

# How intraspecific variation in seed-dispersing animals matters for plants

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## ABSTRACT

Seed dispersal by animals is a complex phenomenon, characterized by multiple mechanisms and variable outcomes. Most researchers approach this complexity by analysing context-dependency in seed dispersal and investigating extrinsic factors that might influence interactions between plants and seed dispersers. Intrinsic traits of seed dispersers provide an alternative way of making sense of the enormous variation in seed fates. I review causes of intraspecific variability in frugivorous and granivorous animals, discuss their effects on seed dispersal, and outline likely consequences for plant populations and communities. Sources of individual variation in seed-dispersing animals include sexual dimorphism, changes associated with growth and ageing, individual specialization, and animal personalities. Sexual dimorphism of seed-dispersing animals influences seed fate through diverse mechanisms that range from effects caused by sex-specific differences in body size, to influences of male *versus* female cognitive functions. These differences affect the type of seed treatment (e.g. dispersal *versus* predation), the number of dispersed seeds, distance of seed dispersal, and likelihood that seeds are left in favourable sites for seeds or seedlings. The best-documented consequences of individual differences associated with growth and ageing involve quantity of dispersed seeds and the quality of seed treatment in the mouth and gut. Individual specialization on different resources affects the number of dispersed plant species, and therefore the connectivity and architecture of seed-dispersal networks. Animal personalities might play an important role in shaping interactions between plants and dispersers of their seeds, yet their potential in this regard remains overlooked. In general, intraspecific variation in seed-dispersing animals often influences plants through effects of these individual differences on the movement ecology of the dispersers. Two conditions are necessary for individual variation to exert a strong influence on seed dispersal. First, the individual differences in traits should translate into differences in crucial characteristics of seed dispersal. Second, individual variation is more likely to be important when the proportions of particular types of individuals fluctuate strongly in a population or vary across space; when proportions are static, it is less likely that intraspecific differences will be responsible for changes in the dynamics and outcomes of plant–animal interactions. In conclusion, focusing on variation among foraging animals rather than on species averages might bring new, mechanistic insights to the phenomenon of seed dispersal. While this shift in perspective is unlikely to replace the traditional approach (based on the assumption that all important variation occurs among species), it provides a complementary alternative to decipher the enormous variation observed in animal-mediated seed dispersal.

*Key words:* behavioural syndromes, conditional mutualism, ecology of individuals, endozoochory, frugivory, granivory, individual specialization, scatterhoarding, seed-dispersal effectiveness.

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## I. INTRODUCTION

The majority of woody plants rely on animals for dispersal of their propagules (Howe & Smallwood, 1982; Jordano, 2000; Herrera, 2002). Plants typically accomplish this goal by producing fleshy fruits that are ingested by frugivores, seeds with elaiosomes that are dispersed by ants, or nuts that are scatter-hoarded in topsoil by corvids, rodents, or small marsupials (Jordano, 2000; Forget & Vander Wall, 2001; Leal *et al.*, 2014; Pesendorfer *et al.*, 2016a). The behaviour of animal vectors determines patterns of seed dispersion, consequently shaping spatial and temporal dynamics of plant recruitment (Beckman & Rogers, 2013; Sasal & Morales, 2013; Razafindratsima & Dunham, 2016). On a local scale, seed dispersal can determine whether seeds escape negative density-dependent mortality near their maternal plant and can result in arrival at especially favourable sites for seedling establishment (Hirsch *et al.*, 2012; Carlo & Tewksbury, 2014). On larger scales, seed dispersal can determine how quickly plants are able to shift their range boundaries in response to climate change (Kremer *et al.*, 2012), influence the pace of invasions of exotic plants (Traveset & Richardson, 2014), and provide demographic and genetic connections between otherwise isolated populations (Nathan, 2006). In addition, animal-mediated seed dispersal exerts selective pressures on multiple plant traits, from morphology and chemistry of fruits and seeds (Tewksbury *et al.*, 2008; Lomáscolo *et al.*, 2010; Vander Wall, 2010; Rodríguez, Alquézar & Peña, 2013; Baldwin & Whitehead, 2015) to life history (Herrera *et al.*, 1998; Zwolak *et al.*, 2016).

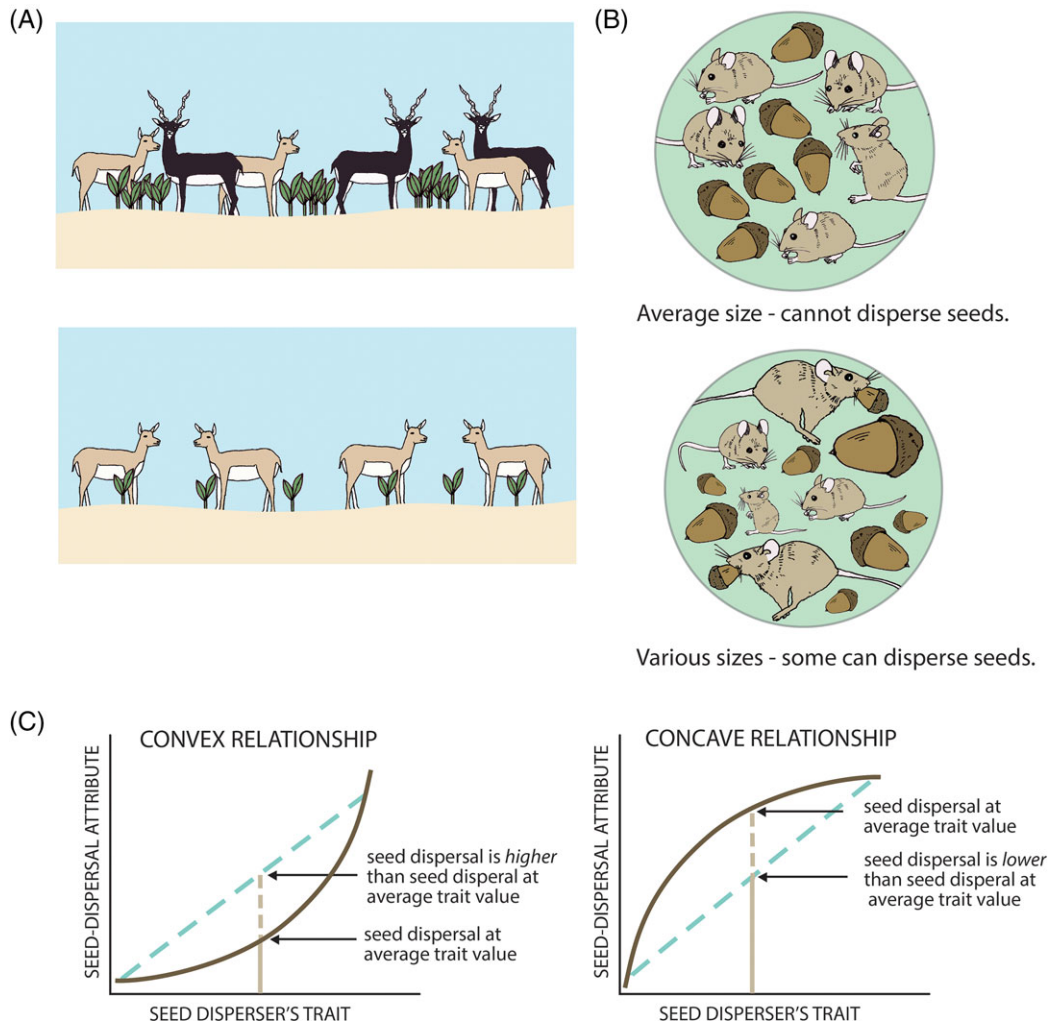
Animal-mediated seed dispersal is a complex process and researchers have grappled for decades to construct predictive frameworks for it (Wang & Smith, 2002; Côrtes & Uriarte, 2013; Schupp, Jordano & Gómez, 2017). A consistent challenge is the inconsistency of seed dispersal patterns and processes: animal seed dispersal is often referred to as ‘highly stochastic’ – its outcomes are thought to be almost impossible to predict and relationships between particular dispersal agents and spatial patterns of plant recruitment are weak (Getzin, Wiegand & Hubbell, 2014). The most common solution has been to focus on ‘context-dependency’ by analysing how a wide range of environmental factors influences who disperses seeds and where they go. Examples of frequently studied factors that shape seed dispersal include seed availability, seed chemistry, predation risk, habitat type, and so-called ‘community context’ (i.e. the abundance and identity of species participating in the interaction; Perea

*et al.*, 2013; Lichti *et al.*, 2014; Griffiths *et al.*, 2015; Ferger *et al.*, 2016; Pesendorfer *et al.*, 2016b; Zwolak *et al.*, 2016). Examining the role of seed dispersers’ intrinsic traits provides a complementary approach, with the goal of identifying links between specific characteristics of particular dispersal agents and dispersal outcomes.

One method to achieve this goal is to combine different species of seed dispersers that share similar traits into functional groups (e.g. Dennis & Westcott, 2006; Jordano *et al.*, 2007; Moran & Catterall, 2010; González-Castro, Calviño-Cancela & Nogales, 2015). A frequent problem, though, is large intraspecific variation in morphological, physiological, and behavioural traits (Bolnick *et al.*, 2003; Sih, Bell & Johnson, 2004). These intraspecific differences can originate from sexual dimorphism (Shine, 1989), ontogenetic niche shifts (Nakazawa, 2015), individual specialization on distinct food resources (Bolnick *et al.*, 2003), and personality differences, also known as ‘behavioural syndromes’ (Sih *et al.*, 2004). Such variation is often treated as random noise that needs to be eliminated or controlled statistically in attempts to identify ‘true’ patterns. However, mounting evidence suggests that differences among individuals should be embraced as a potential driver of patterns in population and community ecology (Violle *et al.*, 2012; Wolf & Weissing, 2012; González-Varo & Traveset, 2016; Pennisi, 2016; Moran, Wong & Thompson, 2017). Thus, dependence on species averages is recognized as a limitation of current frameworks of plant–seed disperser interactions (Schupp *et al.*, 2017).

The key point is that if some individuals contribute disproportionately to seed dispersal or are more likely to provide rare dispersal outcomes, then relying on averages will provide not only an incomplete picture of dispersal but will likely move us away from understanding its mechanistic underpinning (Benton, Plaistow & Coulson, 2006; McConkey & O’Farrill, 2015; Poisot, Stouffer & Gravel, 2015; González-Varo & Traveset, 2016). There are several reasons why this is likely to happen.

First, species-level data can mask unique seed-dispersal functions performed by specific ages, stages, or classes of individuals (Fig. 1A). This is particularly significant in conservation biology: loss or decline of these classes can lead to severe changes in seed dispersal even if the species still persists (McConkey & O’Farrill, 2015, 2016). Furthermore, if individuals differ in their performance as seed dispersers, accounting for the heterogeneity between individuals is crucial for accurate predictions of seed



**Fig. 1.** Seed-dispersal attributes (number of dispersed seeds, distance, seed deposition sites) mediated by a single disperser species typically are described with average values and associated error. In some situations, however, a focus on averages can mask ecological processes. (A) Species-level data can conceal unique seed-dispersal services provided by specific stages or classes of individuals. Spatial or temporal shifts in proportions of these individuals will lead to unexpected (given species-level data) changes in seed dispersal – even when total abundance of the species remains the same (Jadeja *et al.*, 2013; McConkey & O’Farrill, 2016). (B) When only individuals with extreme trait values disperse seeds, relying on averages might lead to an erroneous conclusion that the plant–seed dispersal interaction is ‘forbidden’ due to anatomical or phenological mismatches (González-Varo & Traveset, 2016). (C) When relationships between traits of seed dispersers and seed-dispersal attributes are non-linear (concave or convex: solid black line), seed dispersal predicted by average trait values does not reflect average seed dispersal in the population (Jensen’s inequality: Bolnick *et al.*, 2011; Denny, 2017). Illustration credit: Emily Underwood.

dispersal – particularly under unprecedented conditions created by global changes (Benton *et al.*, 2006).

Second, when functional traits are expressed as mean values, interactions between some species of plants and seed dispersers can be erroneously labelled as ‘forbidden’ due to apparent mismatches in anatomy or phenology (González-Varo & Traveset, 2016; Fig. 1B). However, many interactions are stage- or sex-specific. Thus, reducing intraspecific variability to a single (average) value can lead to biased understanding of interactions and underestimation of connectedness in ecological interaction networks (Poisot *et al.*, 2015; González-Varo & Traveset, 2016).

Third, inferences based on averages might be inaccurate due to Jensen’s inequality (Ruel & Ayres, 1999; Martin & Huey, 2008; Denny, 2017). If the relationship between individual traits and their ecological functions is non-linear (e.g. convex or concave), then the ecological function estimated at the mean trait value is not equal to the mean ecological function in the population; correct estimates need to take into account the amount of variation and shape of the relationship (Bolnick *et al.*, 2011; Denny, 2017; Fig. 1C). Given that non-linear relationships between traits and functions are almost universal, implications of Jensen’s inequality are ubiquitous (Denny, 2017).

Finally and most generally, even when the main interest is in the species, many ecological processes operate at the level of individuals. Such processes should be studied and analysed at the individual scale because aggregating individual-level data to produce species averages often masks crucial ecological patterns (see e.g. Cam *et al.*, 2002; Cohen *et al.*, 2005; Clark *et al.*, 2011; Rudolf & Rasmussen, 2013). In the end, it is individuals that interact with each other, not species (Ings *et al.*, 2009; Clark *et al.*, 2011; Violle *et al.*, 2012). Optimal foraging theory (Pyke, 1984), arguably the backbone of plant–disperser studies, concerns individuals rather than species. Thus, we might gain new insights when we apply it to individual frugivores as they forage, rather than to species averages. Potential outcomes include improved prediction of dispersal distances, sites of seed deposition, variation in seed fates, and ultimately better estimation of plant recruitment patterns.

The importance of intraspecific variation for plant–animal interactions is already documented as a provider of rare but important dispersal events (e.g. to particularly suitable microsites: Wenny & Levey, 1998). However, the ecological effects of such variation are seldom considered. Data on individual variation in frugivore or granivore species often come from unplanned observations (see Pollux, 2017, for a recent exception). Recognition of the consequences of intraspecific variation in seed-dispersing animals could help direct empirical studies of plant–animal interactions.

In this review, I discuss the potential ecological implications of intraspecific variation in seed-dispersing animals (including both frugivores and granivores) and summarize existing empirical evidence on this subject (Table 1). I focus mostly on frugivory and granivory, but will also discuss ectozoochory when relevant. My goal is threefold: (i) identifying multiple ways in which individual variation in seed-dispersing animals affects patterns of seed deposition, (ii) integrating research on ecological differences among individuals with research on animal-mediated seed dispersal, and (iii) suggesting when individual variation is most likely to alter the process and outcome of seed dispersal.

## II. POTENTIAL INFLUENCES ON PLANT ECOLOGY AND EVOLUTION

Individual differences affect populations, communities, and evolution through multiple mechanisms (reviewed by Bolnick *et al.*, 2011; Sih *et al.*, 2012; Violle *et al.*, 2012; Wolf & Weissing, 2012). Here, I focus on potential effects of intraspecific variation on the process of seed dispersal. I categorize effects of individual variation among seed dispersers according to the affected attribute of dispersal: the quantity of dispersed seeds, the quality of seed dispersal, dispersal distance, traits of dispersed seeds, and the number and identity of dispersed plant species.

### (1) Quantity of dispersed seeds

Seed-dispersal effectiveness is often viewed as the product of quantity and quality components of dispersers (Schupp *et al.*, 2017). The number of seeds dispersed by an animal is the ‘quantity’ component (Fig. 2) and can be decomposed into the number of dispersal events multiplied by the average number of seeds dispersed per dispersal event (Schupp *et al.*, 2017). Growing evidence indicates that individuals of seed-dispersing species differ strongly in the number of seeds they disperse, with some individuals responsible for the majority of dispersed seeds (Table 1). Intraspecific variation in dispersal quantity would likely result in unequal contributions to plant dispersal, with some individuals of a given species disproportionately important in this regard.

### (2) Quality of dispersal

The second component of seed dispersal effectiveness, quality, is defined as the probability that a dispersed seed will produce a new adult (Schupp *et al.*, 2017). This probability is influenced by the treatment of seeds in the gut or mouth and the site characteristics where seeds are deposited (Schupp *et al.*, 2017). If individual variation affects dispersal quality, then a single species might function as multiple species that differ in their type of interaction – in extreme cases, some species of disperser may simultaneously play the roles of seed predator and mutualist (Sih *et al.*, 2012). This situation can occur in frugivores if individuals differ in the likelihood of defaecating or regurgitating seeds intact *versus* damaged by mastication or digestive enzymes (Türke & Weisser, 2013; Pollux, 2017). It is also likely to occur in scatterhoarder–plant interactions, where animals disperse some seeds but consume others. These interactions will be mutualistic only when the benefits to the plant of seed dispersal outweigh the costs of seed consumption (Jansen & Forget, 2001; Theimer, 2005; Zwolak & Crone, 2012). Outcomes of such conditional interactions are usually thought to be determined by changes in relative abundance of particular species. However, if populations of seed dispersers are composed of non-identical individuals that differ in behaviour (see e.g. Pan *et al.*, 2013), some of them might consistently act as mutualists in their interactions with plants, and some as antagonists. Under this scenario, fluctuations in the frequency of these types of individuals may fundamentally change that species’ role in interspecific interactions and in the community. In some years, the species may be generally beneficial and in other years generally harmful (Fig. 2).

The neighbourhood in which seeds are deposited often determines the likelihood of successful germination, establishment, and growth (Howe & Miriti, 2004; Swamy *et al.*, 2011, but see also Fricke *et al.*, 2013). Different animals can deposit seeds in different types of locations, yet this process has been studied mostly through interspecific comparisons (e.g. Loayza & Knight, 2010; Mellado & Zamora, 2014; Razafindratsima & Dunham, 2015). However, individuals of the same species might also differ in location-related benefits of seed deposition. This



Table 1. Examples of studies reporting effects of individual variation in animal seed dispersers on plants. The table includes studies that linked seed dispersal characteristics to traits of individual dispersers or reported individual differences in seed dispersal

Source of individual variation	Study	Seed disperser	Plant	Seed-dispersal characteristic	Patterns of individual variation
Differences related to sex	Cords (1986)	<i>Cercopithecus ascanius</i> & <i>C. mitis</i> (mammals)	Multiple species	Quantity <sup>a</sup>	Males more frugivorous than females
	Clarke & Kramer (1994)	<i>Tamias striatus</i> (mammal)	Tests with sunflower seeds	Quality <sup>b</sup>	Females with young scatterhoarded more seeds than males and females without young
	Krijger <i>et al.</i> (1997)	<i>Corapipo gutturalis</i> & <i>Manacus manacus</i> (birds)	Melastomataceae	Quality	Mating behaviour affected seed deposition sites
	Wenny (2000)	<i>Procnias tricarunculata</i> (bird)	<i>Ocotea endresiana</i>	Quality, distance	Mating behaviour affected seed deposition sites
	Herrel <i>et al.</i> (2004)	<i>Anolis</i> spp. (reptiles)	<i>Canella winterana</i> , <i>Ficus cotenifolia</i> & other species	Quantity	Females ate more fruit per unit body size than males
	Barkley & Jacobs (2007)	<i>Dipodomys merriami</i> & <i>D. microps</i> (mammals)	Tests with sunflower seeds	Quality	Females relied on landmarks to recover cached seeds; males did not
	De Camargo <i>et al.</i> (2011)	<i>Gracilinanus agilis</i> (mammal)	<i>Miconia albicans</i>	Quantity	Females defaecated more seeds than males
	Jenkins (2011)	<i>Dipodomys ordii</i> & <i>D. merriami</i> (mammal)	Tests with sunflower seeds	Quality	Sex affected repeatability of seed-hoarding tactics (scatter-versus larderhoarding)
	Karubian <i>et al.</i> (2012)	<i>Cephalopterus penduliger</i> (bird)	<i>Oenocarpus bataua</i> , <i>Virola dixonii</i> & <i>Ficus crassiuscula</i>	Distance	Mating behaviour influenced seed deposition patterns
	Jadeja <i>et al.</i> (2013)	<i>Antilope cervicapra</i> (mammal)	<i>Prosopis juliflora</i>	Quantity, quality, distance	Adult males removed more fruits; mating behaviour affected seed deposition sites
	Mancilla-Leytón, González-Redondo & Vicente (2013)	<i>Oryctolagus cuniculus</i> (mammal)	<i>Myrtus communis</i>	Quality	Females more likely to defaecate intact seeds
	Pan <i>et al.</i> (2013)	<i>Tamias sibiricus</i> (mammal)	<i>Pinus koraiensis</i>	Quality	Males more likely to consume cached seeds
	Rosalino <i>et al.</i> (2013)	<i>Apodemus sylvaticus</i> (mammal)	<i>Quercus faginea</i> , <i>Q. rotundifolia</i> & <i>Q. suber</i>	Traits of dispersed seeds	Females more prone to consume acorns of smaller width
	Oleksy, Racey & Jones (2015)	<i>Pteropus rufus</i> (mammal)	<i>Ficus grevei</i>	Distance	Females had larger home ranges, thus were more likely to disperse seeds further
Zhang <i>et al.</i> (2016)	<i>Tamias sibiricus</i> (mammal)	<i>Pinus koraiensis</i>	Quality	Males, but not females, established seed caches with respect to visual landmarks	
Ontogenetic shift	Cords (1986)	<i>Cercopithecus ascanius</i> & <i>C. mitis</i> (mammals)	Multiple species	Quantity	In juveniles, body size was negatively related to the proportion of fruits in diet
	Clarke & Kramer (1994)	<i>Tamias striatus</i> (mammal)	Tests with sunflower seeds	Quality	Juveniles mostly scatterhoarded and adults mostly larderhoarded seeds
	Kubitzki & Ziburski (1994)	<i>Colossoma macropomum</i> (fish)	<i>Crataeva benthamii</i> & <i>Neolabatia cuprea</i>	Quality	Seeds more likely to survive gut passage in older individuals
	Hampe (2001)	<i>Erithacus rubecula</i> (bird)	<i>Frangula alnus</i>	Quantity, distance	Fruits were ingested mostly by juvenile individuals; juveniles dispersed seeds further
	Herrel <i>et al.</i> (2004)	<i>Anolis</i> spp. (reptiles)	<i>Canella winterana</i> , <i>Ficus cotenifolia</i> & other species	Quantity, traits of dispersed seeds	Larger individuals ate more fruits and ingested larger fruits
	McConkey & Drake (2006)	<i>Pteropus tonganus</i> (mammal)	Multiple species	Distance	Juveniles more likely than adults to be chased from fruiting plants, carrying fruits away
	Galetti <i>et al.</i> (2008)	<i>Piaractus mesopotamicus</i> (fish)	<i>Bactris glaucescens</i>	Quality	Larger individuals had more intact seeds in the gut
	Muñoz & Bonal (2008)	<i>Mus spretus</i> & <i>Apodemus sylvaticus</i> (mammals)	<i>Quercus ilex</i>	Traits of dispersed seeds	Probability of seed removal decreased with ratio of seed size to rodent size

Table 1. Continued

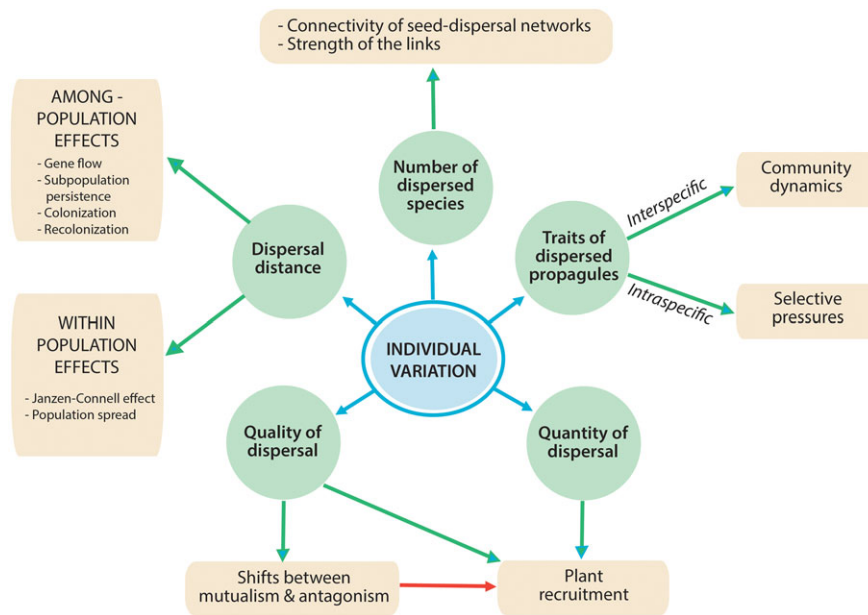
Source of individual variation	Study	Seed disperser	Plant	Seed-dispersal characteristic	Patterns of individual variation
	Reys, Sabino & Galetti (2009)	<i>Brycon hilarii</i> (fish)	Multiple species	Quantity	Longer individuals were more likely to have fruit in their gut
	Anderson, Rojas & Flecker (2009)	<i>Piaractus brachipomus</i> & <i>Colossoma macropomum</i> (fish)	Multiple species	Quality	Larger and older individuals defaecated more intact seeds
	Eisenhauer <i>et al.</i> (2010)	<i>Lumbricus terrestris</i> (earthworm)	Eight different species	Quantity	Heavier individuals ingested more seeds
	Anderson <i>et al.</i> (2011)	<i>Colossoma macropomum</i> (fish)	<i>Duroia duckei</i> , <i>Cecropia latiloba</i> , <i>Cayaponia cruegeri</i> , <i>Cayaponia tubulosa</i> & <i>Annona muricata</i>	Distance	Larger individuals dispersed seeds further
	King, Milicich & Burns (2011)	<i>Hemidenina crassidens</i> (insect)	<i>Fuchsia excorticata</i>	Quality	In large individuals, seeds more likely to germinate after gut passage
	Calvino-Cancela & Rubido-Bará (2012)	<i>Arion ater</i> (gastropod)	Nine different species	Traits of dispersed seeds; number of dispersed species	Body size limited range of ingested seed sizes
	Culliney <i>et al.</i> (2012)	<i>Corvus hawaiiensis</i> (bird)	Multiple species	Number of dispersed species	Juveniles foraged on fruits of more plant species
	Larsen & Burns (2012)	<i>Deinacrida connectens</i> (insect)	<i>Gaultheria depressa</i>	Quantity and quality	Larger individuals consumed more seeds and were more likely to defaecate seeds intact
	Türke & Weisser (2013)	<i>Arion rufus</i> (gastropod)	Seven different species	Quality	Larger individuals more likely to swallow and disperse seeds rather than consume the elaiosome
	Tulipani & Lipcius (2014)	<i>Malaclemys terrapin terrapin</i> (reptile)	<i>Zostera marina</i>	Quantity	Individuals with larger heads were less likely to ingest seeds
	Correa <i>et al.</i> (2015a)	Seven species of fish	Multiple species	Quantity, quality, and number of dispersed species	Larger individuals dispersed more seeds, more plant species, and a greater range of seed sizes; in some species of plants, seeds dispersed by larger individuals had higher probability of surviving gut passage and germinating
	Correa <i>et al.</i> (2015b)	<i>Brycon amazonicus</i> , <i>B. falcatus</i> & <i>B. melanopterus</i> (fish)	Multiple species	Quality	Larger fish more likely to have intact seeds in stomach
	Benitez-Malvido <i>et al.</i> (2016)	<i>Alouatta pigra</i> (mammal)	Multiple species	Number of dispersed species	Adult individuals consumed more plant species than juveniles and infants
Individual specialization	Jung (1992)	<i>Turdus migratorius</i> (bird)	<i>Morus alba</i> , <i>Lonicera × bella</i> & <i>Cornus stolonifera</i>	Traits of dispersed seeds	Individuals differed in preferred fruit species
	Willson & Comet (1993)	<i>Corvus caurinus</i> (bird)	Artificial and natural fruits (multiple species)	Traits of dispersed seeds	Individuals differed in preferred colour and nutrient content of fruits
	Willson (1994)	<i>Turdus migratorius</i> (bird)	Artificial and natural fruits (multiple species)	Traits of dispersed seeds	Individuals differed in preferred colour, nutrient content, and seed load of fruits
	Herrera <i>et al.</i> (2008)	<i>Rousettus aegyptiacus</i> (mammal)	Multiple species	Number of dispersed species	Individuals differed in consumed fruit species
	Araújo <i>et al.</i> (2010)	<i>Gracilinanus microtarsus</i> (mammal)	Multiple species	Number of dispersed species	Population consisted of dietary generalists and specialists
	Rawsthorne, Watson & Roshier (2011)	<i>Acanthagenys rufogularis</i> (bird)	<i>Amyema quandang</i>	Distance	Non-breeding birds predicted to disperse seeds further
	Lenz <i>et al.</i> (2011)	<i>Bycanistes bucinator</i> (bird)	Five different species	Distance	Individuals differed in seed-dispersal distance

Table 1. Continued

Source of individual variation	Study	Seed disperser	Plant	Seed-dispersal characteristic	Patterns of individual variation
	Cantor <i>et al.</i> (2013)	<i>Didelphis albiventris</i> (mammal)	Multiple species	Number of dispersed species	Population consisted of dietary generalists and specialists
	Dáttilo <i>et al.</i> (2014)	<i>Alouatta palliata</i> (mammal)	Multiple species	Number of dispersed species	Population consisted of dietary generalists and specialists
	Yi <i>et al.</i> (2016)	<i>Tamias sibiricus</i> (mammal)	<i>Pinus koraiensis</i>	Quality	Negative association between tendency to scatterhoard and to pilfer cached seeds
	Pollux (2017)	<i>Cyprinus carpio</i> (fish)	<i>Sparganium emersum</i> & <i>Sagittaria sagittifolia</i>	Quantity, quality, distance	Individuals differed in seed ingestion, digestion, and gut retention time
Behavioural syndromes	Dochtermann & Jenkins (2007)	<i>Dipodomys merriami</i> (mammal)	Tests with millet seeds	Distance (?)	Bolder individuals established more-dispersed caches; more-aggressive individuals were more consistent in caching spatial patterns

<sup>a</sup>Quantity of seed dispersal is defined as the number of seeds dispersed by the dispersal agent (Schupp *et al.*, 2017).

<sup>b</sup>Quality of seed dispersal is the probability that seeds handled by the dispersal agents produce a new adult (Schupp *et al.*, 2017).



**Fig. 2.** Individual variation in seed dispersers affects many different aspects of seed dispersal (green circles) that in turn have diverse consequences for plant ecology and evolution (red boxes). Sources of individual variation include differences in: body size, age, social status, cognitive functions, reproductive roles, behavioural types, and dietary preferences. Illustration credit: Emily Underwood.

phenomenon diversifies seed-deposition sites and increases the variation of seed fates. Moreover, plant regeneration in different habitats might depend on different categories of individuals of the disperser species. Likewise, certain individuals might provide crucial dispersal to microsites where recruitment is possible (e.g. into forest gaps: Wenny & Levey, 1998) and consequently determine patterns of plant regeneration (Fig. 2). Thus, taking into account individual variation among seed-dispersing animals can increase our ability to predict recruitment outcomes in many plant species.

### (3) Distance of seed dispersal

Following Schupp, Jordano & Gómez (2010), seed-dispersal distance is treated here separately from seed-dispersal quality because it does not directly translate into plant recruitment. On the one hand, seeds that are dispersed far have a typically low chance of survival and germination because habitat quality tends to be spatially autocorrelated; the chances of being deposited in suitable microsites typically decline with distance from the maternal plant (e.g. John *et al.*, 2007; Condit *et al.*, 2013). On the other hand, seeds that are dispersed far

from parent plants and conspecifics have higher chances of escaping negative density dependence (the Janzen–Connell effect: Jansen, Bongers & van der Meer, 2008; Swamy *et al.*, 2011) and colonizing ephemeral, suitable microsites.

Even though the impact of dispersal distance on plant recruitment is difficult to generalize, it determines several important processes, both within and among populations (e.g. population spread, maintaining gene flow, contributing to persistence of subpopulations, and recolonization of formerly occupied patches: Nathan, 2006; Corlett & Westcott, 2013; Fig. 2). Intraspecific variation in seed-dispersing animals has generally unrecognized potential to influence all these processes. Rare events are often crucial in seed dispersal (Nathan *et al.*, 2008; Loayza & Knight, 2010), and their likelihood is determined by variation around a mean, not the mean itself. Furthermore, most single-distribution dispersal kernels that are frequently used to model seed dispersal implicitly assume that seeds are dispersed by identical individuals, driven by only by extrinsic factors and stochasticity (Russo, Portnoy & Augspurger, 2006; Lowe & McPeck, 2014). However, if different classes of individuals (e.g. males and females) differ in seed-dispersal distance, the resulting seed shadows will be heterogeneous and multimodal. Thus, if we want to understand the ecological and evolutionary roles of seed dispersal, we need to know how different classes of individuals contribute to it. This is particularly important when those classes differ strongly in the distances they disperse seeds. The challenge is to link such differences to specific functional traits (e.g. body size in Amazonian fish: see Section III).

#### (4) Traits of dispersed seeds

Individuals of the same disperser species can use different cues to select fruits and seeds. These choices can occur both interspecifically (i.e. individuals of a given species prefer different species of fruits: Jung, 1992; Willson & Comet, 1993; Willson, 1994; Herrera *et al.*, 2008) and intraspecifically (i.e. individuals of a given species prefer different traits in fruits of the same species: Muñoz & Bonal, 2008; Rosalino *et al.*, 2013). Consequences of preferences towards fruits of different plant species can manifest at the plant community level and affect seed-dispersal networks. Consequences of preferences for particular types of fruits of the same species can influence recruitment success of individual plants and shape selective pressures on fruit traits (Fig. 2). Such pressures will be more diffuse and weaker than in the case of homogeneous preferences by frugivores. As an example, scatterhoarding rodents are usually found to harvest larger seeds preferentially, at least in conspecific comparisons (Lichti, Steele & Swihart, 2017). However, if there is variation in individual preferences of dispersers (e.g. Muñoz & Bonal, 2008), variation in seed size might be beneficial for plants (Geritz, 1998; Shimada *et al.*, 2015). Intriguingly, plants that rely on scatterhoarders for seed dispersal tend to exhibit larger variation in seed size than plants with seeds dispersed by other means (M. Bogdziewicz & R. Zwolak, unpublished data). While this variation might

be maintained by multiple factors and trade-offs (McGinley, Temme & Geber, 1987; Gómez, 2004; Vargas *et al.*, 2015; Wang & Ives, 2017), intraspecific variability in disperser preferences may contribute to intraspecific variability in seed size.

Divergent frugivore preferences could also lead to disruptive selection on fruit traits. However, selective pressures of even very different taxa on fruit characteristics are surprisingly difficult to document (Jordano, 1995; Herrera, 2002; Lomáscolo *et al.*, 2010). Thus, identifying responses to different selective pressures exerted by different individuals within the same species of frugivore is unlikely. To the contrary, perhaps variance in individual preferences contributes to the difficulty of finding so-called ‘dispersal syndromes’ (sets of fruit traits that have co-evolved in response to selection by different types of frugivores: Lomáscolo *et al.*, 2010).

#### (5) Number and identity of dispersed species

If individuals of the same frugivorous or granivorous species differ in the number of plant species they disperse, connectivity of seed-dispersal networks increases, but particular links become weaker (Fig. 2) because only a subset of individuals participates in some of the pairwise interactions (Bolnick *et al.*, 2011; Wolf & Weissing, 2012). Plant–animal mutualisms are generally thought to be diffuse, with many plant species dispersed by many disperser species (Herrera, 2002). Individual differences among seed dispersers make these interactions even more diffuse, which may reduce plant–plant competition for dispersers (Violle *et al.*, 2012) and has important consequences for the persistence of plant–disperser mutualisms: weaker and more diffuse connections stabilize ecological networks, increasing their resilience to species loss and habitat fragmentation (Bascompte, 2009; Moran *et al.*, 2017).

Individual variation among dispersers in the number of plant species they consume can manifest in several ways. For example, individuals can disperse either nested subsets of plant species (Araújo *et al.*, 2010; Cantor *et al.*, 2013; Dáttilo *et al.*, 2014; Benitez-Malvido *et al.*, 2016) or different groups of species (Herrera *et al.*, 2008). It is too soon to tell which form is more common in plant–frugivore interactions but in general, nestedness is a frequent feature of most ecological networks (Montoya, Pimm & Solé, 2006; Pires *et al.*, 2011). If certain classes of individuals (e.g. larger ones: Calvino-Cancela & Rubido-Bará, 2012; Correa *et al.*, 2015a) disperse disproportionately more species of plants than other classes, then the former classes are particularly important for stability of interaction networks (Bascompte, 2009). Eliminating such individuals through, for example, selective harvest might have particularly grave consequences for recruitment in plant communities.

Finally, if different classes of individuals disperse different plant species, then fluctuations in the relative abundance of such classes (e.g. due to shifts in age structure resulting from seasonal or multiannual changes in reproduction) could alter



Table 2. Examples of predicted relationships between individual traits of seed-dispersing animals and characteristics of seed dispersal

Prediction	Comment
<i>Differences related to sex</i>	
Sex with larger home range size disperses seeds further	Applies mostly to ecto- and endozoochory (dispersal distance in scatterhoarders is often limited by transportation costs); differences might be particularly pronounced during mating season when the differences between male and female home range sizes increase
In lek-mating species, lekking individuals show more clumped seed-deposition patterns	Plants that set seed during the breeding season are most likely to be affected
<i>Ontogenetic shifts</i>	
Larger individuals disperse higher quantities of seeds	A consequence of higher food intake or, in the case of ectozoochory, larger body surface
Larger individuals disperse a greater number of plant species	This relationship might be particularly pronounced in species where gape size limits the range of ingested seed sizes
Larger individuals are more likely to act as seed dispersers rather than predators	Applies mostly to species that can swallow or masticate seeds
Larger individuals transport seeds further	A consequence of larger home ranges, longer gut retention times, or both
<i>Individual specialization</i>	
Individuals without territories ('floaters') disperse seeds further than territory owners	Plants that set seed during the breeding season are most likely to be affected
<i>Behavioural syndromes</i>	
Bolder individuals deposit seeds in more risky areas	Risky areas include open habitats and places further from refuge
Individuals with high activity levels disperse seeds further	A consequence of a link between activity levels and home-range size or movement rate
Individuals with high activity levels disperse more seeds	Applies if high resource-acquisition rate is needed to fuel higher activity

patterns of plant recruitment and influence plant community dynamics. Such effects remain unexplored.

### III. PATTERNS OF INTRASPECIFIC VARIATION IN SEED-DISPERSING ANIMALS

In this section, I discuss generalities emerging from empirical studies on intraspecific differences in seed dispersers (see Table 1). I also develop predictions on the effects of variation in particular traits of dispersers on seed dispersal (summarized in Table 2).

#### (1) Differences related to sex

Due to sexual selection, different reproductive roles, and intraspecific niche divergence, females and males differ in numerous traits that might influence interspecific interactions (Shine, 1989; Temeles, Miller & Rifkin, 2010; De Lisle & Rowe, 2015; Thomas *et al.*, 2015). One of the most obvious forms of sexual dimorphism is differences in body size and morphology. In animals that disperse seeds, such differences can influence the size range of handled fruits and nuts (Chen & Moles, 2015). Moreover, even if male and female body sizes are similar, morphological differences in mouthparts can affect food selection and quality of seed treatment. For example, in comparison with males, female wood mice (*Apodemus sylvaticus*) were more likely to consume acorns of smaller width – even though mean body mass did not differ

between tested males and females (Rosalino *et al.*, 2013). In rabbits (*Oryctolagus cuniculus*), more intact seeds passed through the guts of females than of males, probably due to differences in jaw structure (Mancilla-Leytón *et al.*, 2013). Furthermore, individuals of different genders can have different diets, either to avoid competition or as a consequence of differences in size, morphology, and energy requirements (Shine, 1989). Such differences can translate into sex-specific patterns of seed dispersal and predation. In the agile mouse opossum (*Gracilianus agilis*), females consumed more fruits and defaecated more seeds than males (de Camargo *et al.*, 2011), but in guenons (*Cercopithecus ascanius* and *C. mitis*) males were more frugivorous than females (Cords, 1986). In house finches (*Carpodacus mexicanus*), females and males preferred sunflower kernels of different colours (Behbahaninia *et al.*, 2012).

Males and females also differ behaviourally, particularly with regard to their roles during mating and breeding. Sexual dimorphism in behaviour of frugivores can strongly influence patterns of seed dispersal. For instance, males of lek-breeding long-wattled umbrellabirds (*Cephalopterus penduliger*) disperse seeds long distances but mostly within leks, while females transport seeds over shorter distances and distribute them more uniformly in the landscape (Karubian *et al.*, 2012; see also predictions in Table 2). These behaviours influence the genetic structure of dispersed plants: males often bring seeds from remote plants into leks, which can result in stands of genetically diverse trees (Karubian *et al.*, 2010). A similar phenomenon probably occurs in other lekking seed dispersers (e.g. Krijger *et al.*, 1997; Jadeja *et al.*, 2013), and

more generally in species with courtship displays that occur in specific sites. Such sites can become hotspots of plant regeneration or seed death – depending on their quality for seedling establishment. In three-wattled bellbirds (*Procnias tricarunculata*), for example, seed dispersal by males was particularly beneficial for recruitment of a montane tree, *Ocotea andresiana*, because they mostly deposited seeds in canopy openings, which they use as display sites (Wenny & Levey, 1998; Wenny, 2000; see also Jadeja *et al.*, 2013 for broadly analogous findings in blackbuck antelope, *Antilope cervicapra*). The opposite effect was found in white-throated manakins, *Corapipo gutturalis*, whose lek sites were too dark for seedling emergence (Krijger *et al.*, 1997). Differences between sexes can further be broken down into differences between different classes of males and females (e.g. dominant *versus* subordinate or territorial *versus* non-territorial males: see Section III.3). As a rule, where these sex differences are associated with courtship or mating behaviour, they should apply systematically in some seasons and not others – and thus should matter only for plants that fruit during those seasons.

Gender also influences home-range size (e.g. in scramble competition mating systems, males often cover large areas to mate with several females: Stradiotto *et al.*, 2009), activity levels (e.g. Ellsworth *et al.*, 2016), and distance of natal dispersal (male-biased in most mammals; female-biased in most birds: Trochet *et al.*, 2016). These patterns can translate into pronounced, sex-related differences in seed-dispersal distance. For instance, larger home-range size can be linked to routine longer-distance seed dispersal (Oleksy *et al.*, 2015; Table 2). By contrast, natal dispersal is a single episode, but can be important for rare, long-range seed-dispersal events.

Fate of seeds can also be affected by sex-specific differences in cognitive functioning of dispersers. Spatial memory of scatterhoarders determines the proportion of stored food items that the animal will be able to use during a period of food scarcity. For the plant, it determines the risk that cached seeds will be recovered and consumed, which usually precludes successful germination and establishment. Females and males of scatterhoarding species can be expected to differ in spatial memory because it is influenced by sex hormones such as oestrogen and testosterone (e.g. Galea, Kavaliers & Ossenkopp, 1996; Clint *et al.*, 2012). Such a difference was documented in kangaroo rats (*Dipodomys merriami* and *D. microps*): absence of local landmarks deteriorated recovery of experimental caches in females but not in males [Barkley & Jacobs, 2007; see also Pan *et al.*, 2013, Yi *et al.*, 2016, and Zhang *et al.*, 2016 for related findings in Siberian chipmunks, *Tamias sibiricus*]. In pinyon jays (*Gymnorhinus cyanocephalus*), the observed differences in seed recovery were probably related to division of labour during the breeding season: females incubate eggs and keep nestlings warm, and males recover seeds that were cached in the autumn to provide food for themselves, their mates, and nestlings (Dunlap *et al.*, 2006). Only the latter task requires superior memory. In accordance with this reasoning, mated females had less-accurate long-term spatial memory than males and non-mated females (Dunlap *et al.*, 2006). Finally, in kangaroo

rats (*Dipodomys ordii* and *D. merriami*), males had considerably higher repeatability of seed-hoarding tactics (scatterhoarding *versus* larderhoarding) (Jenkins, 2011). It remains to be demonstrated whether these types of difference influence plant recruitment.

In summary, sexual dimorphism of seed-dispersing animals influences seed fate through multiple, diverse mechanisms that range from rather intuitive effects of differences in body size, to more subtle influences of male *versus* female cognitive functions. It is worth noting, however, that studies documenting gender-related effects on seed dispersal are heavily skewed towards mammals and birds (Table 1).

## (2) Ontogenetic shifts

Ontogenetic shifts, usually studied as changes associated with body size or age, can influence many ecological phenomena, including use of resources and interactions with other organisms (Werner & Gilliam, 1984; Nakazawa, 2015). Their impact on plant–animal interactions has been studied relatively often (Table 1). Not surprisingly, larger individuals tend to ingest more seeds and thus disperse them in higher quantities than smaller individuals. This association has been demonstrated in earthworms (Eisenhauer *et al.*, 2010), insects (Larsen & Burns, 2012) and frugivorous fish (Herrel *et al.*, 2004; Reys *et al.*, 2009; Correa *et al.*, 2015a); it appears that the link between body size and dispersal quantity is particularly pronounced in species with indeterminate growth and large variation in adult body sizes. Similar relationships should hold also for ectozoochory (Table 2), but there are no published studies available.

However, the commonly reported positive association between intraspecific variation in body size and the quantity of dispersed seeds is not universal. In northern diamondback terrapins (*Malaclemys terrapin terrapin*), probability of seed ingestion declined with head width. As a consequence, only small individuals (males and young females) acted as dispersal vectors for eelgrass (Tulipani & Lipcius, 2014).

In addition to the number of seeds, larger individuals can ingest and transport a greater range of seed sizes (e.g. Muñoz & Bonal, 2008). Thus, larger individuals often disperse more species than do smaller individuals (Calvino-Cancela & Rubido-Bará, 2012; Correa *et al.*, 2015a; Benitez-Malvido *et al.*, 2016). Due to different treatment in mouthparts (higher probability of swallowing whole seeds), larger individuals are also less likely to act as seed predators than as dispersers (Kubitzki & Ziburski, 1994; Galetti *et al.*, 2008; Anderson *et al.*, 2009; King *et al.*, 2011; Larsen & Burns, 2012; Türke & Weisser, 2013; Correa *et al.*, 2015a,b). Finally, large individuals are often responsible for the majority of long-distance seed-dispersal events because they tend to have larger home ranges and longer gut retention times than small individuals. This effect was documented in Amazonian flooded forests, where frugivorous fish serve as major seed dispersers of trees and lianas (Correa *et al.*, 2007). In these ecosystems, large individuals are disproportionately important in transporting

seeds over long distances (Anderson *et al.*, 2011), but are also particularly vulnerable to overfishing because they are preferentially targeted by fishermen (Correa *et al.*, 2015a). Such overexploitation threatens seed dispersal in wetlands and could lead to changes in plant communities in floodplain forests (Correa *et al.*, 2015a).

Body size and behavioural dominance might also affect individual foraging tactics. Flying foxes in the genus *Pteropus* maintain feeding territories and repel newcomers, who often steal fruits and carry them away (Richards, 1990; McConkey & Drake, 2006). Only the ‘raiders’ provide long-distance seed dispersal, and juvenile bats are more likely than adults to act as ‘raiders’ (McConkey & Drake, 2006). Similar interactions might occur in frugivorous birds (Sallabanks, 1993).

In eastern chipmunks (*Tamias striatus*), juveniles mostly scatterhoard seeds in topsoil, while adults typically larderhoard seeds in deep burrows – presumably because younger animals are smaller than adults and would be unable to defend larders successfully (Clarke & Kramer, 1994). While many scatterhoarded seeds germinate and produce seedlings, larderhoarded seeds are usually stored too deep for successful emergence and perish even when not consumed. Therefore, eastern chipmunks shift from mutualism to antagonism as they age.

While most seed-dispersal studies listed in Table 1 focus on disperser body size, ontogenetic shifts encompass a wide diversity of traits associated with growth and maturation of individuals. For example, when juveniles and adults differ in habitat selection, they might encounter and disperse different subsets of plant species. For instance, young Swainson’s and wood thrushes (*Catharus ustulatus* and *Hylocichla mustelina*) spend the first few weeks after leaving the nest in secondary habitats with particularly dense vegetation and abundant fruiting plants, while their parents typically inhabit more mature vegetation and different habitat types (e.g. riparian; Rivera *et al.*, 1998; White *et al.*, 2005). The ecological consequences of such changes have not been investigated in the context of seed dispersal. However, these patterns suggest that plant regeneration in different habitats might depend on different classes of individuals of the disperser species. Thus, adults and juveniles would not be functionally equivalent in their interactions with plants (Sih *et al.*, 2012; see also Hampe, 2001; Culliney *et al.*, 2012).

### (3) Individual specialization

Individual specialization is defined as inter-individual variation in niche that cannot be attributed to age, sex or discrete morphotype (non-continuous variation in a trait; Bolnick *et al.*, 2003). While this definition is very broad, research on individual specialization tends to focus mostly on differences in resource use and foraging behaviour (Dall *et al.*, 2012). Sometimes variation in diet can be linked to morphological differences, usually associated with food processing. This was documented in classical studies of Darwin’s finches (Geospizinae) on the Galapagos Islands (Grant, 1986). Finches with larger beaks can crack harder seeds, which influences both inter- and intraspecific variation

in diets (Grant, 1986). However, in many other cases, the link between morphology and individual dietary specialization is weak or apparently absent (e.g. Werner & Sherry, 1987; Jung, 1992; De León *et al.*, 2012).

Individual specialization might result from intraspecific variation in sensory abilities. In Siberian chipmunks, individuals with a high propensity to scatterhoard seeds have a low propensity to pilfer cached seeds, and *vice versa* (Yi *et al.*, 2016). These differences are thought to stem from differences in olfactory abilities: individuals with poor olfaction rely mostly on their own caches (and use spatial memory to recover them), while individuals with good olfaction use scent cues to pilfer seeds. While scatterhoarding is generally beneficial to plants (Zwolak & Crone, 2012), seed pilferage can erase these benefits – unless the stolen seeds are re-cached elsewhere (Jansen *et al.*, 2012).

Individual specialization on different food resources has been found both in granivores and frugivores (Table 1). For example, populations of gracile mouse opossums (*Gracilinanus microtarsus*), white-eared opossums (*Didelphis albiventris*), and howler monkeys (*Alouatta palliata*) appear to consist of dietary specialists and generalists, with diets of the former being subsets of the latter (Araújo *et al.*, 2010; Cantor *et al.*, 2013; Dáttilo *et al.*, 2014). Thus, some individuals disperse many species of plants, while other individuals disperse few. Egyptian fruit bats (*Rousettus aegyptiacus*) also show strong intraspecific partitioning of diets, leading to different groups of individuals within populations being responsible for dispersal of distinct groups of plant species (Herrera *et al.*, 2008). Likewise, American robins (*Turdus migratorius*) and northwestern crows (*Corvus caurinus*) have clear individual propensities towards particular fruits, driven partly by colour preferences (Jung, 1992; Willson & Comet, 1993; Willson, 1994). As a consequence, territories of birds with particular preferences might represent centres of recruitment of different plant species (Jung, 1992).

Even if individuals of a given species have similar diets, their effects on seed dispersal can be strikingly different. In an experimental study on the common carp (*Cyprinus carpio*), individuals that tended to ingest many seeds were also more likely to defaecate them intact (Pollux, 2017). This positive association between quantity and quality of seed dispersal resulted in pronounced (up to 31-fold) differences in dispersal effectiveness among individuals. The intraspecific variation in seed dispersal was speculated to result from individual differences in the morphology of the feeding apparatus and gut (Pollux, 2017).

More broadly, individual differences in ecological niches might be expressed not only by differential foraging (which in the case of frugivores leads to dispersal of distinct plant species or differences in dispersal effectiveness), but also through variation in space use (which influences distances and places of seed deposition: e.g. Lenz *et al.*, 2011). In birds, such variation is often related to breeding status; non-territorial birds (‘floaters’), for example, have different seed-dispersal patterns than those holding territories (Hampe, 2001; Rawsthorne *et al.*, 2011; Karubian *et al.*, 2012). During the



breeding season, individuals that do not have territories (usually because the habitat is saturated) move longer distances on a daily basis than territorial individuals, which show high site-fidelity (Rawsthorne *et al.*, 2011). In conclusion, individual specialization represents a source of individual variation that is probably ubiquitous, but often cryptic; individuals that look the same can provide very different seed dispersal.

#### (4) Behavioural syndromes

Behavioural syndromes, also referred to as animal personalities, are defined as distinct sets of behavioural tendencies that are consistent in time and across different ecological situations; e.g. consistent individual differences in boldness, aggressiveness, sociability, activity or exploratory tendency (Sih *et al.*, 2004; Bell, 2007). In recent years, this phenomenon has become a popular research field. Typically, animal personality studies have focused on variation in one aspect of behavioural type (e.g. boldness), on documenting correlations among different behaviours that comprise behavioural syndromes, or on evolutionary mechanisms that could lead to the emergence or maintenance of different personality types in animal populations (Dingemanse & Wolf, 2010; Réale *et al.*, 2010b; Dall *et al.*, 2012). Even though a few high-profile articles have outlined possible ecological implications of animal personalities (Réale *et al.*, 2007; Sih *et al.*, 2012; Wolf & Weissing, 2012), empirical studies linking personalities and ecology are lagging behind theoretical developments (DiRienzo & Montiglio, 2015, but see e.g. Duckworth & Badyaev, 2007; Dunn, Cole & Quinn, 2011; Toscano & Griffen, 2014; Royauté & Pruitt, 2015). As a striking example, there is virtually no overlap between research on animal personalities and on plant–animal interactions. A search for (frugivory OR granivory OR “seed dispersal” OR “seed predation”) AND (personalit\* OR “behavio\* syndrome\*”) conducted on 21 January 2016 on *Web of Science* yielded just one publication (Rockwell, Gabriel & Black, 2012). This single study did not concern seed dispersal, but rather food sampling behaviour in Steller’s jays (*Cyanocitta stelleri*), examined at feeding stations with peanuts.

It is almost certain that animals with different personalities will differ in their effectiveness as seed dispersers, yet we do not know how strong such an effect may be, much less about potential mechanisms linking behavioural traits and seed-dispersal outcomes. Thus, we can only speculate about such mechanisms and outcomes (Table 2). For instance, animal personalities will likely influence seed-dispersal distances. Variation in personalities is ubiquitous among mobile organisms (Pennisi, 2016) and shapes their movement patterns (Boon, Réale & Boutin, 2008; Montiglio *et al.*, 2012; Knotts & Griffen, 2016). Understanding this variation holds great potential for understanding where seeds go. For example, animals that are highly active in behavioural tests often have large home ranges (e.g. Montiglio *et al.*, 2012), and therefore may be predicted to disperse seeds further than less-active individuals. In seed-dispersing fish, locomotion increases gut retention times (van Leeuwen *et al.*, 2016). This phenomenon might additionally inflate the difference

in distances of seed dispersal by individuals with different activity levels.

Furthermore, theoretical (Careau *et al.*, 2008; Biro & Stamps, 2010; Houston, 2010; Réale *et al.*, 2010a) and empirical (Careau *et al.*, 2009; Mathot *et al.*, 2015) studies link behavioural syndromes to energy expenditure and metabolic rate. Fast-exploring, bold and aggressive individuals are more likely to have high metabolic rates and resource demands (e.g. Careau *et al.*, 2009). This connection can influence seed dispersal particularly in scatterhoarding granivores. These animals cache surplus food (Vander Wall, 1990) and for individuals with high energy requirements, situations when food is in excess will be relatively rare (Biro & Stamps, 2010). This might shift plant–scatterhoarder interactions from mutualism (when seed caching is so frequent that it outweighs the costs to the plant of seed consumption) to antagonism (when caching is too rare to balance the costs: Theimer, 2005; Zwolak & Crone, 2012). Finally, animals that are consistently bold might cache seeds in different places than animals that tend to be shy. For example, we can predict that bold individuals will cache more often in riskier (e.g. open) habitats that might be better for seed germination and safer from seed predators that tend to stay in refuges (Muñoz & Bonal, 2011; Steele *et al.*, 2014).

These ideas are largely untested. As a rare exception, a study on Merriam’s kangaroo rats (*Dipodomys merriami*) demonstrated links between boldness (measured as foraging under predation risk), agonistic behaviour towards conspecifics, and spatial patterns of seed caching in small (1.45 m<sup>2</sup>) enclosures (Dochtermann & Jenkins, 2007). Bolder individuals dispersed their caches more widely than shy ones, and more-aggressive animals were more consistent in their caching patterns than less-aggressive individuals (Dochtermann & Jenkins, 2007). Yet, the goal of this study was to analyse correlations among different behaviours rather than to explore the ecological consequences of behavioural syndromes. In general, while behavioural syndromes might play an important role in shaping interactions between plants and dispersers of their seeds, their potential in this regard remains overlooked.

#### IV. PROSPECTS

Compared to research based on species averages, gathering data on intraspecific variation raises the bar of difficulty for study design and execution since it requires linking seed-dispersal characteristics to individual traits of seed dispersers. Because this effort should be directed where it will be most profitable, it is first necessary to identify the most important functional traits of individuals. Likewise, it is important to determine the ecological conditions when individual variation in animals is particularly important for seed dispersal.

Currently, the number of studies on particular traits of seed dispersers might reflect research bias rather than the importance of these traits for plant–animal interactions;



some traits are evident and easy to measure, while others are inconspicuous and require well-designed tests. From the studies reviewed in Table 1, it appears that consequences of differences in body size for seed dispersal are comparatively well documented. On the other hand, research on animal personalities is particularly under-represented. The lack of studies that integrate animal personalities with plant–animal interactions is somewhat surprising, given repeated calls to investigate the ecological consequences of behavioural syndromes (Sih *et al.*, 2004, 2012; Réale *et al.*, 2010b; Wolf & Weissing, 2012).

The paucity of studies demonstrating that individual variation in seed-dispersing animals affects plant recruitment represents another conspicuous gap in current knowledge (but see Wenny, 2000). Impacts on seeds do not necessarily translate into demographic changes in plant populations due to processes such as density-dependence, microsite limitation, and abiotic influences (e.g. Clark *et al.*, 2007; Larios, Pearson & Maron, in press). Similarly, links between individual traits of seed dispersers and plant community structure or evolutionary dynamics remain to be demonstrated.

Two conditions are necessary for individual variation in seed dispersers to matter. First, the individual differences in traits should translate into strong differences in crucial characteristics of seed dispersal. This condition appears to be fulfilled in Amazonian frugivorous fish, where differences in body size cause pronounced differences in seed-dispersal distances, which in turn are positively associated with the likelihood of placing seeds in appropriate habitats (Anderson *et al.*, 2011). Conditional mutualism in plant–animal interactions provides another example of potentially strong impacts. As a hypothetical illustration, personality-driven differences in foraging strategies in rodents could lead to fundamentally different outcomes for plant recruitment, from beneficial to harmful. For instance, masting has been suggested to cause switching between seed dispersal and seed predation (Vander Wall, 2010; Zwolak *et al.*, 2016). The putative mechanism of this change involves behavioural responses of individual scatterhoarders to fluctuations in the relative abundance of seeds (Theimer, 2005; Zwolak & Crone, 2012). However, masting was also found to change personality types in granivore populations (Montiglio *et al.*, 2014), which suggests an alternative mechanism for this phenomenon.

Second, individual variation is more likely to be important when the proportions of particular types of individuals in a population change directionally, fluctuate, or vary across space (Miller & Rudolf, 2011). Examining intraspecific variation in seed-disperser traits might be crucial for a mechanistic understanding of seed dispersal. However, when proportions of different individuals are static, it is less likely that intraspecific differences will be responsible for changes in the dynamics and outcomes of plant–animal interactions. Yet, fluctuations in population structure seem to be the norm rather than the exception in animal populations (Benton *et al.*, 2006). Potential mechanisms of changes in the

proportions of animals with particular traits include harvest by humans (e.g. size: Correa *et al.*, 2015a; sex: McLoughlin, Taylor & Messier, 2005; Milner *et al.*, 2006; Marealle *et al.*, 2010), fluctuations in size and age structure related to the timing of reproductive events in a population, and shifts in personality-type populations triggered by resource pulses (Montiglio *et al.*, 2014). More broadly, since some of the key traits (body size, behavioural type) influence individual performance in multiple other challenges, these other ecological factors affect the mean and variance of these traits and thus seed-dispersal outcomes. For example, predation risk affects the distribution of granivore sizes and personalities (Michaux *et al.*, 2002; Rödel *et al.*, 2015) and therefore might change seed-dispersal patterns. Such indirect interactions represent an exciting direction for future research.

## V. CONCLUSIONS

(1) Intraspecific variation in seed-dispersing animals is rarely investigated (Pollux, 2017). It is likely, however, that research on this subject will be more intense in the near future, due to rapidly growing general interest in intraspecific variation in ecology (Bolnick *et al.*, 2011; Dall *et al.*, 2012; Violle *et al.*, 2012; Pettorelli *et al.*, 2015; Pennisi, 2016).

(2) Ecological theory suggests that consequences of individual variation for seed dispersal might be far-reaching (Fig. 2, Table 2). If individuals differ in the number of dispersed seeds or the quality of seed dispersal, some of them will be disproportionately more important for plant recruitment than others. Variation in the distance of seed dispersal can lead to multimodal seed shadows and heterogeneous patterns of seed deposition. Intraspecific differences in fruit or seed preferences can drive selective pressures on plants, affecting the evolutionary dynamics of plant–animal interactions. If variation in preferences leads to foraging on different species of fruits, the strength and architecture of interaction networks will be affected. Relying on species averages can obscure these patterns and bias our estimates of seed-dispersal characteristics.

(3) Existing empirical evidence strongly supports the notion that individuals of the same species are not equal when dispersing plant seeds. Multiple studies have revealed strong influences of variation in body size, reproductive role, foraging tactics, and other traits of animals on seed fate (Table 1). However, the effects of such variation on plant demography and evolutionary dynamics remain unexplored.

(4) Individual variation in traits of frugivores and granivores provides a new avenue to explain the baffling variation in the number and fates of dispersed seeds. This approach has been used successfully to address similar puzzles in behavioural ecology (Wolf & Weissing, 2012); most likely, it will also help explain variation in plant–disperser interactions and make their outcomes more predictable. While this shift in perspective is unlikely to replace the

traditional approach that focuses on variation that occurs among species, it adds to it with the potential for considerably improving our understanding of animal-mediated seed dispersal.

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