), *Co-evolution of Animals and Plants*. University of Texas Press, Austin, pp. 159–191.
- Medellín, R.A., Gaona, O., 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* 31, 478–485.
- Mello, M.A.R., Marquitti, F.M.D., Guimarães Jr., P.R., Kalko, E.K.V., Jordano, P., de Aguiar, M.A.M., 2011. The missing part of seed dispersal networks: Structure and robustness of bat–fruit interactions. *PLoS One* 62, e17395. <http://dx.doi.org/10.1371/journal.pone.0017395>.
- Melo, F.P.L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol. Evol.* 28, 462–468.
- Mesquita, R.C.G., Ickes, K., Ganade, G., Williamson, G.B., 2001. Alternative successional pathways in the Amazon Basin. *J. Ecol.* 89, 528–537.
- Minteer, B.A., Collins, J.P., 2010. Move it or lose it? The ecological ethics of relocating species under climate change. *Ecol. Appl.* 20, 1801–1804.
- Moran, C., Catterall, C.P., 2014. Responses of seed-dispersing birds to amount of rainforest in the landscape around fragments. *Conserv. Biol.* 28, 551–560.
- Moran, C., Catterall, C.P., Green, R.J., Olsen, M.F., 2004. Functional variation among frugivorous birds: Implications for rainforest seed dispersal in a fragmented subtropical landscape. *Oecologia* 141, 584–595.
- Moran, C., Catterall, C.P., Kanowski, J., 2009. Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biol. Cons.* 142, 541–552.
- Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R., Hubbell, S.P., 2008. Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* 96, 653–667.
- Murray, J. (Ed.), 1986. *Seed Dispersal*. Academic Press, Sidney, Australia.
- Murray, K.G., Russell, S., Picone, C.M., Winnett-Murray, K., Sherwood, W., Kuhlmann, M.L., 1994. Fruit laxatives and seed passage rates in frugivores: Consequences for plant reproductive success. *Ecology* 75, 989–994.
- Muscarella, R., Fleming, T.H., 2007. The role of frugivorous bats in tropical forest succession. *Biol. Rev.* 82, 573–590.
- Naniwadekar, R., Shukla, U., Isvaran, K., Datta, A., 2015. Reduced hornbill abundance associated with low seed arrival and altered recruitment in a hunted and logged tropical forest. *PLoS One* 10 (3), e0120062. <http://dx.doi.org/10.1371/journal.pone.0120062>.
- Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., et al., 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. *Proc. Natl. Acad. Sci. USA* 112, 8013–8018.
- Núñez-Iturri, G., Olsson, O., Howe, H.F., 2008. Hunting reduces recruitment of primate–Dispersed trees in Amazonian Peru. *Biol. Cons.* 141, 1536–1546.
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *Proc. Natl. Acad. Sci. USA* 104, 19891–19896.
- Owen-Smith, N., 1987. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13, 351–362.
- Parrotta, J.A., Turnbull, J.W., Jones, N., 1997. Catalyzing native forest regeneration on degraded tropical lands. *For. Ecol. Manag.* 99, 1–7.
- Pejchar, L., 2015. Introduced birds incompletely replace seed dispersal by a native frugivore. *AoB PLANTS* 7, plv072.
- Peres, C.A., Palacios, E., 2007. Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica* 39, 304–315.
- Perfecto, I., Vandermeer, J., 2010. The agroecological matrix as alternative to the landsparing/agriculture intensification model. *Proc. Natl. Acad. Sci. USA* 107, 5786–5791.
- Pesendorfer, M.B., Sillett, T.S., Koenig, W.D., Morrison, S.A., 2016. Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. *Condor: Ornithol. Appl.* 118, 215–237.
- Peters, H., 2003. Neighbour-regulated mortality: The influence of positive and negative density-dependence on tree populations in species-rich tropical forests. *Ecol. Lett.* 6, 757–765.
- Pires, M.M., Galetti, M., Donatti, C.I., Pizo, M.A., Dirzo, R., Guimarães Jr., P.R., 2014. Reconstructing past ecological networks: The reconfiguration of seed-dispersal interactions after megafaunal extinction. *Oecologia* 175, 1247–1256.
- Prado, F.A., 2013. Feeding behavior, bird visitation and seed dispersal in *Guarea macrophylla* and *Trichilia quadrijuga* (Meliaceae). *Ornitol. Neotrop.* 24, 459–468.
- Prance, G.T., Schaller, G.B., 1982. Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia* 34, 228–251.
- Reid, J.L., Holl, K.D., 2013. Arrival ≠ survival. *Restoration Ecol.* 21, 153–155.
- Reid, J.L., Mendenhall, C.D., Rosales, A., Zahawi, R.A., Holl, K.D., 2014. Landscape context mediates avian habitat choice in tropical forest restoration. *PLoS One* 93, e90573.
- Reis, A., Bechara, F.C., Tres, D.R., 2010. Nucleation in tropical ecological restoration. *Sci. Agricola* 67, 244–250.
- Renner, S.S., 2006. Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In: Waser, N.M., Ollerton, J. (Eds.), *Plant–Pollinator Interactions* (eds. N.M. Waser & J. Ollerton). Univ. Chicago Press, Chicago, pp. 123–144.

- Restrepo, C., Sargent, S., Levey, D.J., Watson, D.M., 2002. The role of vertebrates in the diversification of New World mistletoes. In: Levey, D.J., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI, New York, N.Y., pp. 83–98.
- Rey Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front. Ecol. Environ.* 6, 329–336.
- Ridley, H.N., 1930. *The Dispersal of Plants Throughout the World*. Ashford, Reeve.
- Rother, D.C., Jordano, P., Rodrigues, R.R., Pizo, M.A., 2013. Demographic bottlenecks in tropical plant regeneration: A comparative analysis of causal influences. *Perspect. Plant Ecol. Evol. Syst.* 15, 86–96.
- Rother, D.C., Pizo, M.A., Jordano, P., 2016. Variation in seed dispersal effectiveness: The redundancy of consequences in diversified tropical frugivore assemblages. *Oikos* 125, 336–342.
- Rother, D.C., Pizo, M.A., Siqueira, T., Rodrigues, R.R., Pedro Jordano, P., 2015. Community-wide spatial and temporal discordances of seed-seedling shadows in a tropical rainforest. *PLoS One* 10 (4), e0123346.
- Russo, S., 2003. Response of dispersal agents to tree and fruit traits in *Virola calophylla* Myristicaceae: Implications for selection. *Oecologia* 136, 80–87.
- Russo, S., Portnoy, S., Augspurger, C.K., 2006. Incorporating animal behavior into seed dispersal models: Implications for seed shadows. *Ecology* 87, 3160–3174.
- Schaefer, H.M., Schmidt, V., Bairlein, F., 2003a. Discrimination abilities for nutrients: Which difference matters for choosy birds and why? *Anim. Behav.* 65, 531–541.
- Schaefer, H.M., Schmidt, V., Winkler, H., 2003b. Testing the defence trade-off hypothesis: How contents of nutrients and secondary compounds affect fruit removal. *Oikos* 102, 318–328.
- Schoener, T.W., 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2, 369–404.
- Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108, 15–29.
- Schupp, E.W., Howe, H.F., Augspurger, C.K., Levey, D.J., 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70, 562–564.
- Schupp, E.W., Jordano, P., 2011. The full path of Janzen–Connell effects: Genetic tracking of seeds to adult plant recruitment. *Mol. Ecol.* 20, 3953–3955.
- Schupp, E.W., Jordano, P., Gomez, J.M., 2010. Seed dispersal effectiveness revisited: A conceptual review. *New Phytol.* 188, 333–353.
- Sekar, N., Lee, C.-L., Sukumar, R., 2015. In the elephant's seed shadow: The prospects of domestic bovines as replacement dispersers of three tropical Asian trees. *Ecology* 96, 2093–2105.
- Sekar, N., Sukumar, R., 2013. Waiting for Gajah: An elephant mutualist's contingency plan for an endangered megafaunal disperser. *J. Ecol.* 101, 1379–1388.
- Seltzer, C.E., Ndangalasi, H.J., Cordeiro, N.J., 2013. Seed dispersal in the dark: Shedding light on the role of fruit bats in Africa. *Biotropica* 45, 450–456.
- Sethi, P., Howe, H.F., 2009. Poor recruitment of hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. *Conserv. Biol.* 23, 710–718.
- Sethi, P., Howe, H.F., 2012. Seed dispersal of six hornbill-forage trees in a semi-evergreen forest of the Indian Eastern Himalaya. *J. Trop. Ecol.* 28, 531–541.
- Sezen, U.U., Chazdon, R.L., Holsinger, K.E., 2009. Proximity is not a proxy for parentage in an animal-dispersed Neotropical canopy palm. *Proc. R. Soc. B* 276, 2037–2044.
- Shanahan, M., So, S., Compton, S.G., Corlett, R., 2001. Fig-eating by vertebrate frugivores: A global review. *Biol. Rev.* 76, 529–572.
- Slik, J.W.F., Arroyo-Rodríguez, V., Aiba, S.-I., Alvarez-Loayza, P.F., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., van den Berg, E., et al., 2015. An estimate of the number of tropical tree species. *Proc. Natl. Acad. Sci. USA* 112, 7472–7477.
- Slocum, M.G., 2001. How tree species differ as recruitment foci in a tropical pasture. *Ecology* 82, 2547–2559.
- Sorensen, A.E., 1986. Seed dispersal by adhesion. *Annu. Rev. Ecol. Syst.* 17, 443–463.
- Stevenson, P.R., 2005. Potential keystone plant species for the frugivore community at Tinigua Park, Colombia. In: Dew, J.L., Boubli, J.P. (Eds.), *Tropical Fruits and Frugivores: The Search for Strong Interactors*. Springer, The Netherlands, pp. 37–57.
- Stevenson, P.R., 2011. Pulp–seed attachment is a dominant variable explaining legitimate seed dispersal: A case study on woolly monkeys. *Oecologia* 166, 693–701.
- Stevenson, P.R., Link, A., González-Caro, S., Torres-Jiménez, M.F., 2015. Frugivory in canopy plants in a western Amazonian forest: Dispersal systems, phylogenetic ensembles and keystone plants. *PLoS One* 10, e0140751.
- Terborgh, J.T., 1986. In: Estrada, A., Fleming, T.H. (Eds.), *Community Aspects of Frugivory in Tropical Forests*. Frugivores and Seed Dispersal. Dr. W. Junk Publishers, Dordrecht, pp. 371–384.
- Terborgh, J.T., 2013. Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biol. Cons.* 163, 7–12.
- Terborgh, J.T., Nuñez-Iturri, G., Pitman, N.C.A., Valverde, F.H.C., Alvarez, P., Swamy, V., Pringle, E.G., Paine, C.E.T., 2008. Tree recruitment in an empty forest. *Ecology* 89, 1757–1768.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Carolina, V., Castilho, C.V., Magnusson, W.E., et al., 2013. Hyperdominance in the Amazonian tree flora. *Science* 342, <http://dx.doi.org/10.1126/science.1243092>.
- Tewksbury, J.J., Reagan, K.M., Machnicki, N.J., Carlo, T.A., Haak, D.C., Calderón Peñaloza, A.L., Levey, D.J., 2008. Evolutionary ecology of pungency in wild chilies. *Proc. Natl. Acad. Sci. USA* 105, 11808–11811.
- Theimer, T.C., 2005. Rodent scatterhoarders as conditional mutualists. In: Forget, P.-M., Lambert, J.E., Hulme, P.E., Vander Wall, S.B. (Eds.), *Seed Fate*. CAB International, Wallingford, pp. 283–295.
- Thompson, J.N., Willson, M.F., 1979. Evolution of temperate fruit/bird interactions: Phenological strategies. *Evolution* 33, 973–982.
- Toledo, V.M., Ortiz-Espejel, B., Cortés, L., Moguel, P., Ordoñez, M.D.J., 2003. The multiple use of tropical forests by indigenous peoples in Mexico: a case of adaptive management. *Conserv. Ecol.* 7 (3), 9. [online] URL: <http://www.consecol.org/vol7/iss3/art9>.
- Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspect. Plant Ecol. Evol. Syst.* 1/2, 151–190.
- Traveset, A., Robertson, A.W., Rodríguez-Pérez, J., 2007. A review on the role of endozoochory on seed germination. In: Dennis, A.J., Schupp, E.W., Green, R.J., Westcott, D.A. (Eds.), *Seed Dispersal: Theory and its Application in a Changing World*. CAB International, Cambridge, Massachusetts, pp. 78–103.
- Turner, I.M., Corlett, R., 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. *Trends Ecol. Evol.* 11, 330–333.
- Tylianakis, J.W., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Cons.* 143, 2270–2279.
- Valiente-Banuet, A., Aizen, M., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, M.B., Jordano, P., et al., 2015. Beyond species loss: The extinction of ecological interactions in a changing world. *Funct. Ecol.* 29, 299–307.
- Van der Pijl, L., 1982. *Principles of Dispersal in Higher Plants*, third ed. Springer-Verlag, Berlin.
- Vander Wall, S.B., 2010. *Food Hoarding in Animals*. Univ. Chicago Press, Chicago.
- Vanthomme, H., Bellé, B., Forget, P.M., 2010. Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. *Biotropica* 42, 672–679.
- Wang, B.C., Smith, T.B., 2002. Closing the seed dispersal loop. *Trends Ecol. Evol.* 17, 379–385.
- Wenny, D.G., 1999. Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *J. Trop. Ecol.* 15, 481–496.
- Wenny, D.G., Devault, T.L., Johnson, M.D., Kelly, D., Sekercioglu, C.H., Tomback, D.F., Whelan, C.F., 2011. The need to quantify ecosystem services provided by birds. *Auk* 128, 1–14.
- Wenny, D.G., Levey, D.J., 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl. Acad. Sci.* 95, 6204–6207.
- Wheelwright, N.T., 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66, 808–818.
- Wheelwright, N.T., Haber, W.A., Murray, K.G., Guindon, C., 1984. Tropical fruit-eating birds and their food plants: A survey of a Costa Rican lower montane forest. *Biotropica* 16, 173–192.
- Wheelwright, N.T., Janson, C.H., 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126, 777–799.
- Whelan, C.J., Schmidt, K.A., Steele, B.B., Quinn, W.J., Dilger, S., 1998. Are bird-consumed fruits complementary resources? *Oikos* 83, 195–205.
- Wijdeven, S.M.J., Kuzeev, M.E., 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecol.* 8, 414–424.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5, 475–482.
- Willson, M.F., Whelan, C.J., 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus Drummondii*. *Ecol. Monogr.* 63, 151–172.
- Witmer, M.C., 2001. Nutritional interactions and fruit removal: Cedar waxwing consumption of *Viburnum opulus* fruit in Spring. *Ecology* 82, 3120–3130.

- Witmer, M.C., Van Soest, P.J., 1998. [Contrasting digestive strategies of fruit-eating birds](#). *Funct. Ecol.* 12, 728–741.
- Wright, S.J., Carrasco, C., Calderón, O., Paton, S., 1999. [The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest](#). *Ecology* 80, 1632–1647.
- Wright, S.J., Muller-Landau, H.C., Calderon, O., Hernandez, A., 2005. [Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest](#). *Ecology* 86, 848–860.
- Wunderle Jr., J.M., 1997. [The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands](#). *For. Ecol. Manag.* 99, 223–235.
- Zahawi, R.A., Holl, K.D., Cole, R.J., Reid, J.L., 2013. [Testing applied nucleation as a strategy to facilitate tropical forest recovery](#). *J. Appl. Ecol.* 50, 88–96.
- Zaya, D., Howe, H.F., 2009. [The anomalous Kentucky Coffee Tree: Megafaunal fruit sinking to extinction?](#) *Oecologia* 161, 221–226.