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Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal

Marina Corrêa Côrtes* and María Uriarte

Department of Ecology, Evolution and Environmental Biology, Columbia University in the City of New York, 1200 Amsterdam Avenue, New York, New York 10027, USA

ABSTRACT

General principles about the consequences of seed dispersal by animals for the structure and dynamics of plant populations and communities remain elusive. This is in part because seed deposition patterns emerge from interactions between frugivore behaviour and the distribution of food resources, both of which can vary over space and time. Here we advocate a frugivore-centred, process-based, synthetic approach to seed dispersal research that integrates seed dispersal ecology and animal movement across multiple spatio-temporal scales. To guide this synthesis, we survey existing literature using paradigms from seed dispersal and animal movement. Specifically, studies are discussed with respect to five criteria: selection of focal organisms (animal or plant); measurement of animal movement; characterization of seed shadow; animal, plant and environmental factors included in the study; and scales of the study. Most studies focused on either frugivores or plants and characterized seed shadows directly by combining gut retention time with animal movement data or indirectly by conducting maternity analysis of seeds. Although organismal traits and environmental factors were often measured, they were seldom used to characterize seed shadows. Multi-scale analyses were rare, with seed shadows mostly characterized at fine spatial scales, over single fruiting seasons, and for individual dispersers. Novel animal- and seed-tracking technologies, remote environmental monitoring tools, and advances in analytical methods can enable effective implementation of a hierarchical mechanistic approach to the study of seed dispersal. This kind of mechanistic approach will provide novel insights regarding the complex interplay between the factors that modulate animal behaviour and subsequently influence seed dispersal patterns across spatial and temporal scales.

Key words: animal behaviour, animal-plant interaction, foraging behaviour, gut retention time, intrinsic traits, maternity analysis, resource selection, scale, seed shadow, tracking technology.

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* Address for correspondence Tel: (917) 749 2090; Fax: (212) 854–8188; E-mail: mcc2149@columbia.edu.

I. INTRODUCTION

Seed dispersal is a crucial component of plant population dynamics with consequences for colonization of new habitats, spatial structure and maintenance of diversity (Schupp, Milleron & Russo, 2002; Wang & Smith, 2002; Trakhtenbrot *et al.*, 2005; Bascompte & Jordano, 2006). Twenty five to 80% of temperate plant species and 40–90% of tropical rainforest woody species depend on frugivores for seed dispersal (Howe & Smallwood, 1982; Jordano, 2000). Despite the critical role frugivores play in the organization of plant communities, a mechanistic understanding of the principles affecting animal dispersers and their consequences for the spatial and genetic organization of plant populations and communities remain elusive. Studies of seed dispersal have historically focused on individual components of the seed dispersal loop (Wang & Smith, 2002), with numerous comparisons of seed dispersal patterns among units at the same scale (e.g. between habitats or dispersers). However, only a handful of these provide a comprehensive understanding of how seed dispersal 'plays out' across spatial (García, Obeso & Martínez, 2005; Carlo & Morales, 2008; García, Zamora & Amico, 2011) or temporal (Prasad & Sukumar, 2010) scales. Scaling seed dispersal is especially important given the rapid changes natural systems are currently facing. Deforestation and forest fragmentation, selective logging and defaunation modify plant-animal interactions with direct implications for the conservation and regeneration of natural habitats (da Silva & Tabarelli, 2000; Galetti *et al.*, 2006; Cordeiro *et al.*, 2009).

Two key questions are relevant to all studies of seed dispersal by frugivores (Jordano, 2007): (*i*) which frugivore species (or individuals) contribute seeds, and to which locations, (*ii*) which source plants contribute seeds, and to which locations? Together, these two processes generate the seed shadow, that is, the location where seeds from single plants are deposited (Nathan & Muller-Landau, 2000). Our understanding of the processes generating seed shadows is primarily limited by the difficulties involved in tracking seeds back to their source and in teasing apart the relative contributions of different dispersal agents to the spatial distribution of seeds. By using diverse methods, however, we can now begin to characterize some of the components that determine seed shadows, such as the distance and density from source tree, the density of dispersed seeds arriving at the target site, and less commonly, the number and extent of overlapping seed shadows (Jordano, 2007; García & Grivet, 2011).

The approaches used to characterize seed shadows can be divided into two broad classes: backward and forward tracking. Backward tracking, or source-based approaches (Jordano, 2007), examine the spatial patterns of seed distribution with respect to distance from source plants (Muller-Landau *et al.*, 2008) and then trace the movement of the seed back to its putative source. Backward approaches have commonly relied on inverse modelling, a statistical method in which the likelihood of obtaining the observed spatial patterns of seed dispersal or seedling establishment is calculated, based on a probability density function, linking the location of seed deposition with respect to the source (i.e. dispersal kernel) (Ribbens, Silander & Pacala, 1994; Clark *et al.*, 1999; Nathan & Muller-Landau, 2000; Bullock, Shea & Skarpaas, 2006). These approaches have some limitations. For instance, commonly used kernels generally capture dispersal of wind-dispersed species quite well, but fail to do so for animal-dispersed species (Hardesty, Hubbell & Bermingham, 2006; Russo, Portnoy & Augspurger, 2006; Holbrook & Loiselle, 2007; Moran & Clark, 2011). More recently, backward approaches have included the use of isotopes to track the seeds of ^{15}N-enriched maternal plants (Carlo, Tewksbury & Martínez del Río, 2009) and the application of molecular markers to assign more accurately the offspring to its maternal source (Godoy & Jordano, 2001; García & Grivet, 2011). Ultimately, molecular tools represent the only direct way to characterize the contribution of individual seed sources to a particular patch (e.g. seed trap, latrine, or roost), and to measure the number and extent of overlapping seed shadows (García *et al.*, 2009a; García & Grivet, 2011).

Forward, or target-tracking methods (Jordano, 2007), follow the movement of seeds from the source plant to the deposition site. These methods include observing disperser foraging activity and tracking subsequent movements either remotely (i.e. radio-telemetry) or visually to infer seed displacement (Jordano & Schupp, 2000; Westcott & Graham, 2000), tagging fruits or seeds with threads (Forget, 1990), attaching radio-tracking devices (Pons & Pausas, 2007) or coded labels (Mack, 1995) to seeds, and spraying fruits with fluorescent microspheres (Levey & Sargent, 2000).

Forward-tracking mechanistic approaches offer an alternative to backward-tracking techniques for modelling the seed shadow. In this case, plant and disperser traits and characteristics of the dispersal event itself can be directly incorporated into a predictive model of dispersal (Nathan & Muller-Landau, 2000). Given the large number of variables that affect animal behaviour and movement (Nathan & Muller-Landau, 2000), these approaches are often difficult to apply. This is because animals do not move randomly in space. Rather, traits intrinsic to the dispersal vectors (e.g. physiology), together with extrinsic environmental factors,

including landscape structure, food availability, competition and predation processes may ultimately determine how animals forage, move, and deposit seeds over space and time (Nathan, 2008; Cousens *et al.*, 2010; García *et al.*, 2011). Unfortunately, forward-tracking approaches rarely account for extrinsic factors.

Developing a mechanistic understanding of animal-mediated seed dispersal requires that we ask a third focal question in seed dispersal studies: why and how do frugivore species (or individuals) disperse seeds from an individual plant to a given deposition site? To answer this question, we must comprehensively embrace the study of animal ecology (Giuggioli & Bartumeus, 2010). These efforts should include studies of foraging behaviour, the factors that shape the behavioural responses of animals to habitat and landscape structure, and the physiological traits that constrain foraging behaviour. The nature of this third question demands the mechanistic study of the different intrinsic and extrinsic factors that modulate disperser behaviour and seed deposition. Because the relative importance of these factors on animal-plant interactions is highly context- and scale-specific (Lehouck *et al.*, 2009; Schupp, Jordano & Gomez, 2010), finding general patterns may prove challenging (Agrawal *et al.*, 2007). Instead, future work needs to go beyond the study of a single temporal or spatial snapshot of a particular dispersal system (Burns, 2004) to investigate how the relative importance of the intrinsic and extrinsic factors governing animal foraging behaviour changes across spatio-temporal and taxonomic scales.

Our objective here is to motivate the adoption of a frugivore-centred seed dispersal research framework that goes beyond the pattern-based and snapshot view to a process-based and multi-scale examination of animal-mediated seed dispersal. To this end, we first combine elements from two existing frameworks, the seed dispersal effectiveness (Schupp, 1993; Schupp *et al.*, 2010) and movement ecology paradigm (Nathan *et al.*, 2008), to examine the frugivore and plant traits, and environmental factors that influence the way animals interact with fruiting plants, shape seed shadows, and potentially influence plant recruitment. Second, we combine these frameworks to survey studies that explicitly link frugivory and seed deposition. Third, we survey promising technological developments and propose future directions for research aimed at advancing our understanding of the mechanisms influencing seed dispersal processes across spatial, temporal and taxonomic scales.

II. LINKING FRUGIVORES, FRUITING PLANTS, AND SEED SHADOWS

From a disperser perspective, seed dispersal effectiveness (SDE) can be described as the relative contribution of an individual disperser to a particular plant's seed shadow (Schupp, 1993), although it can be more inclusive and also refer to the overall effectiveness of dispersal a plant receives from the complete suite of dispersers (Schupp *et al.*,
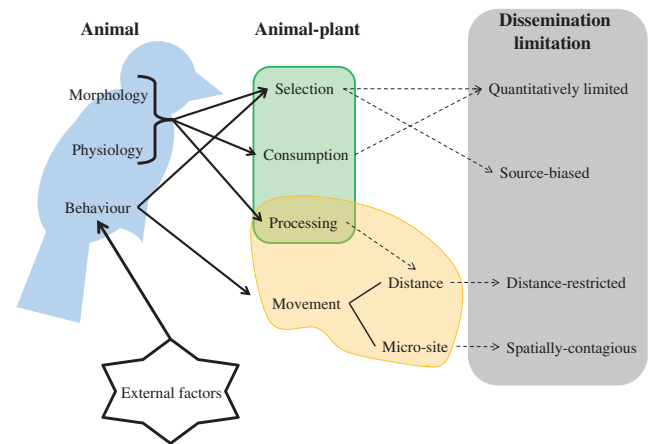

Fig. 1. The effects of animal characteristics during the frugivory phase (green box) and the seed deposition phase (yellow box). From the plant's perspective (grey box), different aspects of animal-plant interactions may result in distinct kinds of seed dispersal and dissemination limitation.

2010). Ultimately, SDE is the product of the quantity (visitation frequency and rate of fruit consumption) and quality (treatment given to the seed and characteristics of the deposition site and pattern) components of seed dispersal (Schupp, 1993; Schupp *et al.*, 2010). Animal movement, one of the sub-components of seed dispersal quality, is the process that links frugivores, fruiting plants and seed shadows and thus deserves further attention. The movement ecology paradigm (Nathan *et al.*, 2008) conceptualizes the drivers and components of animals' movement and, in so doing, can add useful information to seed dispersal studies. In this paradigm, individual movement can be characterized by an internal state (why move?), motion capacity (how to move?), and a navigation capacity (when and where to move?), which are all modulated by biotic and abiotic stimuli (Nathan *et al.*, 2008).

To help us integrate the elements of these two frameworks and organize our literature survey, we compartmentalize seed dispersal into two phases: frugivory and seed deposition. This two-phase compartmentalization aims to capture the effects that distinct plant and animal traits together with environmental characteristics have on the discrete sequence of disperser behaviours that lead to seed deposition (Fig. 1). Hereafter we will use intrinsic factors to refer to inherent traits of the focal plant and animal, whereas extrinsic factors refer to abiotic or biotic environmental characteristics that influence either of these phases (Table 1).

(1) Frugivory phase: what fruits are consumed and in which manner?

The frugivory phase is governed by the behaviours associated with fruit preference and selection, manipulation, and ingestion of fruits by animal dispersers (Fig. 1). The frugivory phase incorporates quantity and quality components of the SDE framework (Schupp, 1993; Schupp *et al.*, 2010). It is a cognitive process, with fruits as the intended targets

Table 1. Intrinsic and extrinsic factors related to individual and population traits of frugivores and plants, and abiotic characteristics of the environment that may affect the frugivory and seed deposition phases

Factors	Frugivore	Plant	Abiotic
Intrinsic	Body size	Fruit size	NA
	Nutrient requirements	Crop size	—
	Age/sex	Nutrient content	—
	Digestive system	Colour	—
	Territory or home-range size	Accessibility	—
	Reproductive status Spatial memory	—	—
Extrinsic	Abundance	Abundance	Light incidence
	Competition	Plant aggregation	Temperature
	Predation	Community phenology	Topography
	—	Vegetation structure	Climate
	—	—	Soil

NA, not applicable.

that trigger the internal state of frugivores. The type and quantity of seeds taken and dispersed by frugivores are determined during this phase and are primarily influenced by morphological (e.g. size), physiological (e.g. nutritional requirements) and behavioural (e.g. reproductive status, social interactions) characteristics of the animals relative to those of the dispersed plants (Martin, 1985). As a result, fruits of some species may be preferred over others, leading to disproportionally greater fruit removal rates for preferred species relative to other plant species in the community (Wheelwright, 1983; Carlo, Collazo & Groom, 2003). Animal morphology and physiology further determine whether a seed will be dispersed or predated, and also the speed of passage through the gut, which together with animal movement, determines where seeds are deposited (Will & Tackenberg, 2008; Cousens *et al.*, 2010). Moreover, disperser's life-history traits interact with environmental factors to generate large variation in fruit removal across plant populations and communities (Table 1). For instance, males of manakins (Pipridae) may establish leks on environmental hotspots, such as sites with high density of fruiting plants, to optimize foraging and attract females during the breeding season (Ryder, Blake & Loiselle, 2006), resulting in aggregated fruit removal and increased density of the local seed bank (Krijger *et al.*, 1997). Extensive lists and description of the myriad intrinsic and extrinsic factors that can influence these patterns are provided elsewhere (Howe & Smallwood, 1982; Schupp, 1993; Jordano, 2000; Corlett, 2011).

From the plant's perspective, seed dispersers may affect the abundance of plants when dissemination is quantitatively limited (Schupp *et al.*, 2002), meaning that independent of fruit production, dispersers remove a low proportion of fruits from the parents (Fig. 1). Reduced visitation rate and fruit removal may be due to low disperser abundance (Jordano & Schupp, 2000), low consumption rates, or avoidance of plant species, possibly as the result of dispersers' diet preference or morphological constraints (Jordano, 2000; Carlo *et al.*, 2003). Another type of dissemination limitation during this phase is source-biased limitation (Jordano, 2007) (Fig. 1),

the result of unequal fruit removal among individual plants (Carlo & Morales, 2008). In this case, few plants contribute seeds disproportionately to a given micro-site (García *et al.*, 2009a) or to the whole population (Sezen, Chazdon & Holsinger, 2005), whereas other individuals fail to have their seeds dispersed. The most striking consequence of source-biased limitation is genetic. Dissemination limitation can be studied indirectly by observing animals' feeding behaviour on individual plants (Fuentes *et al.*, 2001), by marking individual plants and monitoring the number of fruits removed over time (Pizo & Almeida-Neto, 2009), or by genotyping disseminated seeds and assessing the number of seed donors and the relative contributions of maternal plants to the population seed rain (Grivet, Smouse & Sork, 2005; García & Grivet, 2011).

(2) Seed deposition phase: how and where are seeds deposited?

The seed deposition phase includes all behaviours that dictate where seeds are deposited, after consumption and digestion (Fig. 1), and largely incorporates SDE quality variables (Schupp, 1993; Schupp *et al.*, 2010). Animals' daily and seasonal activities will affect how and where seeds are deposited, and ultimately, disperser movement will be the most important post-frugivory factor affecting all three components of seed shadows (distance of seed from source tree, density and distribution of dispersed seeds, and number and extent of seed shadows overlapping with conspecifics).

The study of animal movement has advanced steadily, by virtue of increases in temporal and spatial accuracy of global positioning system (GPS) tracking technology (Tomkiewicz *et al.*, 2010), miniaturization of tracking devices (Wikelski *et al.*, 2010), and the conceptualization of movement models borrowed from physics theory, such as random walk (or diffusion models if population-based), correlated and biased random walks, and Lévy statistics (Borger, Dalziel & Fryxell, 2008; Smouse *et al.*, 2010).

Mechanistic models of animal's movement and home-range have emerged as an alternative to description of

patterns of habitat use and selection. The models are based on stochastic rules of movement associated with probability distributions of movement lengths, orientations and turning angles (Moorcroft & Lewis, 2006). Models of animal movement patterns have improved by considering the heterogeneous and complex nature of animal behavioural responses to intrinsic and extrinsic factors (Morales & Ellner, 2002; Kie *et al.*, 2010; Smouse *et al.*, 2010). For instance, different speed or turning distributions can be assigned for distinct behavioural modes, or switches between modes can be modelled based on variations in internal states or environmental stimuli (Moorcroft & Lewis, 2006). Navigation capacity accounts for the animal's ability to orient in space, determining the position and direction of each movement event. In order to predict seed dispersal events, we need to understand how external conditions affect animal internal states, in turn influencing the navigation status of the disperser (Cousens *et al.*, 2010).

Social organization, territoriality and mating system are important aspects of animal behaviour that play a role in determining the patterns of seed dispersal (Karubian & Durães, 2009). Many of these behaviours could explain the motivation (internal state) behind frugivore movement and navigation capacity. For example, one of the most important seed dispersers of the neotropical tree *Ocotea endresiana*, the three-wattled bellbird *Procnias tricarunculata*, disperses most of the seeds under song perches in canopy gaps (Wenny & Levey, 1998). Here, the internal state is represented by the urge to attract females *via* display, and the navigation-dictated target is the song perch located in a gap. Such predictable seed deposition patterns favouring the recruitment of *O. endresiana* in gaps can be directly linked to disperser mating behaviour.

Habitats are composed of a set of biotic and abiotic environmental variables that are heterogeneous in space and time (Beyer *et al.*, 2010). How animals use habitat reflects a trade-off between their internal motivations and intended targets and the external conditions restricting their accessibility to those targets (Borger *et al.*, 2008). An animal's movement is generally bounded by its home range and by the territories of neighbouring individuals or groups. Thus, home range determines the scale over which most of the animal seed dispersal occurs by any particular individual. Within these broad boundaries, various environmental characteristics can determine direction, length and speed of movement and frequency of use for specific habitats (Moorcroft & Barnet, 2008) following a feeding event. Vegetation structure, water availability, topography, presence of competitors or predators, and abundance of a given food item are only a few of the many environmental factors that may exert an influence on the internal state of frugivores or modify their navigation capacities (Table 1).

In summary, understanding animal movement is essential to connect frugivores to seed shadows. The study of animal movement is still analytically challenging but the continuous application and subsequent refinement of analytical tools will help to advance the field of study by providing the means to investigate the internal triggers and external conditions influencing how animals move and where they deposit ingested seeds.

III. A REVIEW OF STUDIES OF SEED SHADOWS FROM THE DISPERSER PERSPECTIVE

Numerous reviews have synthesized empirical work or discussed theoretical aspects of frugivore-mediated seed dispersal. These include a detailed description of morphological and physiological characteristics of frugivores and quality and distribution of food resources that ultimately affect plant-animal interactions (Schupp, 1993; Jordano, 2000; Corlett, 2011), the importance of seed dispersal to the ecology, evolution (Howe & Smallwood, 1982; Wang & Smith, 2002; Levin *et al.*, 2003; Levine & Murrell, 2003), and genetics of plant populations and communities (Broquet & Petit, 2009; García & Grivet, 2011), and a survey of the scale at which seed dispersal processes are studied (Kollmann, 2000; Burns, 2004). In parallel, there have been a number of recent reviews in the field of animal movement (Borger *et al.*, 2008; Moorcroft & Barnet, 2008; Nathan, 2008; Schick *et al.*, 2008; Cagnacci *et al.*, 2010). None of these reviews, however, has simultaneously considered seed dispersal, animal movement, and scaling issues. This is a critical need because integrating these processes will enable the development of a more mechanistic understanding of frugivore-mediated seed dispersal and open new avenues for researching the feedbacks between interacting organisms and the strength of biotic and abiotic context on modulating mutualisms (Agrawal *et al.*, 2007).

To aid in this effort, we compiled studies that explicitly link fruiting plants, frugivores, and seed shadows. We carried out a literature search up to September 2011 and found 30 studies that met the following two criteria: (*i*) individual plants, as fruit sources, were spatially linked to their seed shadow; (*ii*) frugivore (individual or species) behaviour was linked directly or indirectly to both the fruiting plant and seed shadow. The studies cover a broad range of frugivores (birds, mammals and reptiles), plant life-forms (trees, shrubs and herbs), and biomes (tropical rainforests, deserts, temperate forests) (Table 2).

For each of the selected studies, we determined: (*i*) which and how many plants and animals were included and whether the study was centred on the plant or animal perspective; (*ii*) how animal movement was measured or inferred; (*iii*) how seed shadows were characterized; (*iv*) the number of intrinsic and extrinsic factors (see Table 1) included in the study; and (*v*) the spatial and temporal scale over which the studies were conducted. Below, we summarize and discuss our findings (Table 2).

(1) Selection of focal plant and animal disperser species

Overall, studies of seed shadows evaluated either the seed dispersal role of chosen animals or seed dispersal pattern

Table 2. Characteristics of the reviewed studies

Focus	Plant life form (no. of species)	Disperser (no. of species)	Habitat (location)	Spatial extent	Period of study	Plant traits	Animal traits			DSC	SS	References
							GRT	Mov	Other			
Animal	Diverse	Monkey (1)	Atlantic forest and chaco (Argentina)	4 ha	2 y	0	F	O	5	Yes	O	Bravo (2009)
	Tree (1)	Elephant (1)	Deciduous forest (Sri Lanka/Myanmar)	NA	1 y	0	C	GPS	2	No	P	Campos-Arceiz et al. (2008)
	Diverse	Tortoise (1)	Amazonian forest (Peru)	1420 ha*	1 y	0	F	RT	4	Yes	O	Guzman & Stevenson (2008)
	Diverse (8)	Hornbill (2)	Forest (Cameroon)	526000 ha*	1 y	1	C	RT	0	No	P	Holbrook & Smith (2000)
	Diverse	Tortoise (1)	Amazonian forest (Brazil)	8000 ha*	3 y	0	F	RT, SL	1	No	P	Jerozolimski et al. (2009)
	Diverse (5)	Hornbill (1)	Fragmented sub-tropical forest (South Africa)	NA	2 y	0	C	GPS	0	Yes	P	Lenz et al. (2011)
	Bush (1)	Bird (1)	Open temperate forest (USA)	8 areas (50 ha each)	2 y	0	C	O	3	Yes	P	Levey et al. (2008)
	Bush (1)	Bird (1)	Open temperate forest (USA)	8 areas (50 ha each)	2 y	0	C	O	3	Yes	P	Levey et al. (2005)
	Diverse	Gibbon (1)	Dipterocarp forest (Indonesia)	< 50 ha†	1 y	1	F	O	0	Yes	P	McConkey & Chivers (2007)
	Diverse (6)	Turacos (3)	Tropical forest (Rwanda)	350 ha	14 mo	1	C	O	3	No	P	Sun et al. (1997)
	Diverse (9)	Monkey (1)	Tropical forest (Panama)	50 ha	4 mo	0	C	O	1	Yes	P	Wehncke et al. (2003)
	Diverse	Bird (3)	Vegetation mosaic (Hong Kong)	NA	2 y	0	C	RT, O	0	No	P	Weir & Corlett (2007)
	Shrub/treelet (6)	Bird (1)	Tropical forest (Costa Rica)	115 ha	1 y	0	C	RT	3	No	P	Westcott & Graham (2000)
	Diverse	Cassowary (1)	Tropical forest (Australia)	NA	2 / 7 y	0	C	RT	0	No	P	Westcott et al. (2005)
Plant	Diverse	Monkey (2)	Tropical forest (Colombia)	17−70 ha†	21 d	0	F	O	1	Yes	O	Yumoto et al. (1999)
	Tree (1)	Mice (1)	Evergreen forest (Japan)	0.1 ha	< 5 mo	0	-	G	0	Yes	G	Abe et al. (2006)
	Shrub (1)	Bird (2)	Cattle ranch (Puerto Rico)	18 ha	3 mo	3	T	T, O	1	No	P	Carlo & Morales (2008)
	Tree (1)	Bird (3 groups)	Mediterranean (Spain)	25 ha	< 1.5 mo	8	—	G	0	Yes	G	García et al. (2009a)
	Mistletoe (1)	Bulbul (1)	Desert (Israel)	7 wadis (area NA)	14 mo	0	C	O	1	Yes	P	Green et al. (2009)
	Tree (1)	Toucans (2 groups)	Tropical forest (Ecuador)	84 ha	≈2 y	1	C	RT	1	No	P	Holbrook & Loiselle (2007)
	Tree (1)	Bird (3 groups)	Mediterranean (Spain)	26 ha	4 y	0	—	G	1	Yes	G	Jordano et al. (2007)
	Theoretical	Bird	Theoretical	2500 ha	30 d	2	T	T	2	No	P	Morales & Carlo (2006)
	Herb/shrubs (3)	Bird (3)	Tropical forest (Costa Rica)	14 plots (0.013 −0.24 ha)	2 y	2	C	RT	0	Yes	P	Murray (1988)
	Tree (1)	Monkey (1)	Amazonian forest (Peru)	≈300 ha	2 y	1	F	O	4	Yes	P	Russo et al. (2006)
	Shrub (1)	Lizard (1)	Insular Mediterranean (Spain)	2.91 ha	7 d	1	C, F	RT	4	Yes	P	Santamaría et al. (2007)

Table 2. *(Cont.)*

Focus	Plant life form (no. of species)	Disperser (no. of species)	Habitat (location)	Spatial extent	Period of study	Plant traits	Animal traits			DSC	SS	References
							GRT	Mov	Other			
	Tree (1)	Woodpecker (1)	Oak savannah (USA)	2380 ha*	1 y	0	—	G	0	Yes	G	Scofield *et al.* (2010)
	Shrub (1)	Bird (2)	Desert (Israel)	Wadis (50–800 m wide)	4 mo	1	C	RT, O	2	Yes	P	Spiegel & Nathan (2007)
	Herb (1)	Bird (2 groups)	Fragmented Amazonian forest (Brazil)	13 plots (0.5 ha each)	1 y	2	C	RT	4	Yes	P	Uriarte *et al.* (2011)
Plant/animal	Palm (1)	Umbrellabird (1)	Tropical forest (Ecuador)	30 ha	NA	0	—	G	0	Yes	G	Karubian *et al.* (2010)
	Tree (1)	Macaque (1)	Evergreen forest (Japan)	70 ha	1 mo	0	—	G	0	No	G	Terakawa *et al.* (2009)

*Spatial extent based on area reported for reserve not for study.
†Spatial extent based on area reported for animal(s) home range.
Plant traits are related to the maternal plant and thus affect the frugivory phase. Animal traits affect seed deposition (GRT and Mov) and frugivory (Other). Deposition site characteristics (DSC) affect the seed deposition phase. Gut retention time (GRT) was estimated observing animals in the field (F) or in captivity (C), or extracted from theoretical probability distributions (T). Movement (Mov) of animals was directly observed in the field (O), measured using GPS-loggers (GPS), radio-telemetry (RT), spool-and-line (SL), inferred by conducting maternity analysis on dispersed seeds (G), or characterized theoretically (T). Other represents the number of other animal traits used to characterize frugivory. Seed shadow (SS) was characterized by direct observation (O), predicted using movement and GRT (P) or measured through maternity analysis on dispersed seeds (G). d, days; mo, months; y, years.

of specific plants and, thus, have primarily taken either the animal ($N = 15$ studies) or plant perspective ($N = 13$ studies), with only two studies addressing dispersal from both perspectives (Table 2). There are good reasons behind this pattern. Reciprocal specialization in seed dispersal systems is very rare because frugivore diet is often diversified and most fleshy fruit bearing plants rely on a large assemblage of animals for their dispersal (Joppa *et al.*, 2009).The research focus often reflects the interests of the investigators and the characteristics of the study system, while logistical restrictions limit the number of focal organisms and the taxonomic (e.g. species and genus) or organizational level (e.g. functional groups) considered in the study.

From an animal perspective, evaluating the outcomes of seed dispersal of all plant species consumed by a disperser species is often impractical. For instance, animal-focused studies (Table 2) took one of the following approaches to estimate gut retention time: seed shadows were generated using gut retention time obtained for a few plant species (Holbrook & Smith, 2000), categories of plant species were created based on similar gut retention time [e.g. slow *versus* fast seeds (Sun *et al.*, 1997)], gut retention times of different plant species were combined into a single average (Wehncke *et al.*, 2003), or a model plant was used to understand seed dispersal patterns (Levey *et al.*, 2005; Campos-Arceiz *et al.*, 2008).

From a plant's perspective, tracking movement of all frugivores consuming a particular plant species is costly and time-demanding. Different approaches have been used to constrain the number of dispersers included in a study. The most straightforward method is to select the single most important seed disperser of the focal plant species. For instance, the spider monkey *Ateles paniscus* was selected for evaluating the seed shadow of the neotropical tree *Virola calophylla* (Russo *et al.*, 2006) because it was responsible for dispersing 92% of removed seeds (Russo, 2003). Seed dispersers, however, often have equivalent or similar roles in dispersing seeds from multiple, different focal plant species. Often, the few most important frugivores were studied individually (Murray, 1988; Holbrook & Loiselle, 2007), or subdivided into functional groups, based on their gut retention time [e.g. manakins *versus* thrushes (Uriarte *et al.*, 2011)], bodysize or micro-habitat preference [small-*versus* medium-sized birds *versus* mammals (Jordano *et al.*, 2007)]. Although measuring the individual contribution of each disperser is ideal, detailed information about individual dispersers may not always be necessary to understand or predict seed shadows.

(2) Measuring animal movement

Frugivore movement was measured directly, through observation ($N = 12$) and/or remote tracking ($N = 13$), and indirectly by conducting maternity analysis on seeds ($N = 6$) (Table 2). The most common method was to observe visually and record the time and location of animals throughout the day (e.g. Sun *et al.*, 1997; Wehncke *et al.*, 2003; McConkey & Chivers, 2007; Green, Ward & Griffiths, 2009). Depending

on the homerange and patterns of habitat use, however, it may be difficult to sample longer movement bouts using these methods (Spiegel & Nathan, 2007). Nevertheless, some of the selected studies successfully used radio and GPS telemetry to overcome this problem (e.g. Holbrook & Smith, 2000; Campos-Arceiz *et al.*, 2008; Lenz *et al.*, 2011).

Indirect measures of animal movement can be obtained by using genetic markers to assign seeds (i.e. offspring) to their source (i.e. maternal plant). The use of molecular tools can provide valuable insights into frugivores' social, reproductive and foraging behaviour. For instance, Karubian *et al.* (2010) examined the effect of lekking behaviour of the umbrellabird *Cephalopterus penduliger* on the directed seed dispersal of the palm *Oenocarpus bataua* under leks. Directed seed dispersal leads to the disproportionate dissemination of seeds to a particular micro-site, which has been hypothesized to result in the formation of pronounced genetic structure within the seed pool. The seed pools under leks were genetically characterized and they were highly heterogeneous, presenting weaker spatial genetic structure than seeds outside leks. These results have important implications for our understanding of how spatially contagious dispersal interacts with source-biased dispersal (García & Grivet, 2011).

In sum, different techniques used to measure movement elucidate different aspects of animal-plant interactions with some clear trade-offs. Observational methods allow detailed recording of animal behaviour at limited spatial and temporal extents, while remote tracking methods allow for accurate measurements of animal locations across larger areas, but fail to provide information on individual behavioural states. Expanding results from observational data to larger scales through modelling has been successfully employed (Levey *et al.*, 2005), however given our lack of understanding on how frugivore behaviour transitions across scales in most systems, extrapolating fine-scale behaviour may generate uncertainties and false predictions as we scaleup (see Section V.2 for scaling seed dispersal). Molecular tools can accurately describe seed dispersal events, but cannot capture detailed information on disperser foraging behaviours, therefore limiting mechanistic generalization.

(3) Characterizing the seed shadow

Seed shadows were characterized through observations of seed deposition in realtime ($N = 3$), predicted using movement and gut retention time data ($N = 21$), or through maternity analysis ($N = 6$) (Table 2). Visual tracking of animals' foraging and post-feeding movement until seeds are deposited requires that researchers have an initial estimate of average or maximum gut retention time for the disperser. This method can capture isolated feeding (Yumoto, Kimura & Nishimura, 1999). But, if an animal consumes fruits from conspecifics within the gut retention timeframe, identification of the exact maternal tree is impossible, unless genetic maternity analysis is also employed (Terakawa *et al.*, 2009). Some of the selected studies, however, have bypassed this issue by assigning individual seeds to different plants when

individual faeces contained more than one seed (Russo *et al.*, 2006; Bravo, 2009).

Alternatively, some of the studies measured movement and gut retention time separately and later estimated seed dispersal curves by calculating the probability that a given seed consumed at time zero would be voided at a certain distance from the maternal plant, after a specific time of gut retention has elapsed. Four studies used fixed median, minimum and/or maximum values of gut retention time for calculating these probabilities (e.g. Westcott & Graham, 2000; Levey *et al.*, 2005) and, in some cases, different curves were generated using temporal categories of gut retention time [e.g. fast, medium and long retention time (Weir & Corlett, 2007)]. However, gut retention times are highly variable, even within the same animal species and for the same plant species (Traveset, 1998; Tewksbury *et al.*, 2008), so dispersal curves generated using fixed values may be unrealistic. For this reason, several of the reviewed studies ($N = 13$) sampled gut retention time values from empirical frequency distributions or probability distribution functions, which were then used to simulate seed dispersal events (e.g. Murray, 1988; Levey, Tewksbury & Bolker, 2008; Uriarte *et al.*, 2011).

Studies often assume that seed dispersal decays with distance to putative maternal individuals and characterize seed movement by reporting maximum or mean distance to sources. These metrics are chosen because they are hypothesized to reflect the two main advantages of dispersal (Howe & Smallwood, 1982): the escape hypothesis, which assumes that longer dispersal distances are beneficial because of high density-dependent mortality below maternal plants (Janzen, 1970), and the colonization hypothesis, which assumes dispersal into a new environment is beneficial (e.g. tree-fall gaps) (Cain, Milligan & Strand, 2000). Furthermore, distance metrics are useful to evaluate whether the seed dispersal of a particular plant population is distance-restricted (i.e. dissemination limitation) (Fig. 1), with implications for the fine-scale recruitment, distribution and long-distance dispersal of plants (Clark *et al.*, 1999; Cain *et al.*, 2000; Schupp *et al.*, 2002).

However, the idea that seed dispersal obeys a decay function with respect to distance from the source plant has recently come into question. For instance, parentage analysis has shown that seeds dispersed beneath a conspecific canopy need not be from that specific mother tree (Godoy & Jordano, 2001) and that the adult plant nearest to the seedling is rarely the parent (Hardesty *et al.*, 2006; Sezen, Chazdon & Holsinger, 2009). Thus, basing models of seed dispersal on distance alone may yield unrealistic predictions about the spatial distribution and gene flow of many plant species (Ashley, 2010). Although some of the reviewed studies went beyond reporting distance metrics and acknowledged the fact that seed movement is anisotropic and non-random (Santamaría *et al.*, 2007; Scofield, Sork & Smouse, 2010), few evaluated the factors that underlie spatial variance in seed dispersal (Russo *et al.*, 2006). Often, seeds may be disproportionately deposited in certain sites,

leading to clumped patterns of seed dispersal and spatially contagious dissemination limitation (Fig. 1) (Schupp *et al.*, 2002). For instance, Russo *et al.* (2006) demonstrated that the distribution of *Virola calophylla* seeds dispersed by the spider monkey *Ateles paniscus* was strongly leptokurtic (many seeds were dropped beneath the sleeping trees), with a long fat tail (due to longer seed dispersal events during in-transit movements) and multimodality (due to the clumped deposition under sleeping sites at various distances from the parent tree).

In summary, seed shadows are more accurately measured by using molecular tools, but can be mechanistically described by combining animal movement and gut retention time data. As gut retention time is highly variable, probability distribution of retention times should be used over single values (e.g. average or maximum). Moreover, components of seed dispersal other than distance from source plants should be considered. Mapping seed shadows allows for a two-dimensional examination of seed deposition and additional components, such as the density of seeds at different deposition microsites, can be uncovered.

(4) Incorporating intrinsic and extrinsic factors into seed dispersal studies

Many of the selected studies evaluated other extrinsic and intrinsic factors that may influence dispersal (Table 1). These factors included plant traits ($N = 12$ studies), animal traits ($N = 19$) and environmental factors ($N = 17$) (Tables 1 and 2). Commonly, however, the variation in these factors was not incorporated in the characterization of the seed shadow ($N = 8$). Plant traits included crop size (Carlo & Morales, 2008), plant aggregation patterns (Morales & Carlo, 2006; Carlo & Morales, 2008), and distance to distinct microhabitats (García *et al.*, 2009a). Animal traits included abundance of dispersers (Uriarte *et al.*, 2011), digestive physiology [e.g. effect of ingestion on germination (Santamaría *et al.*, 2007)], behavioural states [e.g. foraging, sleeping, defaecating (Russo *et al.*, 2006)] and movement states [e.g. perching time, move length and move direction (Sun *et al.*, 1997; Levey *et al.*, 2005)]. A few studies also characterized quality of the deposition site as a function of presence and size of gaps (Murray, 1988), vegetation height (García *et al.*, 2009a), and availability of sleeping trees (Russo *et al.*, 2006) (Table 2).

Animals move purposefully, their internal states and navigation capacities change over time according to the influence and interplay of intrinsic and extrinsic factors. In general, however, seed dispersal models integrating displacement and gut retention time probabilities make no assumptions about the reasons animals move (Cousens *et al.*, 2010). Some studies have added realism to seed dispersal models by making displacement probabilities a function of intrinsic and extrinsic factors. For example, in order to understand the effect of forest fragmentation on seed dispersal of the understorey herb *Heliconia acuminata*, Uriarte *et al.* (2011) parameterized a mechanistic simulation model which incorporated the effects of landscape structure on animal movement decisions and resulting seed shadows.

Other studies examined effects of corridors (Levey *et al.*, 2005), patch shape and landscape heterogeneity (Levey *et al.*, 2008), and daily activity of frugivores (Russo *et al.*, 2006).

We advocate the explicit inclusion of a greater number of intrinsic and extrinsic factors in studies that aim to link frugivory to seed deposition. The use of predictive models driven by a set of foraging and dispersal rules may help us test hypotheses about the relevance of such factors for seed dispersal under different environmental conditions and along natural and human-modified gradients.

(5) Scale of analyses

The relative importance of individual factors on determining frugivory and seed deposition processes and patterns differed with the choice of spatial, temporal, or taxonomic scales (Kollmann, 2000; Schupp *et al.*, 2010; García *et al.*, 2011) (Fig. 2). Among the reviewed studies, seed shadows were mostly studied at fine spatial scales (0.1–50 ha) and over single fruiting seasons (days to months) (Table 3, third and fourth level in Fig. 2). Furthermore, most studies were conducted at the individual disperser level, and multiple seed shadows were summed or averaged to generate composite population-level seed shadows (Holbrook & Loiselle, 2007; Santamaría *et al.*, 2007).

At the population level, factors measured at fine scales are considered to influence the observed pattern of dispersal (Fig. 2). However, factors occurring at larger scales, such as phylogenetic constraints of frugivores or biome structural characteristics, may influence fine-scale processes (Fig. 2). This is a critical issue if we are to scale up from individual studies to a general understanding of the factors that influence variation in seed dispersal patterns across years and regions. Despite the important effect that the choice of scale may have on our understanding of seed shadows, very little has been done actually to disentangle the influence of factors acting at different scales on seed shadows. Among the reviewed studies, Carlo & Morales (2008) examined the effect of plant aggregation at the neighbourhood (fine-scale) and landscape (5000 × 5000 m plot) scales on fruit removal rates and seed dispersal of individual plants. Westcott & Graham (2000) analysed the fractal geometry of the trajectory of an understorey bird *Mionectes oleagineus* to find that its movement complexity was not scale invariant.

Although the majority of studies included in this survey did not attempt to perform cross-scale analysis, many of them conducted comparisons within spatial, temporal and/or taxonomic categories (Table 3). Spatially, seed deposition was compared among different micro-habitats, habitats, landscapes or geographical regions. Despite the well-known striking temporal variation in fecundity (e.g. mast seeding) for many tree species (Kelly & Sork, 2002), annual and inter-decadal comparisons remain rare in studies of seed dispersal (but see Jordano, 1994; Herrera, 1998). Finally, taxonomic comparisons were conducted in the selected literature between congeneric species (e.g. Holbrook & Smith, 2000), or functional groups (Jordano *et al.*, 2007).
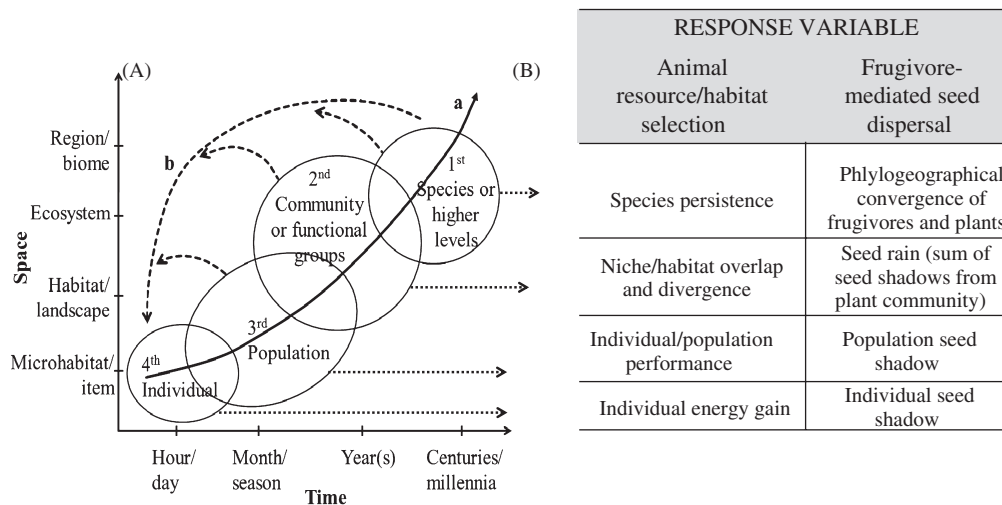
RESPONSE VARIABLE	
Animal resource/habitat selection	Frugivore-mediated seed dispersal
Species persistence	Phlyogeographical convergence of frugivores and plants
Niche/habitat overlap and divergence	Seed rain (sum of seed shadows from plant community)
Individual/population performance	Population seed shadow
Individual energy gain	Individual seed shadow

Fig. 2. (A) Cross-scale variation in the processes that determine the organizational level of frugivory and seed deposition along a spatial and temporal gradient. Plant-frugivore interactions can be examined from different perspectives as follows: (a) seed shadows are summed across individuals from single plants (fourth order) to higher organizational levels (third and second orders) and matched to appropriate factors in each level (e.g. abundance of conspecifics or other fruiting plants). (b) Factors included in the first order (e.g. regional species pool, rainfall) can influence individual seed shadows at finer scales. (B) Proxies for measuring the response variables in seed dispersal studies at each scale, adopting the framework for animal studies of habitat and resource selection (see text for details).

IV. TECHNICAL PROSPECTS FOR STUDIES OF DISPERSAL

The study of seed dispersal in the wild confronts a series of logistical and technical limitations. Researchers have creatively adapted existing tools to collect data relevant to understanding seed shadows (Bullock et al., 2006). As we make use of the newly available tools, we expect advances in our understanding of the components of the frugivore-plant system that remain largely unexplored [e.g. the effect of odour and sound on fruit-animal interactions (Corlett, 2011)]. In this section, we discuss the potential of new technical tools to help unveil the factors that determine disperser activities.

(1) Animal-specific contribution to seed shadows

One technical difficulty that often impedes linking individual species of frugivores to the disseminated seed is to identify and quantify the contribution of different animal dispersers to a plant seed shadow. Seed dispersal interactions are highly complex and often involve multiple frugivore species shaping the combined seed shadow of one focal plant species. With a few exceptions, identifying which frugivore dispersed which seed is a daunting task. In some cases, system particularities, such as noticeable signatures of seed deposition by different frugivores (e.g. regurgitation versus defaecation) or microhabitat use by a single frugivore, might make it possible to track a seed back to its disperser and then back to its seed source (Jordano et al., 2007; Fedriani, Wiegand & Delibes, 2010). Many dispersers, however, do not have distinguishable deposition patterns and the definition of discrete, biologically meaningful microsites can be difficult.

One way to overcome this limitation is to identify the dispersers using genetic tools. DNA barcoding has been used by ecologists to identify animal species based on samples of hair, faeces or urine (Valentini, Pompanon & Taberlet, 2009). Defaecated or regurgitated seeds can provide enough animal material to isolate DNA and run the analysis to assign unknown specimens to known species using public databases (GenBank, Barcode of Life Database). This approach can provide useful information on the contributions of different frugivores to seed shadows (Marrero et al., 2009).

(2) Tools for monitoring intrinsic and extrinsic factors

Understanding the environmental and physiological variables that trigger different internal states of animals can be challenging primarily because obtaining appropriate data on animal behavioural states and environmental characteristics is not always easy. At fine scales, ground surveys can be conducted to gather information on certain intrinsic and extrinsic factors, such as abundance and distribution of fruit sources, which can be appropriate for animals that forage within restricted areas. Often, however, frugivores rely on patchy resources scattered across large areas or highly heterogeneous and inaccessible habitats (Lehouck et al., 2009). Satellite and aerial imagery is a valuable tool to help map points of interest [e.g. fruiting trees (Caillaud et al., 2010)] and characterize habitats at broader scales. Remote monitoring data (e.g. land use, climate) collected at different temporal and spatial resolutions has become increasingly available allowing detailed characterization of association between biota and

Table 3. Spatial, temporal and taxonomic scales considered by some of the reviewed studies

	Scale aspects	Examples	References
Spatial	Fine *versus* broad scale	Neighbourhood *versus* landscape	Westcott & Graham (2000), Jordano *et al*. (2007), Spiegel & Nathan (2007), and Carlo & Morales (2008)
	Micro-habitat	Conspecific plants, sleeping trees	Yumoto *et al*. (1999), Wehncke *et al*. (2003), Russo *et al*. (2006), McConkey & Chivers (2007), Spiegel & Nathan (2007), Bravo (2009), and Green *et al*. (2009)
	Habitat	Gaps, rock outcrop, shrub-dominated, grassland	Murray (1988), Yumoto *et al*. (1999), Westcott & Graham (2000), Abe *et al*. (2006), Jordano *et al*. (2007), Santamaría *et al*. (2007), Guzman & Stevenson (2008), García *et al*. (2009a), and Karubian *et al*. (2010)
	Landscape	Fragmented forest	Levey *et al*. (2005, 2008), Lenz *et al*. (2011), and Uriarte *et al*. (2011)
	Geographical	Biomes	Campos-Arceiz *et al*. (2008)
Temporal	Daily	Morning *versus* afternoon	Westcott *et al*. (2005), Russo *et al*. (2006), McConkey & Chivers (2007), and Santamaría *et al*. (2007)
	Monthly	Across months	McConkey & Chivers (2007)
	Seasonal	Dry *versus* wet	Weir & Corlett (2007), Campos-Arceiz *et al*. (2008), Guzman & Stevenson (2008), and Jerozolimski *et al*. (2009)
	Year	Between years	Levey *et al*. (2005)
Taxonomic	Plants	Among plants	Murray (1988), Holbrook & Smith (2000), and Westcott & Graham (2000)
	Animals	Small *versus* large birds	Murray (1988), Sun *et al*. (1997), Yumoto *et al*. (1999), Holbrook & Smith (2000), Holbrook & Loiselle (2007), Jordano *et al*. (2007), Spiegel & Nathan (2007), Weir & Corlett (2007), and Uriarte *et al*. (2011)
	Within animals	Groups of monkeys	McConkey & Chivers (2007)

environment (Kearney & Porter, 2009), including disperser-plant interactions (Marquez, Real & Vargas, 2004). Light detection and ranging (LiDAR) provides information on vertical habitat structure (e.g. presence of gaps, vegetation stratification) as another tool to model animal-habitat relationships (Vierling *et al*., 2008).

Biotelemetry, on the other hand, enables the characterization of the intrinsic factors that modulate animal foraging and movement. This promising advance involves remote monitoring of animal activities, physiological states and environmental conditions, such as temperature, frequency of wing beats, or heart rate, using specialized sensors (Cooke *et al*., 2004). Combining biotelemetry and movement-tracking technology can provide information on frugivore activities and their specific location in space and time. For instance, to understand better the role of the nocturnal frugivorous oilbird *Steatornis caripensis* on seed dispersal, Holland *et al*. (2009) used GPS-telemetry and accelerometers to monitor behavioural changes remotely. They were able to identify when birds were inactive in roosts or foraging in trees, and could distinguish flights to roost or foraging sites, based on the frequency of wing beats. Their results indicated that oilbirds are effective seed dispersers, due to their extensive foraging activities outside caves and non-overlap of foraging and roosting sites. Valuable information about animal behaviours, such as resting, feeding, walking or flying, can be retrieved remotely using these tools.

Although many of these tools are new, costly, and logistically challenging, their increasing application in a broad range of studies will expand our understanding of seed dispersal across a broad range of scales. When combined with ground surveys, they may allow a more accurate and detailed understanding of links between environment and animal behaviour, providing us with the material to explore the mechanisms behind frugivore-mediated seed dispersal at different scales.

V. A PROPOSAL FOR INTEGRATED ANALYSES

As ecologists we are faced with the challenge of linking processes that are highly space-time dependent and identifying general patterns that we can seldom extrapolate to other systems. In this section we first propose a flexible mechanistic approach as a way to integrate multiple processes within a comprehensive framework in order to shed some light on the effects of different assumptions on specific patterns, in our case, seed dispersal. Second, we focus on scaling issues as a way to pinpoint generalities in complex systems. Instead of looking for pattern similarities across systems, we propose concentrating on the mechanisms that lead to differences across temporal, spatial and taxonomic scales.

(1) Building a spatially explicit mechanistic model: a hypothetical example

To understand how biotic and abiotic factors affect seed dispersal one useful approach is to apply a spatially explicit

mechanistic model in which sub-models are tested and simulations are constructed using a series of nested routines. This approach allows for a comprehensive analysis of the processes taking place and predicting the relative effects of factors on seed dispersal according to alternative scenarios. Inspired by many existing studies (Russo *et al.*, 2006; Carlo & Morales, 2008; Levey *et al.*, 2008; Uriarte *et al.*, 2011) we describe a hypothetical example to demonstrate how one can test for the relevance of different factors on the generation of seed shadow.

In our example, we are interested in the seed shadow of a canopy tree T generated by a medium-sized canopy bird B in a dense forest. Specifically, we ask what is the relative importance of abiotic and biotic factors on shaping the seed shadow? The first step is to identify underlying models describing aspects of the frugivory and seed deposition phases, and thus select a series of traits and factors believed to influence each one of these aspects. Appropriate data on animal and plant natural history and ecology should be collected, and for that a myriad of traditional and modern techniques are available (see Section IV). Alternatively, data from similar systems can be used to parameterize some of the sub-models. For instance, gut retention time of a related disperser species can be used in the absence of specific information for the disperser under study (Levey *et al.*, 2008).

Here, we have data on the location of every tree T and all heterospecific trees that also produce bird-eaten fruits during the tree T fruiting period within a pre-defined plot of 300×300 m. Available data for intrinsic plant traits for plant T include crop size for a sample of trees, mean fruit size per plant, and fruit removal (based on observations of bird visitation) for a sample of trees. For intrinsic traits of bird B we have: gape size and body size for males and females (from a sample of captured birds), gut retention time for males and females from experiments in captivity, and movement behaviour (from radio-telemetry); as extrinsic bird factors: abundance/activity of other frugivorous birds (from bird counts and mistnet captures established in a grid system within the plot); as abiotic factors: location of gaps.

The second step is to build statistical models given our scientific hypotheses and select the best one. Given a set of nested alternative sub-models we drop the covariates that do not improve the likelihood of a particular hypothesis given the dataset and select the most parsimonious one based on Akaike information criterion (AIC) values. The components included and the respective covariates considered in each of our models are (Fig. 3):

Model 1. Probability that a tree T is visited by bird B: hypothesized to be affected by crop size, number of heterospecifics in the neighbourhood, number of conspecifics in the neighbourhood, distance to nearest gap, and number of other frugivores in the neighbourhood. This model represents the attractiveness of each tree T to birds B. Larger crop size and number of plants in the neighbourhood are predicted to increase tree attractiveness to frugivores (Sargent, 1990; Carlo, 2005; Saracco *et al.*, 2005). Plants located in gaps or close to them may be less attractive, as open environments
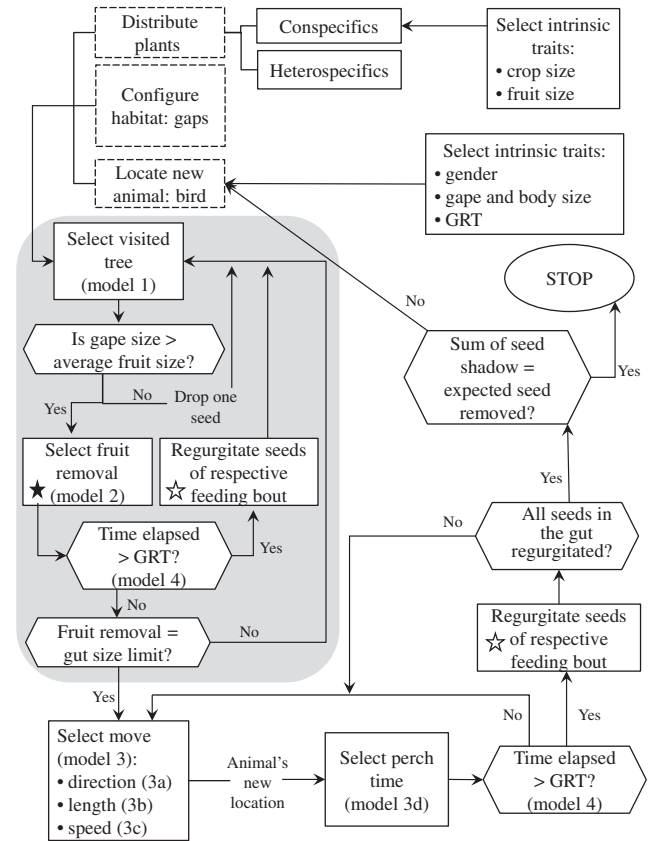

Fig. 3. Flow diagram representing the steps within the seed dispersal simulation. The grey box encompasses the animal's internal state in which the feeding behaviours are governed by the urge to eat fruits from tree T (frugivory phase). It is assumed that after the animal is satiated, its internal state changes to an unknown state and navigation is mediated by environment and motion capacity (taking most of the seed deposition phase). Black filled star indicates that the identity of the maternal plant, location and time of feeding bout are registered. White filled star indicates the moment that the time, location and number of deposited seeds are registered. See text for further details. GRT, gut retention time.

make birds more vulnerable to predators (Howe, 1979; Martin, 1985). It is worth noting that high fruit production in gaps, however, can concentrate activity of understorey birds (Levey, 1988, 1990), which may outweigh predation risk. Also, the activity of other frugivores in the area represents the level of competition in the neighbourhood (Carlo, 2005); high levels may repel birds B from approaching certain trees (Pratt, 1984; Martin, 1985; Fadini *et al.*, 2009).

Model 2. Fruit removal rates (number of fruits removed per visit): hypothesized to be affected by the probability that a bird can swallow the fruit, body size, distance to gaps, and activity of other frugivores in the area. Larger birds are able to consume more fruits per bout (Jordano & Schupp, 2000), so if there is sexual dimorphism in body size, we expect that males, on average, will remove different amounts of fruit compared to females. Fruit removal rates are strongly affected by visit duration (Pratt & Stiles, 1983), which in turn

can be influenced by distance to gaps and activity of other frugivores. Birds visiting trees that are close to gap openings or located in neighbourhoods with higher frugivore activity are expected to spend less time in the tree due to predation risk (Howe, 1979) and competition pressure (Pratt, 1984; Martin, 1985), respectively.

Model 3. Bird's movement: analysed through four components. (*i*) Direction of movement: hypothesized to be affected by previous move direction and location of gaps, under the prediction that birds avoid flying into gaps; (*ii*) move length; (*iii*) speed; and (*iv*) perch time: hypothesized to be affected by distance to gaps (i.e. predation risk) and frugivore activity in the neighbourhood (i.e. competition pressure).

Model 4. Gut retention time: affected by bird's gender and body size (which may be correlated).

The second step is to use the parameters estimated from the most parsimonious sub-models for each of the four models to define probability distributions to be sampled in a series of simulations. The simulation routines start from scenarios created from our empirical data. We create a plot with the same size and distribute plant *T* and heterospecifics in the same numbers as observed. Plants and gap openings are randomly distributed (but location can follow a specific spatial distribution model). Crop size and average fruit size are assigned to each tree *T* from probability distributions fitted to data. Each simulation starts from a bird randomly located in the map. We assume that the bird's internal state is motivated by eating fruit *T* and thus it moves in the landscape searching for tree *T* at a constant speed, until the gut is satiated (the maximum number of eaten fruits can be measured from experiments in captivity and may vary according to size and gender). Movement rules are dictated by model 1. After satiated, the bird's internal state changes and rules governing behaviour are then based on model 3. Steps go as follows (Fig. 3):

(1) Bird is randomly located in the map. Assign gender to the bird [given natural proportions from mistnet data, although basing sex ratio on mistnet data can be biased given that capture rates for males and females may differ because of specific movement patterns (Remsen & Good, 1996)]. If sexual dimorphism in size was detected (see models 2 and 4), each gender is associated with a different body and gape size average and GRT. If there is no dimorphism, a combined body and gape size and GRT are used.

(2) The bird visits the most attractive tree *T* within a 20 m radius (expected visual field). Level of attractiveness is based on model 1 and distance to each plant. Attractiveness decreases with distance from bird *B* to plant *T*.

(3) The bird stays and consumes fruits if gape size is wider than the average fruit size of tree *T*, meaning that the bird will more likely swallow the fruits from that tree. If there is gape size dimorphism between males and females, than the probability of removal is affected by gender. If the bird consumes fruits, go to step 4, otherwise the bird drops pecked fruit under the crown and moves to a different tree (step 2).

(4) Number of fruits removed is defined by model 2, sampled from a distribution bounded between 1 and a maximum number given gut size limits (which may vary according to gender). At this point, plant identity and time are recorded. Perch time is conditional on the number of fruits removed. If the bird consumes less than the maximum gut size, we repeat steps 2–4 (movement dictated by the urge to eat fruit *T*) until the bird is satiated. Seeds may be voided during perching if time elapsed since first feeding bout exceeds gut retention time. If the bird is satiated, go to step 5.

(5) Movement is now dictated by an unknown internal state. Direction, move length and speed are chosen based on the sub-models 3a, 3b, and 3c. The bird lands at a point in the map and remains perched given sub-model 3d. Seeds may be voided during perching if time elapsed since first feeding bout exceeds gut retention time. The bird regurgitates as many seeds as eaten in the respective feeding bout and the specific location where seeds are deposited is recorded. If the bird does not regurgitate all seeds, repeat step 5. If all seeds are regurgitated, go to step 6.

(6) Sum total of dispersed seeds by all simulated birds. If the sum corresponds to the total expected fruit removal by birds *B* during the fruiting season of tree *T*, stop the simulation. If not, start with a new bird in step 1.

At the end of each of the many simulations, seed shadows can be evaluated individually for each tree or summed across individuals to characterize the population seed shadow. Probability distribution functions can be fitted to the simulated data and two-dimensional depictions of the resulting seed shadows can be created to assess the variance in the spatial distribution of seeds. Assessment of the relative importance of different factors included in the model can be made by conducting sensitivity analyses by changing the input values of different factors one at a time and studying the outcomes (Calviño-Cancela & Martín-Herrero, 2009; Uriarte *et al.*, 2011). For instance, in the hypothetical example, we can remove variability in fruit removal per visit or change proportion of males and females in the population, in case gender differences were found.

Stochastic mechanistic simulation models are also useful for hypothesis testing, so that, for example, one may test the effect of bird extinction or reduced plant abundance on seed shadow. Likewise, genetic data can be incorporated, and differential gene shadows can also be simulated and modelled given a set of assumptions and factors.

Building such a comprehensive model is not a trivial task. The challenges are to gather a complete data set on animal, plant and environmental characteristics and to develop adequate algorithms for the simulation models. Clearly, the field of seed dispersal would benefit immensely from interdisciplinary collaborations between plant, animal and quantitative ecologists and, particularly, by developing such initiatives within long-term studies in permanent plots for which environmental data and mapped plant data are already available.

(2) Multi-scale analysis

Our compilation of the existing literature identified only a few studies that examined seed dispersal across multiple spatial, temporal, or taxonomic scales. This finding is in line with Kollmann (2000), who reviewed 136 studies to examine the spatial scale (e.g. microhabitats, habitats, regions) in which the intensity of particular components of seed dispersal (e.g. frugivore abundance, fruit removal, seed rain) were more strongly determined. Kollmann (2000) and Burns (2004) argue that the lack of studies investigating seed dispersal at different scales may have so far precluded the emergence of general principles in the field. We believe that uncovering general principles and patterns will occur as frugivore-mediated seed dispersal is treated as a complex and integrated process that varies within and among scales rather than as a series of components examined individually at arbitrary scales.

Although literature on scaling issues in frugivory and seed deposition is scant, studies of animal movement and habitat selection undertaken at multiple scales can provide some insights on animal-mediated seed dispersal research. In animal ecology, four hierarchical spatio-temporal levels of resource selection have been identified (Johnson, 1980; Gaillard *et al.*, 2010): first-order level refers to the geographical distribution range of the animal species; second order to selection of home range; third order to selection of a patch or habitat; and fourth order to selection of a micro-site (e.g. nest) or item (e.g. prey). These levels are tied to spatio-temporal scales with relevant resource selection and habitat performance parameters chosen according to the scale of study (Gaillard *et al.*, 2010). For example, a proxy for studying resource selection and habitat performance at the species level (first order) is the probability of extinction, a process that should be investigated at the scale at which the pattern emerges, that is, across biomes and over millions of years. By contrast, at the individual level (fourth order), a useful proxy for measuring performance is energy gain from a food item (Fig. 2, Gaillard *et al.*, 2010). At fine spatial and temporal scales animals tend to select resources and habitats that increase their immediate performance. As scales increase, behavioural decisions influence demographic parameters and population performance. And finally, environmental niches emerge at broad scales, over evolutionary time (Gaillard *et al.*, 2010).

From fine to intermediate temporal scales, some effort has focused on understanding how animals' daily (e.g. sleeping, foraging, moving) and seasonal (e.g. mating, migrating) activities are tied to the spatio-temporal extent of analysis (Johnson *et al.*, 2002; Morales & Ellner, 2002; Fryxell *et al.*, 2008; Amano & Katayama, 2009; Mayor *et al.*, 2009). Aside from searching for invariant scaling properties, multi-scale analysis provides a means to investigate the correlations between specific behavioural states and landscape features and how these are conditional to specific scales (Schick *et al.*, 2008). For instance, Fryxell *et al.* (2008) used datasets from different sources (radio and GPS tracking devices) to test how the movement modes of elks (*Cervus elaphus*)

change across spatio-temporal scales, ranging from minutes to years and meters to 100 km. At coarser scales, elks shifted from dispersive, exploratory movement to home-ranging behaviour through time. At finer scales, however, elks responded to patchiness in local resources, displaying shorter moves and greater turning frequency when foraging than when exploring for food. Fryxell *et al.* (2008) concluded that multiphasic movement patterns were present at all spatio-temporal scales, as a result of a combination of internal state, resource abundance, distribution of other individual elks, and navigational capability.

Here we propose a similar hierarchical approach for seed dispersal studies, in which a set of intrinsic and extrinsic factors are selected based on research questions and study system and then located along spatial and temporal gradients (Fig. 4). For instance, in our hypothetical example described above (Section V.1), we can evaluate how rates of fruit removal vary with the abundance of plants in the fruiting community at the regional level, which in turn may be determined by underlying gradients of soil fertility and rainfall (Gentry & Emmons, 1987). The ultimate goal is to link causal relationships to dispersal outcomes from fine to large scales, using factors related to different organization levels (Fig. 2) as the covariates. Although not explicitly linking frugivores activity to seed deposition, a handful of studies have investigated the exact scale in which seed dispersal operates (Aukema, 2004; García & Chacoff, 2007; García, Rodríguez-Cabal & Amico, 2009b; García *et al.*, 2011). García *et al.* (2011), for example, assessed the relative importance of food availability and habitat structure on explaining scale-dependent variability on seed-frugivore interactions and looked for generalities by comparing patterns across three distinct ecosystems.

Scaling frugivory and seed deposition to higher levels in the temporal and spatial continuum over evolutionary time (right upper corner of Fig. 2A) requires a more powerful conceptual approach and may bring another level of uncertainty into the models. The same four hierarchical levels identified in animal ecology studies can be translated to animal-mediated seed dispersal and pertinent proxies for studying these interactions and outcomes should be chosen according to the scale (Fig. 2). Seed shadows are predominantly viewed as the deterministic outcome of local processes at finer scales, with no considerations of the larger spatio-temporal context in which they are embedded. Historical, systematic, and biogeographic information are seldom incorporated in investigations of seed dispersal (but see Garrido *et al.*, 2002; Almeida-Neto *et al.*, 2008; Kissling, Bohning-Gaese & Jetz, 2009). Biotic interactions are pervasive in all environments and have been recorded in the geologic past (Tiffney, 2004; Jablonski, 2008). Because of their relatively transient nature, however, biotic interactions have been mostly dismissed as an important force moulding species- and clade-level dynamics, largely because we lack understanding of how local processes cascade upwards to clade dynamics, and *vice versa* (Jablonski, 2008). At fine scales (fourth and third order), seed shadows are the first template over which plant recruitment takes

place (Wang & Smith, 2002), and thus are the means by which plants expand their range, exchange genes (or conversely lead to genetic differentiation and speciation), and colonize new habitats. Ultimately, population-level processes mould community composition and reflect on biogeographic and phylogeographic patterns over evolutionary time scales (first order) (Givnish, 2010) (Fig. 2Aa). Community-wide and multi-trophic interactions are particularly important given that multiple animal dispersers are shared among plant species. Networks of mutualistic interactions are often affected by other trophic levels through cascading effects, with consequences for evolution and coevolution of species and implications for conservation of system stability and robustness (Carlo & Yang, 2011; Guimarães, Jordano & Thompson, 2011; Pocock, Evans & Memmott, 2012). Conversely, seed shadows are also contingent on large-scale patterns (Fig. 2Ab). To address these feedbacks between scales more explicitly (Agrawal *et al.*, 2007), we will have to assemble large data sets, spanning environmental gradients over time and space, using for instance molecular analysis (see below) or palaeoecological data (Tiffney, 2004).

By examining contemporary and historic gene flow across environmental gradients, molecular markers can help us elucidate some of these feedbacks (Oddou-Muratorio *et al.*, 2010). Using a hierarchical approach, one can scale from individual gene shadows to analyses of variance in allele frequency among populations and regions to measure levels of genetic differentiation and connectivity, with implications for incipient speciation (Broquet & Petit, 2009). For instance, Voigt *et al.* (2009) studied the spatial genetic structure of two congeneric *Commiphora* plant species at the local and regional level. At the local scale (i.e. within forest sites), the Malagasy species with few dispersers and shorter seed dispersal distances exhibited greater genetic structure than the South African species, with a diverse assemblage of frugivores and longer seed dispersal distances. At the regional scale (i.e. among forest sites), however, this pattern was reversed. This unexpected result was associated with the historical habitat distribution of *Commiphora* in both sites: longer persistence of ecosystems in Madagascar allowed for some level of gene flow across the island, until recent human-induced forest fragmentation. By contrast, naturally isolated patches of scarp forests since the Last Glacial Maximum in South Africa may have precluded high levels of gene flow across the region.

Estimating the relative contributions of different factors acting at local, regional and historical scales on seed shadows (Fig. 4) would be extremely helpful, not only for understanding processes of seed dispersal, but to evaluate better its role in maintaining natural populations, communities and shaping the spatial distribution of plants over large geographical ranges and evolutionary time.

VI. CONCLUSIONS

(1) A mechanistic understanding of frugivore-mediated seed dispersal requires that we embrace animal ecology
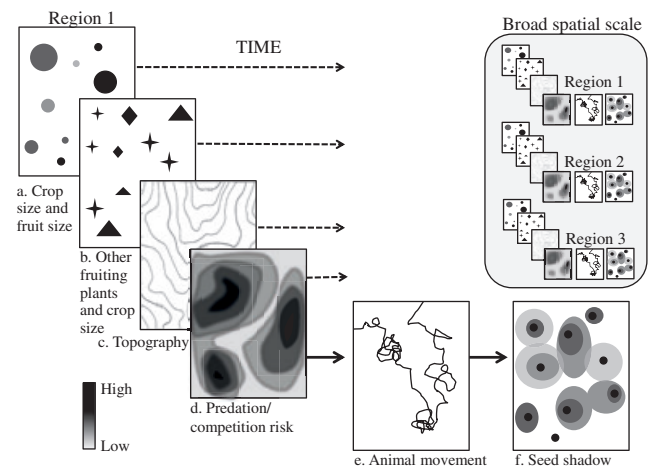

Fig. 4. Schematic representation of a hierarchical multi-scale analysis of the factors that determine animal movement (e) and seed shadow (f) across multiple temporal and spatial dimensions. Different factors are spatially mapped and layers are overlaid to search for relationships among plant traits (a), biotic (b) and abiotic (c) environmental characteristics, and animal traits (d). Each map can be replicated over time at distinct resolutions generating, for example, a plant phenology map for the focal species (a, over time) and plant community (b, over time). The relationship among factors can be additionally studied at different spatial scales, from fine (individuals within maps) to regional scale (comparison of different regions at a broadspatial scale).

and characterize the environment more fully and comprehensively within an integrated framework. The number of variables that modulate seed dispersal outcomes, however, is very large; they can relate to characteristics of the dispersed plants, animal dispersers, or environmental factors. Building a bridge between frugivory and seed deposition will require that we take full advantage of the new tools available for studying animal and seed movement, monitoring environmental and physiological factors, and analysing large plant and animal community datasets.

(2) Which variables to include in our studies will depend on the study system, the questions we aim to address, and the availability and cost of techniques. Studying all pertinent variables may sound impractical, but simulation models based on empirical data or theoretical concepts can help to evaluate particular hypotheses and predict resulting outcomes across relevant natural or anthropogenic gradients.

(3) Seed dispersal processes and outcomes are highly context dependent, and results will mostly differ according to the scale. Advances in seed dispersal research are likely to emerge as we move from describing patterns to actually exploring the reasons why processes differ as we shift scales. To forecast seed dispersal and its outcomes (e.g. spatial distribution of plants), we first need to be able to identify relevant correlations between specific biotic and abiotic factors and pinpoint the scales at which these relationships emerge. Instead of predicting patterns, we should start

predicting the magnitude of the effects certain factors and their interactions have on processes of interest.

(4) Assessing how the relative importance of the factors that modulate frugivory and seed deposition scales up over time and space and across taxonomic levels will require a hierarchical multi-scale approach. Such an approach is likely to foster the development of general principles in the study of frugivory and seed dispersal.

(5) Building spatially explicit mechanistic models that incorporate several plant, animal and environmental factors and investigating such processes at multiple spatial, temporal and taxonomic scales are challenging tasks. Much can be gained, however, from building collaborative working groups, which bring together plant, behavioural and physiological ecology with those studying movement ecology and mathematical modelling.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

Abe, H., Matsuki, R., Ueno, S., Nashimoto, M. & Hasegawa, M. (2006). Dispersal of *Camellia japonica* seeds by *Apodemus speciosus* revealed by maternity analysis of plants and behavioral observation of animal vectors. *Ecological Research* 21, 732–740.

Agrawal, A. A., Ackerly, D. D., Adler, F., Arnold, A. E., Cáceres, C., Doak, D. F., Post, E., Hudson, P. J., Maron, J., Mooney, K. A., Power, M., Schemske, D., Stachowicz, J., Strauss, S., Turner, M. G. & Werner, E. (2007). Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5, 145–152.

Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P. & Oliveira, A. (2008). Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography* 17, 503–513.

Amano, T. & Katayama, N. (2009). Hierarchical movement decisions in predators: effects of foraging experience at more than one spatial and temporal scale. *Ecology* 90, 3536–3545.

Ashley, M. V. (2010). Plant parentage, pollination, and dispersal: how DNA microsatellites have altered the landscape. *Critical Reviews in Plant Sciences* 29, 148–161.

Aukema, J. E. (2004). Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* 27, 137–144.

Bascompte, J. & Jordano, P. (2006). The structure of plant-animal mutualistic networks. In *Ecological Networks* (eds M. Pascual and J. Dunne). Oxford University Press, Oxford.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M. & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2245–2254.

Borger, L., Dalziel, B. & Fryxell, J. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters* 11, 637–650.

Bravo, S. P. (2009). Implications of behavior and gut passage for seed dispersal quality: the case of black and gold howler monkeys. *Biotropica* 41, 751–758.

Broquet, T. & Petit, E. J. (2009). Molecular estimation of dispersal for ecology and population genetics. *Annual Review of Ecology Evolution and Systematics* 40, 193–216.

Bullock, J. M., Shea, K. & Skarpaas, O. (2006). Measuring plant dispersal: an introduction to field methods and experimental design. *Plant Ecology* 186, 217–234.

Burns, K. C. (2004). Scale and macroecological patterns in seed dispersal mutualisms. *Global Ecology and Biogeography* 13, 289–293.

Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. (2010). Preface. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2155.

Caillaud, D., Crofoot, M. C., Scarpino, S. V., Jansen, P. A., Garzon-Lopez, C. X., Winkelhagen, A. J. S., Bohlman, S. A. & Walsh, P. D. (2010). Modeling the spatial distribution and fruiting pattern of a key tree species in a Neotropical Forest: methodology and potential applications. *PLoS ONE* 5, e15002.

Cain, M. L., Milligan, B. G. & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *American Journal of Botany* 87, 1217–1227.

Calviño-Cancela, M. & Martín-Herrero, J. (2009). Effectiveness of a varied assemblage of seed dispersers of a fleshy-fruited plant. *Ecology* 90, 3503–3515.

Campos-Arceiz, A., Larrinaga, A. R., Weerasinghe, U. R., Takatsuki, S., Pastorini, J., Leimgruber, P., Fernando, P. & Santamaría, L. (2008). Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology* 89, 2684–2691.

Carlo, T. A. (2005). Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. *Ecology* 86, 2440–2449.

Carlo, T. A., Collazo, J. A. & Groom, M. J. (2003). Avian fruit preferences across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. *Oecologia* 134, 119–131.

Carlo, T. A. & Morales, J. M. (2008). Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology* 96, 609–618.

Carlo, T. A., Tewksbury, J. J. & Martínez del Río, C. (2009). A new method to track seed dispersal and recruitment using N-15 isotope enrichment. *Ecology* 90, 3516–3525.

Carlo, T. A. & Yang, S. (2011). Network models of frugivory and seed dispersal: Challenges and opportunities. *Acta Oecologica* 37, 619–624.

Clark, J. S., Silman, M., Kern, R., Macklin, E. & HilleRisLambers, J. (1999). Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80, 1475–1494.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. & Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* 19, 334–343.

Cordeiro, N. J., Ndangalasi, H. J., McEntee, J. P. & Howe, H. F. (2009). Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90, 1030–1041.

Corlett, R. T. (2011). How to be a frugivore (in a changing world). *Acta Oecologica* 37, 674–681.

Cousens, R. D., Hill, J., French, K. & Bishop, I. D. (2010). Towards better prediction of seed dispersal by animals. *Functional Ecology* 24, 1163–1170.

Fadini, R. F., Fleury, M., Donatti, C. I. & Galetti, M. (2009). Effects of frugivore impoverishment and seed predators on the recruitment of a keystone palm. *Acta Oecologica-International Journal of Ecology* 35, 188–196.

Fedriani, J. M., Wiegand, T. & Delibes, M. (2010). Spatial pattern of adult trees and the mammal-generated seed rain in the Iberian pear. *Ecography* 33, 545–555.

Forget, P.-M. (1990). Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6, 459–468.

Fryxell, J. M., Hazell, M., Borger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T. & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America* 105, 19114–19119.

Fuentes, M., Guitian, J., Guitian, P., Bermejo, T., Larrinaga, A., Amezquita, P. & Bongiomo, S. (2001). Small-scale spatial variation in the interactions between *Prunus mahaleb* and fruit-eating birds. *Plant Ecology* 157, 69–75.

Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M. & Van Moorter, B. (2010). Habitat-performance relationships: finding the right metric at a given spatial scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2255–2265.

Galetti, M., Donatti, C. I., Pires, A. S., Guimaraes, P. R. & Jordano, P. (2006). Seed survival and dispersal of an endemic Atlantic forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society* 151, 141–149.

García, D. & Chacoff, N. P. (2007). Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology* 21, 400–411.

García, C. & Grivet, D. (2011). Molecular insights into seed dispersal mutualisms driving plant population recruitment. *Acta Oecologica* 37, 632–640.

García, C., Jordano, P., Arroyo, J. M. & Godoy, J. A. (2009a). Maternal genetic correlations in the seed rain: effects of frugivore activity in heterogeneous landscapes. *Journal of Ecology* 97, 1424–1435.

García, D., Rodríguez-Cabal, M. A. & Amico, G. C. (2009b). Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. *Journal of Ecology* 97, 217–229.

García, D., Obeso, J. R. & Martínez, I. (2005). Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *Journal of Ecology* 93, 693–704.

García, D., Zamora, R. & Amico, G. C. (2011). The spatial scale of plant-animal interactions: effects of resource availability and habitat structure. *Ecological Monographs* 81, 103–121.

GARRIDO, J. L., REY, P. J., CERDA, X. & HERRERA, C. M. (2002). Geographical variation in diaspore traits of an ant-dispersed plant (*Helleborus foetidus*): are ant community composition and diaspore traits correlated? *Journal of Ecology* **90**, 446–455.

GENTRY, A. H. & EMMONS, L. H. (1987). Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* **19**, 216–227.

GIUGGIOLI, L. & BARTUMEUS, F. (2010). Animal movement, search strategies and behavioural ecology: a cross-disciplinary way forward. *Journal of Animal Ecology* **79**, 906–909.

GIVNISH, T. J. (2010). Ecology of plant speciation. *Taxon* **59**, 1326–1366.

GODOY, J. A. & JORDANO, P. (2001). Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology* **10**, 2275–2283.

GREEN, A. K., WARD, D. & GRIFFITHS, M. E. (2009). Directed dispersal of mistletoe (*Plicosepalus acaciae*) by Yellow-vented Bulbuls (*Pycnonotus xanthopygos*). *Journal of Ornithology* **150**, 167–173.

GRIVET, D., SMOUSE, P. & SORK, V. (2005). A novel approach to an old problem: tracking dispersed seeds. *Molecular Ecology* **14**, 3585–3595.

GUIMARÃES, P. R., JORDANO, P. & THOMPSON, J. N. (2011). Evolution and coevolution in mutualistic networks. *Ecology Letters* **14**, 877–885.

GUZMAN, A. & STEVENSON, P. R. (2008). Seed dispersal, habitat selection and movement patterns in the Amazonian tortoise, *Geochelone denticulata*. *Amphibia-Reptilia* **29**, 463–472.

HARDESTY, B. D., HUBBELL, S. P. & BERMINGHAM, E. (2006). Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters* **9**, 516–525.

HERRERA, C. M. (1998). Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecological Monographs* **68**, 511–538.

HOLBROOK, K. M. & LOISELLE, B. (2007). Using toucan-generated dispersal models to estimate seed dispersal in Amazonian Ecuador. In *Seed Dispersal: Theory and its Application in a Changing World*, pp. 300–321. CAB International, Wallingford.

HOLBROOK, K. M. & SMITH, T. B. (2000). Seed dispersal and movement patterns in two species of Ceratogymna hornbills in a West African tropical lowland forest. *Oecologia* **125**, 249–257.

HOLLAND, R. A., WIKELSKI, M., KUMMETH, F. & BOSQUE, C. (2009). The secret life of oilbirds: new insights into the movement ecology of a unique avian frugivore. *PLoS ONE* **4**, e8264.

HOWE, H. F. (1979). Fear and frugivory. *The American Naturalist* **114**, 925–931.

HOWE, H. F. & SMALLWOOD, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**, 201–228.

JABLONSKI, D. (2008). Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* **62**, 715–739.

JANZEN, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104**, 501–528.

JEROZOLIMSKI, A., RIBEIRO, M. B. N. & MARTINS, M. (2009). Are tortoises important seed dispersers in Amazonian forests? *Oecologia* **161**, 517–528.

JOHNSON, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**, 65–71.

JOHNSON, C. J., PARKER, K. L., HEARD, D. C. & GILLINGHAM, M. P. (2002). A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* **12**, 1840–1860.

JOPPA, L. N., BASCOMPTE, J., MONTOYA, J. M., SOLE, R. V., SANDERSON, J. & PIMM, S. L. (2009). Reciprocal specialization in ecological networks. *Ecology Letters* **12**, 961–969.

JORDANO, P. (1994). Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb* – Patterns and consequences. *Oikos* **71**, 479–491.

JORDANO, P. (2000). Fruits and frugivory. In *Seeds: The Ecology of Regeneration in Plant Communities* (ed M. FENNER), pp. 125–166. CAB International, Wallingford.

JORDANO, P. (2007). Frugivores, seeds and genes: analysing the key elements of seed shadows. In *Frugivory and Seed Dispersal: Theory and Applications in a Changing World* (eds A. J. DENNIS, R. GREEN, E. W. SCHUPP and D. A. WESTCOTT), pp. 229–251. CAB International, Wallingford.

JORDANO, P., GARCIA, C., GODOY, J. & GARCIA-CASTANO, J. (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences* **104**, 3278–3282.

JORDANO, P. & SCHUPP, E. W. (2000). Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* **70**, 591–615.

KARUBIAN, J. & DURÃES, R. (2009). Effects of seed disperser social behavior on patterns of seed movement and deposition. *Oecologia Brasiliensis* **13**, 45–57.

KARUBIAN, J., SORK, V. L., ROORDA, T., DURÃES, R. & SMITH, T. B. (2010). Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology* **19**, 1745–1753.

KEARNEY, M. & PORTER, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**, 334–350.

KELLY, D. & SORK, V. L. (2002). Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**, 427–447.

KIE, J. G., MATTHIOPOULOS, J., FIEBERG, J., POWELL, R. A., CAGNACCI, F., MITCHELL, M. S., GAILLARD, J.-M. & MOORCROFT, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2221–2231.

KISSLING, W. D., BOHNING-GAESE, K. & JETZ, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography* **18**, 150–162.

KOLLMANN, J. (2000). Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics* **3**, 29–51.

KRIJGER, C. L., OPDAM, M., THERY, M. & BONGERS, F. (1997). Courtship behaviour of manakins and seed bank composition in a French Guianan rain forest. *Journal of Tropical Ecology* **13**, 631–636.

LEHOUCK, V., SPANHOVE, T., VANGESTEL, C., CORDEIRO, N. J. & LENS, L. (2009). Does landscape structure affect resource tracking by avian frugivores in a fragmented Afrotropical forest? *Ecography* **32**, 789–799.

LENZ, J., FIEDLER, W., CAPRANO, T., FRIEDRICHS, W., GAESE, B. H., WIKELSKI, M. & BOHNING-GAESE, K. (2011). Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes. *Proceedings of the Royal Society B-Biological Sciences* **278**, 2257–2264.

LEVEY, D. J. (1988). Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* **69**, 1076–1089.

LEVEY, D. J. (1990). Habitat-dependent fruiting behavior of an understorey tree, *Miconia centrodesma*, and tropica treefall gaps as keystone habitats for frugivores in Costa Rica. *Journal of Tropical Ecology* **6**, 409–420.

LEVEY, D. J., BOLKER, B. M., TEWKSBURY, J. J., SARGENT, S. & HADDAD, N. M. (2005). Effects of landscape corridors on seed dispersal by birds. *Science* **309**, 146–148.

LEVEY, D. J. & SARGENT, S. (2000). A simple method for tracking vertebrate-dispersed seeds. *Ecology* **81**, 267–274.

LEVEY, D. J., TEWKSBURY, J. J. & BOLKER, B. M. (2008). Modelling long-distance seed dispersal in heterogeneous landscapes. *Journal of Ecology* **96**, 599–608.

LEVIN, S. A., MULLER-LANDAU, H. C., NATHAN, R. & CHAVE, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology Evolution and Systematics* **34**, 575–604.

LEVINE, J. M. & MURRELL, D. J. (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution, and Systematics* **34**, 549–574.

MACK, A. (1995). Distance and nonrandomness of seed dispersal by the dwarf *Cassowary casuarius-Bennetti*. *Ecography* **18**, 286–295.

MARQUEZ, A. L., REAL, R. & VARGAS, J. M. (2004). Dependence of broad-scale geographical variation in fleshy-fruited plant species richness on disperser bird species richness. *Global Ecology and Biogeography* **13**, 295–304.

MARRERO, P., FREGEL, R., CABRERA, V. M. & NOGALES, M. (2009). Extraction of high-quality host DNA from feces and regurgitated seeds: a useful tool for vertebrate ecological studies. *Biological Research* **42**, 147–151.

MARTIN, T. E. (1985). Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia* **66**, 563–573.

MAYOR, S. J., SCHNEIDER, D. C., SCHAEFER, J. A. & MAHONEY, S. P. (2009). Habitat selection at multiple scales. *Ecoscience* **16**, 238–247.

MCCONKEY, K. R. & CHIVERS, D. J. (2007). Influence of gibbon ranging patterns on seed dispersal distance and deposition site in a Bornean forest. *Journal of Tropical Ecology* **23**, 269–275.

MOORCROFT, P. R. & BARNET, A. (2008). Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology* **89**, 1112–1119.

MOORCROFT, P. & LEWIS, M. A. (2006). *Mechanistic Home Range Analysis*. Princeton University Press, Princeton, NJ.

MORALES, J. M. & CARLO, T. A. (2006). The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* **87**, 1489–1496.

MORALES, J. M. & ELLNER, S. P. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. *Ecology* **83**, 2240–2247.

MORAN, E. V. & CLARK, J. S. (2011). Estimating seed and pollen movement in a monoecious plant: a hierarchical Bayesian approach integrating genetic and ecological data. *Molecular Ecology* **20**, 1248–1262.

MULLER-LANDAU, H. C., WRIGHT, S. J., CALDERON, O., CONDIT, R. & HUBBELL, S. P. (2008). Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* **96**, 653–667.

MURRAY, K. (1988). Avian seed dispersal of 3 neotropical gap-dependent plants. *Ecological Monographs* **58**, 271–298.

NATHAN, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* **105**, 19050–19051.

NATHAN, R., GETZ, W. M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZ, D. & SMOUSE, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 19052–19059.

NATHAN, R. & MULLER-LANDAU, H. C. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution* **15**, 278–285.

ODDOU-MURATORIO, S., BONTEMPS, A., KLEIN, E. K., CHYBICKI, I., VENDRAMIN, G. G. & SUYAMA, Y. (2010). Comparison of direct and indirect genetic methods for

estimating seed and pollen dispersal in *Fagus sylvatica* and *Fagus crenata*. *Forest Ecology and Management* **259**, 2151–2159.

Pizo, M. A. & Almeida-Neto, M. (2009). Determinants of fruit removal in *Geonoma pauciflora*, an understory palm of neotropical forests. *Ecological Research* **24**, 1179–1186.

Pocock, M. J. O., Evans, D. M. & Memmott, J. (2012). The robustness and restoration of a network of ecological networks. *Science* **335**, 973–977.

Pons, J. & Pausas, J. G. (2007). Acorn dispersal estimated by radio-tracking. *Oecologia* **153**, 903–911.

Prasad, S. & Sukumar, R. (2010). Context-dependency of a complex fruit-frugivore mutualism: temporal variation in crop size and neighborhood effects. *Oikos* **119**, 514–523.

Pratt, T. K. (1984). Examples of tropical frugivores defending fruit-bearing plants. *Condor* **86**, 123–129.

Pratt, T. K. & Stiles, E. W. (1983). How long fruit-eating birds stay in the plants where they feed: implications for seed dispersal. *The American Naturalist* **122**, 797–805.

Remsen, J. V. & Good, D. A. (1996). Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* **113**, 381–398.

Ribbens, E., Silander, J. A. Jr. & Pacala, S. W. (1994). Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**, 1794–1806.

Russo, S. E. (2003). Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* **136**, 80–87.

Russo, S. E., Portnoy, S. & Augspurger, C. K. (2006). Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* **87**, 3160–3174.

Ryder, T. B., Blake, J. G. & Loiselle, B. R. A. (2006). A test of the environmental hotspot hypothesis for lek placement in three species of Manakins (Pipridae) in Ecuador. *Auk* **123**, 247–258.

Santamaría, L., Rodríguez-Perez, J., Larrinaga, A. R. & Pias, B. (2007). Predicting spatial patterns of plant recruitment using animal-displacement kernels. *PLoS ONE* **2**, e1008.

Saracco, J. F., Collazo, J. A., Groom, M. J. & Carlo, T. A. (2005). Crop size and fruit neighborhood effects on bird visitation to fruiting *Schefflera morototoni* trees in Puerto Rico. *Biotropica* **37**, 81–87.

Sargent, S. (1990). Neighborhood effects on fruit removal by birds – a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* **71**, 1289–1298.

Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M. & Clark, J. S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* **11**, 1338–1350.

Schupp, E. W. (1993). Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **108**, 15–29.

Schupp, E. W., Jordano, P. & Gomez, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* **188**, 333–353.

Schupp, E. W., Milleron, T. & Russo, S. E. (2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. In *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation* (eds W. R. Silva, D. J. Levey and M. Galetti), pp. 19–33. CAB International, Wallingford, UK.

Scofield, D. G., Sork, V. L. & Smouse, P. E. (2010). Influence of acorn woodpecker social behaviour on transport of coast live oak (*Quercus agrifolia*) acorns in a southern California oak savanna. *Journal of Ecology* **98**, 561–572.

Sezen, U. U., Chazdon, R. L. & Holsinger, K. E. (2005). Genetic consequences of tropical second-growth forest regeneration. *Science* **307**, 891.

Sezen, U. U., Chazdon, R. L. & Holsinger, K. E. (2009). Proximity is not a proxy for parentage in an animal-dispersed Neotropical canopy palm. *Proceedings of the Royal Society B: Biological Sciences* **276**, 2037–2044.

da Silva, J. M. C. & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* **404**, 72–74.

Smouse, P. E., Focardi, S., Moorcroft, P. R., Kie, J. G., Forester, J. D. & Morales, J. M. (2010). Stochastic modelling of animal movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2201–2211.

Spiegel, O. & Nathan, R. (2007). Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters* **10**, 718–728.

Sun, C., Ives, A., Kraeuter, H. & Moermond, T. (1997). Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia* **112**, 94–103.

Terakawa, M., Isagi, Y., Matsui, K. & Yumoto, T. (2009). Microsatellite analysis of the maternal origin of *Myrica rubra* seeds in the feces of Japanese macaques. *Ecological Research* **24**, 663–670.

Tewksbury, J. J., Levey, D. J., Huizinga, M., Haak, D. C. & Traveset, A. (2008). Costs and benefits of capsaicin-mediated control of gut retention in dispersers of wild chilies. *Ecology* **89**, 107–117.

Tiffney, B. H. (2004). Vertebrate dispersal of seed plants through time. *Annual Review of Ecology Evolution and Systematics* **35**, 1–29.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. & Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 2163–2176.

Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D. M. (2005). The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions* **11**, 173–181.

Traveset, A. (1998). Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution and Systematics* **1**, 151–190.

Uriarte, M., Anciães, M., da Silva, M. T. B., Rubim, P., Johnson, E. & Bruna, E. M. (2011). Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. *Ecology* **92**, 924–937.

Valentini, A., Pompanon, F. & Taberlet, P. (2009). DNA barcoding for ecologists. *Trends in Ecology & Evolution* **24**, 110–117.

Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S. & Clawges, R. M. (2008). Lidar: shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment* **6**, 90–98.

Voigt, F. A., Arafeh, R., Farwig, N., Griebeler, E. M. & Böhning-Gaese, K. (2009). Linking seed dispersal and genetic structure of trees: a biogeographical approach. *Journal of Biogeography* **36**, 242–254.

Wang, B. C. & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution* **17**, 379–386.

Wehncke, E. V., Hubbell, S. P., Foster, R. B. & Dalling, J. W. (2003). Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species. *Journal of Ecology* **91**, 677–685.

Weir, J. E. S. & Corlett, R. T. (2007). How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology* **22**, 131–140.

Wenny, D. G. & Levey, D. J. (1998). Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America* **95**, 6204–6207.

Westcott, D. A., Bentrupperbaumer, J., Bradford, M. G. & McKeown, A. (2005). Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia* **146**, 57–67.

Westcott, D. A. & Graham, D. L. (2000). Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* **122**, 249–257.

Wheelwright, N. T. (1983). Fruits and the ecology of resplendent quetzals. *The Auk* **100**, 286–301.

Wikelski, M., Moxley, J., Eaton-Mordas, A., Lopez-Uribe, M. M., Holland, R., Moskowitz, D., Roubik, D. W. & Kays, R. (2010). Large-range movements of neotropical orchid bees observed via radio telemetry. *PLoS ONE* **5**, e10738.

Will, H. & Tackenberg, O. (2008). A mechanistic simulation model of seed dispersal by animals. *Journal of Ecology* **96**, 1011–1022.

Yumoto, T., Kimura, K. & Nishimura, A. (1999). Estimation of the retention times and distances of seed dispersed by two monkey species, *Alouatta seniculus* and *Lagothrix lagotricha*, in a Colombian forest. *Ecological Research* **14**, 179–191.