# Tansley review

# Seed dispersal effectiveness revisited: a conceptual review

Author for correspondence:
*Eugene W. Schupp*
*Tel: +1 435 797 2475*
*Email: eugene.schupp@usu.edu*

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Eugene W. Schupp[1,2], Pedro Jordano[2] and José María Gómez[3]

[1]Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT 84322-5230, USA; [2]Integrative Ecology Group, Estación Biológica de Doñana, CSIC, c/Americo Vespucio s/n, Isla de La Cartuja, E–41092 Sevilla, Spain; [3]Grupo de Ecología Terrestre, Dpto Ecología, Facultad de Ciencias, Universidad de Granada, E–18071 Granada, Spain

## Contents

## Summary

Growth in seed dispersal studies has been fast-paced since the seed disperser effectiveness (SDE) framework was developed 17 yr ago. Thus, the time is ripe to revisit the framework in light of accumulated new insight. Here, we first present an overview of the framework, how it has been applied, and what we know and do not know. We then introduce the SDE landscape as the two-dimensional representation of the possible combinations of the quantity and the quality of dispersal and with elevational contours representing isoclines of SDE. We discuss the structure of disperser assemblages on such landscapes. Following this we discuss recent advances and ideas in seed dispersal in the context of their impacts on SDE. Finally, we highlight a number of emerging issues that provide insight into SDE. Overall, the SDE framework successfully captures the complexities of seed dispersal. We advocate an expanded use of the term dispersal encompassing the multiple recruitment stages from fruit to adult. While this entails difficulties in estimating SDE, it is a necessary expansion if we are to understand the central relevance of seed dispersal in plant ecology and evolution.

# I. Introduction

Growth in seed dispersal publications over the last two decades is impressive (Fig. 1; see also Levey *et al.*, 2002; Forget *et al.*, 2005; Dennis *et al.*, 2007; Bullock & Nathan, 2008; and associated special feature papers). While scientific literature in general has increased, we believe the growth in seed dispersal publications is largely driven by increasing appreciation that seed dispersal is critical to many ecological questions; it is central to understanding plant population dynamics (Jordano & Herrera, 1995; Schupp & Fuentes, 1995; Beckage & Clark, 2003; Ness *et al.*, 2006) and community structure and dynamics (Levin *et al.*, 2003; Levine & Murrell, 2003; Howe & Miriti, 2004). Seed dispersal has a prominent role in recent studies on recruitment limitation (Clark *et al.*, 2007), gene flow (Jordano *et al.*, 2007), metapopulation dynamics (Spiegel & Nathan, 2007), plant migration in response to historic and future climate change (Ibáñez *et al.*, 2006), evolutionary trade-offs (Clark *et al.*, 2004b), structure of interaction networks (Bascompte & Jordano, 2007), scale dependence of ecological processes (Burns, 2004), maintenance of biodiversity (Bascompte & Jordano, 2007), structuring of species–area curves (Rosindell & Cornell, 2009), ecological consequences of habitat fragmentation (Cordeiro & Howe, 2003), weed invasions (Buckley *et al.*, 2006), ecological restoration (Nuttle & Haefner, 2007), the effectiveness of corridors for conservation (Levey *et al.*, 2005), and more. Implicit in most if not all of these themes is that seed dispersal is effective – that is, not only are seeds being dispersed but seed dispersal is resulting in the successful establishment of new individuals.
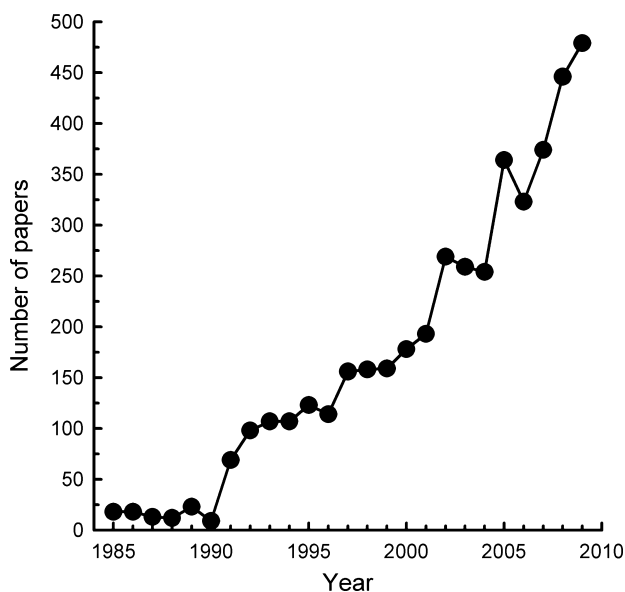


**Fig. 1** The number of published papers by year in the ISI Web of Knowledge SCI-EXPANDED database (searched 24 January 2010) located with the search term 'seed dispers*'.

But what does effective seed dispersal really entail? A framework of seed disperser effectiveness was introduced 17 yr ago. While we still consider that framework valid, we now prefer to refer to it as seed dispersal effectiveness, or simply SDE; see caveats in the next section for justification. This framework was introduced with two objectives (Schupp, 1993). The first was to standardize terminology because a variety of terms were used interchangeably to mean the same thing while individual terms meant different things to different authors. Although the relatively widespread acceptance of SDE terminology has improved clarity in discussions of the consequences of seed dispersal, the second objective was of much greater importance: to develop a quantitative framework for estimating the contributions of individual dispersal agents to plant fitness. Such a framework itself had two goals, one 'empirical' and the other 'organizational.' Empirically, by using such a framework to estimate the contributions of distinct dispersal agents to plant population growth we can better link studies of seed dispersal and of plant demography, and thus more fully understand the consequences of dispersal (Schupp & Fuentes, 1995). However, even in the absence of reaching this ideal the SDE concept is a valuable organizing framework for studying ecological and evolutionary consequences of dispersal – it can structure thinking about what the processes of seed dispersal actually contribute to the successful recruitment of plants. As such, it can add clarity to studies that do not even attempt to quantify effectiveness. Note that similar frameworks have been developed for pollination (Herrera, 1987, 1989) and ant–plant (Ness *et al.*, 2006) mutualisms.

Over the last 17 yr the SDE concept has been widely adopted in studies of seed dispersal by agents as diverse as ants (Boulay *et al.*, 2007), primates (Valenta & Fedigan, 2009), bats (Godínez-Alvarez *et al.*, 2002), rodents (Gómez *et al.*, 2008), ungulates (Ramos *et al.*, 2006), carnivores (Fedriani & Delibes, 2009), frugivorous birds (Ortiz-Pulido & Rico-Gray, 2006), waterfowl (Figuerola *et al.*, 2002), lizards (Valido & Olesen, 2007), tortoises (Jerozolimski *et al.*, 2009), fishes (Galetti *et al.*, 2008) and crabs (Staddon *et al.*, 2010). At the same time, our knowledge of the processes and consequences of seed dispersal has also increased tremendously. Consequently, we believe the time is ripe to revisit the SDE concept. We do not attempt a comprehensive review of the literature relevant to SDE, but instead present a selective review to highlight what we know and do not know about SDE, emphasize new ideas and emerging issues that can influence our view of effectiveness and point the way to important lines of inquiry.

Section II outlines three important caveats. Section III presents an overview of SDE, how it has been addressed empirically, what types of dispersal systems it has been applied to, what aspects we know best, and what aspects we still know little about. Section IV introduces the idea of SDE landscapes and their quantitative and qualitative axes,

while Section V briefly discusses how seed disperser assemblages are distributed on SDE landscapes. Implications of three relatively recent ideas relevant to understanding and studying SDE are then discussed: complementary dispersal, complex seed shadows, and diplochory (Section VI); the context dependence of SDE (Section VII); and 'distance-dependent SDE' (Section VIII). Section IX briefly highlights a selection of emerging issues relevant to SDE. Lastly, brief concluding remarks are in Section X.

## II. Caveats

There are three important caveats for this review, the first of which was introduced above. We believe 'seed disperser effectiveness' is more appropriate than the original 'seed disperser effectiveness' in that semantically it is more inclusive of the overall value of the framework. As reviewed later, the framework was originally focused primarily on quantifying the effects of distinct dispersal agents on plant recruitment. However, the concept is also valuable for assessing the overall effectiveness of dispersal that a plant receives from its assemblage of dispersal agents. While 'seed disperser effectiveness' emphasizes the former – the effectiveness of distinct dispersers – 'seed dispersal effectiveness' applies equally to either – the dispersal effectiveness a disperser provides as well as the dispersal effectiveness a plant receives.

The second caveat is more subtle. We argue that the SDE framework is flexible and can be adapted to a wide variety of dispersal systems. Nonetheless, the original emphasis was on endozoochorous dispersal systems, and to this date the vast majority of studies of SDE have addressed seed dispersal by birds and mammals that consume fruit and defecate or regurgitate intact seeds. Consequently, this review heavily emphasizes endozoochorous seed dispersal. This is a bias based on availability of information and maturation of ideas rather than on importance.

The third caveat concerns the definition of seed dispersal, for which there is no universally accepted meaning. In this review, as in other places, the definition varies with the type of dispersal agent. For wind dispersal we consider seed dispersal to begin with release from the parent. For animal-dispersed species we consider seed dispersal to be horizontal movement of the seed by an animal from the place it was encountered. Thus, an *Acer* seed is dispersed by wind when released from the parent, while a *Quercus* acorn is dispersed by a rodent when the rodent encounters it already on the ground and moves it. In addition, in this review, seed dispersal does not require movement outside the crown of the parent. For example, a bird pecking or consuming pulp and dropping seeds *in situ* has not dispersed seeds while a bird consuming fruits and flying to another branch of the same tree to process the meal and regurgitate seeds has dispersed seeds, even though in both cases seeds fall beneath the parent. Note, however, that the utility of the SDE framework is not restricted to any particular definition of dispersal, as long as the definition used in an empirical study is clear.

## III. What is an effective disperser?

As originally presented, SDE is ideally measured as the 'number of new adults produced by the dispersal activities of a disperser' (Schupp, 1993; p. 16). Although quantifying the production of reproductive adults is challenging, it is ultimately critical. Fig. 2 shows the hierarchical nature of SDE from the viewpoint of endozoochorous seed dispersal of fleshy-fruited plants. This basic framework could be modified for other dispersal agents such as scatter-hoarding animals or wind. For example, with *Quercus* dispersal by rodents, 'quality of treatment in mouth and gut' can be replaced with 'probability of being cached rather than consumed immediately' (Gómez *et al.*, 2008). Obviously, more extensive modifications would be necessary for abiotic dispersal.

In the framework of Fig. 2, SDE can be quantified as the number of seeds dispersed by a dispersal agent multiplied by the probability that a dispersed seed produces a new adult: SDE = Quantity × Quality. Quantity and quality in turn are each determined by two subcomponents. Quantity is (1) the number of visits a dispersal agent makes multiplied by (2) the number of seeds dispersed per visit (Fig. 2), while quality is (1) the probability that a dispersed seed survives handling by the dispersal agent in a viable condition (quality of treatment in the mouth and gut) multiplied by (2) the probability that a viable dispersed seed will survive, germinate, and produce a new adult (quality of deposition) (Fig. 2).

Before addressing variables used to assess SDE, it is important to appreciate its flexibility. The original framework emphasized population-level interactions, especially the SDE a seed disperser population provides a plant population, and endozoochorous dispersal of fleshy-fruited species, and these perspectives continue to dominate. A common approach is to assess the SDE(s) of the population(s) of one or more dispersal agents feeding on a population of a plant, as with the gecko *Hoplodactylus maculatus* dispersing *Coprosoma propinqua* (Wotton, 2002) and bats and birds dispersing *Neobuxbaumia tetetzo* (Godínez-Alvarez *et al.*, 2002). However, the concept can be applied to other levels of organization, and can be viewed from the perspective of either the SDE that dispersers provide or that plants receive. For example, the SDE framework was used to address effects of two primate species on community-level fruit consumption (Martins, 2006), effects of geographic landscape context on the SDE that *Miconia* spp. received from the overall frugivore community (Luck & Daily, 2003), and SDEs of functional groups of dispersal agents dispersing functional groups of trees in order to scale
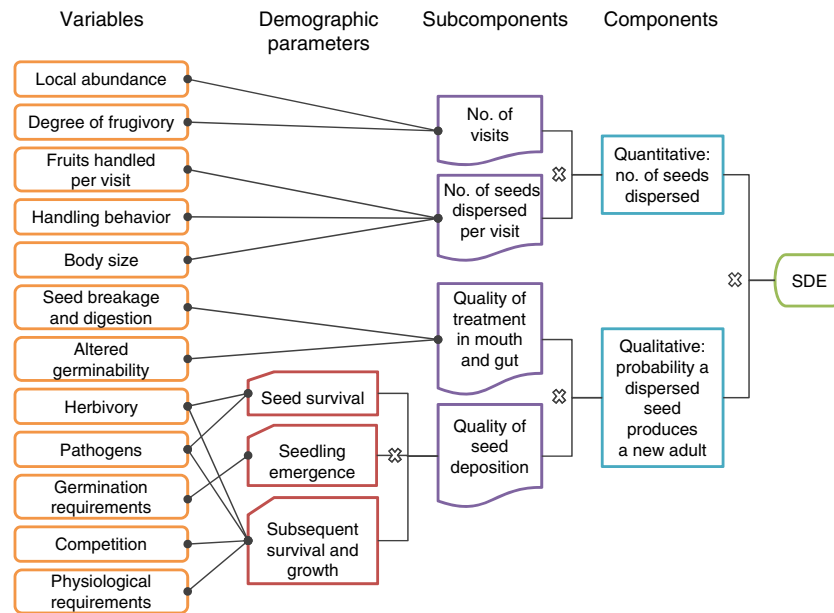
**Fig. 2** A hierarchical flow chart representing the determinants of seed dispersal effectiveness (SDE) for a model endozoochorous seed dispersal system. 'Components' and 'subcomponents' provide the major organizing framework for developing studies and calculating SDE. 'Demographic parameters' represent a simplified life table for determining the 'quality of seed deposition.' 'Variables' are representative measurable variables that are relevant to studies of SDE. Boxes connected by right-angled lines with an '×' represent factors that are, at least in principle, multiplicative (e.g. the number of visits × the number of seeds dispersed per visit = the number of seeds dispersed). Straight lines with closed circles on the ends indicate that the variable affects the 'subcomponent' or 'demographic parameter,' but not multiplicatively.

up to entire diverse communities (Dennis & Westcott, 2006, 2007).

Similarly, most studies of SDE focus on endozoochorous dispersal of fleshy-fruited species, but the concept has been applied to waterfowl dispersing grass seeds (Figuerola *et al.*, 2002) and scatter-hoarding rodents dispersing nuts (Hollander & Vander Wall, 2004; Gómez *et al.*, 2008). It could also be adapted to epizoochorous dispersal of seeds attached to fur or dispersal by wind or water, although, to our knowledge, it has not been yet.

## IV. The SDE landscape and its quantitative and qualitative axes

With sufficient knowledge, disperser species can be plotted on an SDE landscape, as represented in Fig. 3(a). Isoclines connect all values of quantity and quality yielding the same SDE. Loosely based on the adaptive landscape (Wright, 1932; Simpson, 1944), the SDE landscape is a two-dimensional representation of the possible combinations of the quantity (*x*-axis) and the quality of dispersal (*y*-axis). Elevation contours, rising from lower left to upper right, are the SDE isoclines. Obviously, the same SDE can be achieved many ways: relatively high quantity and moderate quality, relatively high quality and moderate quantity or any combination between. One visual insight from this SDE landscape (Fig. 3a) is that the SDE of a very low-quality disperser will not increase much even with large increases

in the quantity dispersed through population increases or resource switching; the species may shift dramatically along the *x*-axis with little crossing of SDE isoclines. Similarly, a species with a very low quantity of dispersal will not increase its SDE much even if the quality of dispersal increases considerably owing to, for example, a change in the environment (see section VII, the context dependence of SDE). By contrast, changes in the quantity of seeds dispersed by a relatively high-quality disperser can have large effects on SDE; the shift along the *x*-axis results in substantial movement downslope or upslope on the SDE landscape.

The essential details of SDE in terms of operational variables contributing to quantitative and qualitative components for a model endozoochorous seed dispersal system are shown in Fig. 2 (that is, the variables determining where dispersers lie along the quantitative and qualitative axes). Numerous variables have been used as proxies to estimate components and subcomponents of SDE, and this variety reflects the methodological approaches that have been used empirically.

Most attempts have primarily studied either the quantitative or the qualitative component, rather than comprehensively assessing SDE (Godínez-Alvarez & Jordano, 2007). Nonetheless, a number of studies give important insight into various aspects of SDE (Howe, 1977; Herrera & Jordano, 1981; Murray, 1988; Reid, 1989; Wenny & Levey, 1998; Jordano & Schupp, 2000; Wenny, 2000; Figuerola *et al.*, 2002; Traveset *et al.*, 2003; Calviño-Cancela & Martín-
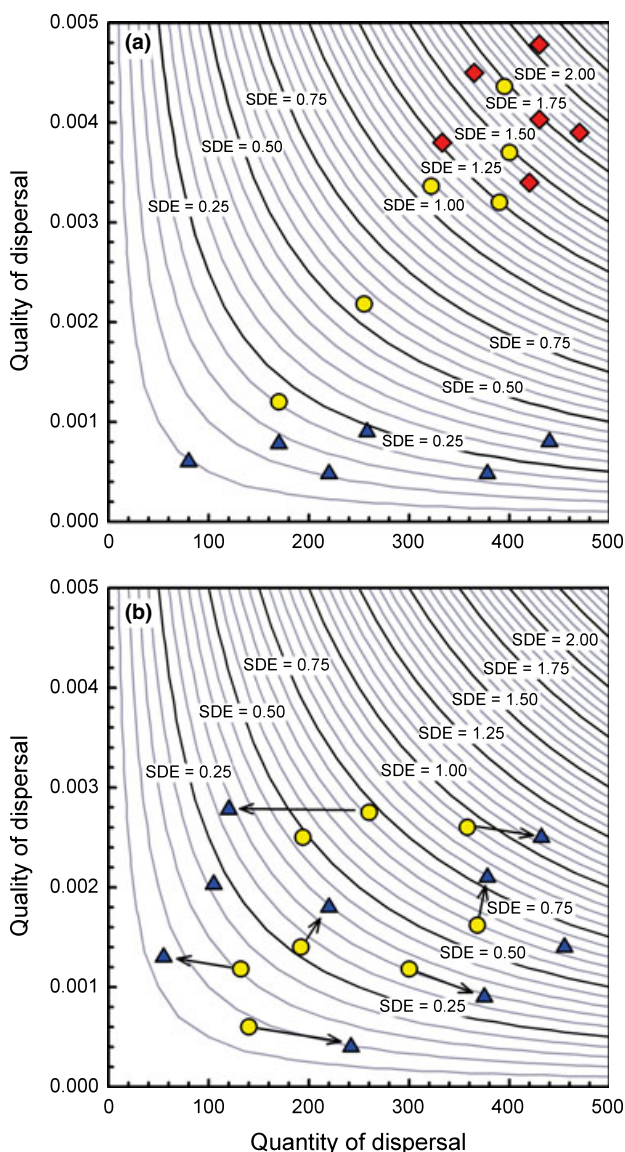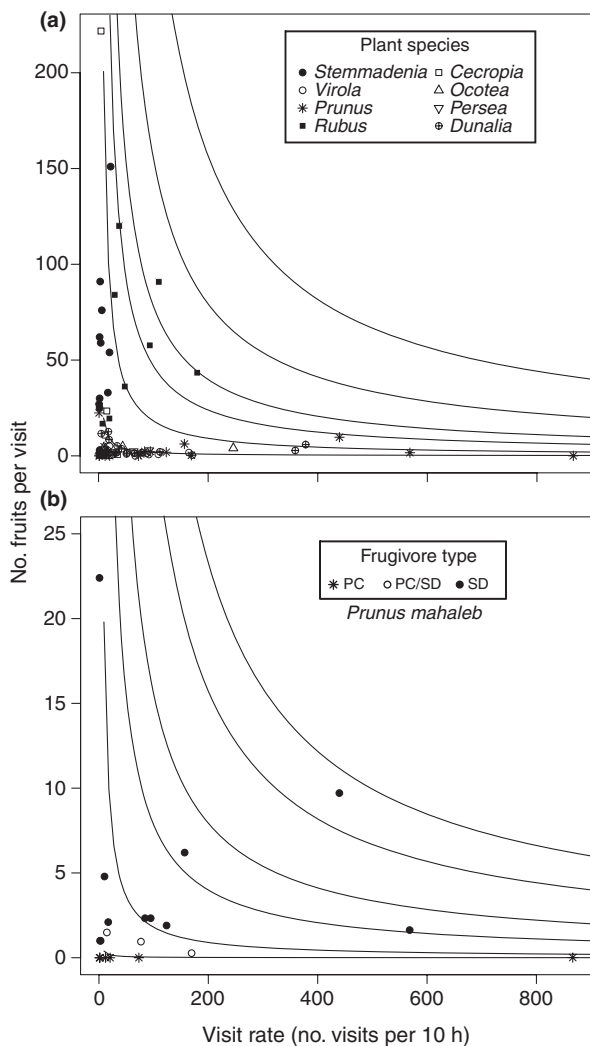
**Fig. 3** The seed dispersal effectiveness (SDE) landscape. Isoclines represent all combinations of quantity and quality that yield the same SDE. Symbols represent the positions of species on the landscape. (a) Shows the distributions of three hypothetical disperser assemblages on the landscape. Diamonds depict an assemblage with some variation among species in both components, but with all species being relatively effective quantitatively and qualitatively. Circles depict an assemblage where quantity and quality are positively correlated, with dispersers ranging from those providing relatively low quality and quantity dispersal to those providing relatively high quality and quantity dispersal. Triangles represent an assemblage with species varying greatly in the quantity of seeds dispersed but with all species providing low-quality dispersal. (b) The context dependence of the quantity and the quality of dispersal demonstrating the dynamic SDE landscape. For example, circles might represent the assemblage dispersing a given plant species in year 1 while triangles represent the assemblage in year 2. Arrows show the SDE trajectory of given disperser species. Some species increase and others decrease quantitatively owing to changes in population size, availability of alternative resources, etc. One species drops out of the assemblage and two others are added in the second year. Similarly, some species increase, some decrease, and some are unchanged qualitatively owing to changes in the balance between interference and facilitation, changes in herbivore population sizes, densities of seeds of the same and different species, etc. Consequently, the SDE that the plant population receives, and the contributions of individual disperser species to the SDE of the population, can vary greatly from year to year.

number of seeds per visit) are multiplicative, we can plot the location of dispersal agents on a quantitative component landscape similar to the SDE landscape (Fig. 4a,b). There are many routes to the same quantitative effectiveness. At low numbers of fruits removed per visit, even dramatic changes in visitation rate would not result in major changes in the quantitative component. An expectation would be that in assemblages in which variation in visitation rate is large, variation among disperser species in the number of seeds dispersed per visit would have negligible effects on the quantitative component (Fig. 4a; Vázquez *et al.*, 2005). By contrast, variation in the quantitative component in small disperser assemblages with greater ecological similarity (i.e. similar local abundances, body size and visit rates) would be driven mainly by variation in fruit handling, rather than in visits (Fig. 4a; Jordano & Schupp, 2000; Vázquez *et al.*, 2005). This appears a general trend for pollination mutualisms as well (Vázquez *et al.*, 2005).

Where species lie on the quantitative component landscape is determined by a variety of variables. Species in a disperser assemblage can differ in visitation rate, the number of seeds handled per visit, the probability a handled seed is dispersed away from the mother plant, and more. While variation across dispersers in the number of seeds dispersed per visit is unlikely to fully compensate for variation in visitation rate (that is, effective dispersers are likely to be frequent visitors), small differences in the probability that a handled seed is dispersed can cause dramatic differences in effectiveness. However, the seed handling ability of a given

Herrero, 2009; Figueroa-Esquivel *et al.*, 2009; Christianini & Oliveira, 2010; Rodríguez-Pérez & Traveset, 2010). The frequency of visits and the number of seeds dispersed – that is the subcomponents of the quantitative component – are frequently documented, while handling behavior, movement patterns and gut passage effects on germination are some of the best-studied qualitative variables (Godínez-Alvarez & Jordano, 2007).

Numerous studies have assessed the quantitative component of SDE, generally using surveys at feeding trees and observations of disperser activity and feeding behavior. Both the frequency of visits and the number of seeds dispersed per visit are frequently obtained during focal tree watches (Howe & Vande Kerckhove, 1981; Jordano & Schupp, 2000) or 'spot' censuses (Howe & Vande Kerckhove, 1981). Because the subcomponents (visit rate and the

**Fig. 4** Examples of the distributions of eight dispersal assemblages on the quantitative component landscape. Isoclines represent all combinations of visit rate and number of fruits consumed per visit that yield the same quantitative component value of seed dispersal effectiveness (SDE). (a) Symbols indicate the average visit rate and number of fruits taken per visit for each frugivore species visiting and dispersing seeds of eight different plant genera representing both tropical and nontropical species. (b) The quantitative component landscape for *Prunus mahaleb*, showing variation among frugivore species categorized into major functional groups: SD, legitimate seed dispersers; PC/SD, pulp consumers–dispersers; and PC, pulp consumers. See Vázquez *et al.* (2005) and Jordano & Schupp (2000) for details.

disperser species is probably largely controlled by ecomorphological/anatomical characteristics, limiting the ability of a species to alter the number of seeds dispersed per visit very much. In the example of a frugivore species, if fruit is handled in such a manner that many seeds are dispersed per visit (Fig. 4a), a small increase in visitation rate (e.g. driven by increased abundance) can result in a large increase in the number of seeds dispersed (i.e. the species moves upslope on the quantitative component landscape rapidly; Fig. 4a). By

contrast, a species with an intrinsically low feeding rate can only marginally increase the absolute quantitative component of SDE by increasing its visitation rate (i.e. the species moves nearly parallel to the slope of the quantitative component landscape; Fig. 4a).

As an example of an assemblage on the quantitative component landscape, *Prunus mahaleb* dispersers form three groups with respect to variation in the probability that a handled fruit will be dispersed, irrespective of visitation and feeding rates (Jordano & Schupp, 2000). Legitimate dispersers that ingest most handled fruits vary in the quantitative component of SDE mainly because of variation in visitation rate, although the large wood pigeon (*Columba palumbus*) visits rarely but consumes many seeds per visit (SD; Fig. 4b). A second group composed of a few granivorous species are quantitatively ineffective because they consume seeds or peck fruits they handle, dropping seeds *in situ* (PC; Fig. 4b). Finally, finches (*Fringilla coelebs*) and tits (*Parus* spp.) are frequent visitors with relatively high feeding rates (fruits handled per visit), yet they drop most of the seeds *in situ* without moving them, often even eating the fruit while it is still attached to the plant (PC/SD; Fig. 4b). This tends to be a general pattern with avian frugivores that mash fruits to get pulp and drop the seeds (Levey, 1987). Which subcomponent ultimately drives variation in the quantitative component of SDE is thus largely dependent on the foraging characteristics of the dispersal agents in the assemblage and the interactions of disperser traits with plant traits such as fruit size, seed size and number, and the fruiting display.

There is wide variation in the potential quantitative effectiveness owing just to variation in visitation and immediate handling behaviors. When a composite variable is estimated (e.g. the proportional dispersal service, or the proportion of total dispersed seeds dispersed by a given species; Fig. 5), it appears that most disperser species account for < 0.25 of the dispersal services the plant receives, frequently << 0.25. Thus, in general, most of the dispersal service a plant species receives is provided by only a few species (Fig. 5; see also Schupp, 1993). This probably reflects the many ways dispersers can be quantitatively ineffective. For example, most species with < 0.25 dispersal service (Fig. 5) rely on the plant only marginally or have low abundance, both of which result in low visitation rates. In addition, some species might be frequent visitors but disperse few seeds (Fig. 4), again resulting in a small proportional dispersal service. Independent of the cause, the general pattern of one to a few species being responsible for dispersing most seeds has implications for temporal variability in the number of seeds dispersed and for resiliency of dispersal systems. In particular, such a structure suggests that overall SDE might be more sensitive to changes in the abundance of a single quantitatively important species than would be the case if there was more redundancy of high-quantity dispersers.

**Fig. 5** Variation in proportional dispersal service (a combined measure incorporating visitation rate and number of fruits consumed per visit) across plant-disperser assemblages. It represents the relative contribution of each species (symbols) to the overall quantity of seed dispersal the plant receives. The *y*-axis is the rank of each species in the disperser assemblage with decreasing proportional dispersal service represented by increasing *y* – the only reason for using the *y*-axis in this Fig. rather than a simple one-dimensional spread along the *x*-axis is that it separates the symbols at the lower range of proportional dispersal service so that the number of species in these low ranges is visually evident. Species abbreviations: bsima, *Bursera simaruba*; ccory, *Casearia corymbosa*; cpelt, *Cecropia peltata*; darbo, *Dunalia arborescens*; fcoti, *Ficus cotinifolia*; gglab, *Guarea glabra*; gsanc, *Guaicum sanctum*; oinsu, *Ocotea insularis*; pmaha, *Prunus mahaleb*; rulmi, *Rubus ulmifolius*; sdonn, *Stemmadenia donnell-smithii*; sgris, *Stenocereus griseus*; tpana, *Tetragastris panamensis*; vsebi, *Virola sebifera*; vsuri, *Virola surinamensis*. See Vázquez *et al.* (2005) for references.
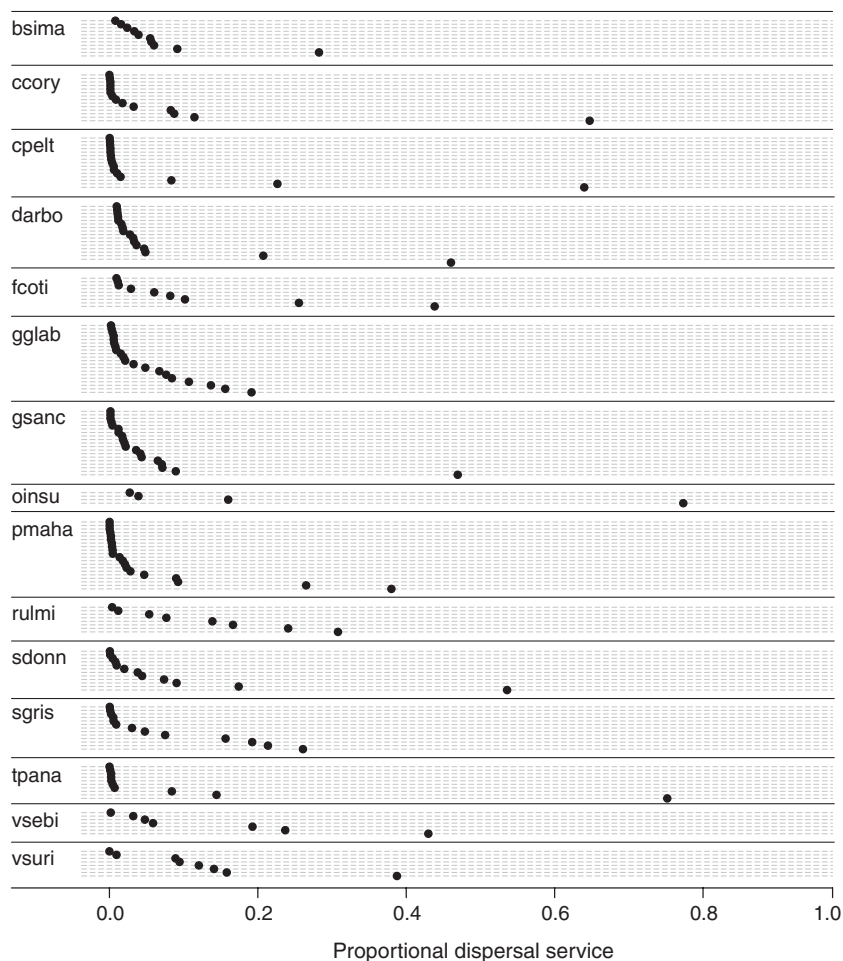
There is ample evidence that dispersal agents also vary broadly in their impacts on the qualitative component of SDE. The treatment in the mouth and gut subcomponent of dispersal quality has been addressed by assessing various combinations of seed crushing in the beak or mouth, the proportion of seeds passed intact, and changes in per cent germination and speed of germination (Coates-Estrada & Estrada, 1986; Figuerola *et al.*, 2002; Martins, 2006; Ortiz-Pulido & Rico-Gray, 2006; Traveset *et al.*, 2007; Fedriani & Delibes, 2009; Rodríguez-Pérez & Traveset, 2010). Dispersers appear to vary continuously from dispersing all seeds intact to destroying nearly all seeds (Schupp, 1993).

The quality of deposition subcomponent is frequently thought of in terms of safe sites, as defined by Harper (1977), although it is important to realize that deposition sites are not safe vs unsafe, but rather vary continuously in suitability for recruitment, and that the quality of deposition is affected by processes operating on survival and growth long after a seedling has established, the end-point of Harper's safe site (see Schupp, 2007). Variables that have been studied can be lumped into three broad categories: distance from conspecifics, habitat variability across a range of

spatial scales, and seed neighborhood effects. Of these, the positive effects of increasing distance from conspecifics, or Janzen–Connell effects, have been considered most extensively (Clark & Clark, 1984; Howe *et al.*, 1985; Gómez *et al.*, 2008; Martínez *et al.*, 2008; Fedriani & Delibes, 2009; Valenta & Fedigan, 2010). The suggestion by Janzen (Janzen, 1970) and Connell (Connell, 1971) that distance- and density-responsive seed and seedling enemies result in disproportionate mortality near conspecific adults provided not only a hypothesis for the maintenance of high species richness in the tropics but also the first hypothesized selective advantage of local seed dispersal away from the parent.

The quality of seed deposition has also frequently been addressed from the perspective of environmental variability at scales ranging from habitats to small scale microsites. For example, at a larger scale the consequences of dispersal to treefall gaps vs forest interior (Schupp, 1988; Schupp & Frost, 1989; Herrera *et al.*, 1994; Wenny & Levey, 1998) and to shrub lands vs forest (Vander Wall, 2002; Ortiz-Pulido & Rico-Gray, 2006; Côrtes *et al.*, 2009) have been considered. At an intermediate scale, the microhabitat of seed deposition, such as open interspace vs beneath a shrub

or functional group of shrubs, is often a major factor affecting dispersal quality, especially in more arid environments (Herrera *et al.*, 1994; Alcántara *et al.*, 2000; Godínez-Alvarez *et al.*, 2002; Ortiz-Pulido & Rico-Gray, 2006; Martínez *et al.*, 2008; Rodríguez-Pérez & Traveset, 2010). Finally, at the microsite scale the role of seed burial through caching in improving survival and germination and thus dispersal quality has been stressed (Vander Wall, 2001; Hollander & Vander Wall, 2004; Gómez *et al.*, 2008).

Lastly, effects of seed neighborhoods on dispersal quality have also been assessed at a range of scales. At a small scale, the number of seeds and the identity of species in local seed neighborhoods can affect the quality of dispersal by affecting seed harvesting by predators (García *et al.*, 2007) and the outcome of seedling competition (Loiselle, 1990). At a larger neighborhood scale, it has become increasingly clear that high densities of seeds resulting from spatially contagious dispersal to primate sleeping sites, fruit-processing roosts, latrines and other sites can reduce the quality of dispersal independent of distance from parents and other conspecifics (Schupp *et al.*, 2002; Russo & Augspurger, 2004; Kwit *et al.*, 2007).

Unfortunately, although the qualitative component of SDE has been widely addressed in diverse ways, we still know much less about it than we do about the quantitative component because it is considerably more difficult to study and measure. Studies of the qualitative component tend to be incomplete, focusing on only one or a few early stages such as seed survival, germination or seedling emergence and short-term survival rather than attempting to assess overall quality with respect to the likelihood of recruiting a new adult. Thus, although in theory we could construct a figure parallel to Fig. 4 that represents the qualitative component landscape, we do not as it would be hypothetical.

This highlights a major weakness of applications of SDE. While assessing the quality of dispersal with respect to seed survival or seedling emergence and early survival is very valuable, it is insufficient. Carrying the assessment through later life stages to reproductive adults is a challenge for long-lived species, but the challenge must be met. Because of potential life stage conflicts, or decoupling (Jordano & Herrera, 1995; Schupp, 1995, 2007), conclusions based only on early life stages can be misleading – dispersal favoring germination ('qualitatively effective') might disfavor seedling survival ('qualitatively ineffective') – thus, if only the former is studied, the estimate of overall effectiveness might be very biased.

To determine the SDE of distinct dispersal agents we ideally should link disperser behavior with actual spatially explicit patterns of seed arrival. Some studies have used data on fruit consumption and seed removal, disperser movements and gut passage rates (Murray, 1988; Holbrook & Smith, 2000; Westcott & Graham, 2000) or traits of wind-dispersed fruits (e.g. terminal velocity, release height) and

atmospheric conditions (e.g. sensible heat flux, wind speed and direction) (Wright *et al.*, 2008) to model seed shadows. Although these studies are extremely enlightening, we still have a shortage of studies directly linking dispersal agent activity with the actual seed rain reaching specific microsites, rather than simply distance and directionality from the parent, and perhaps microhabitat type. This contributes to the difficulty in assessing the qualitative aspects of SDE (Wenny & Levey, 1998; Jordano & Schupp, 2000). Making this assessment would be facilitated by understanding the relative contribution of each disperser to seed arrival in specific locations in the landscape, ideally in a spatially explicit framework (Howe & Miriti, 2004), and how this bridges with variable recruitment probabilities.

In order to determine the role of dispersal agents in plant population dynamics – their SDE – it is necessary to improve knowledge of predissemination and especially postdissemination stages of seed dispersal, and then identify and overcome methodological limitations for linking disperser activity to the fates of seeds, seedlings and later stages, and ultimately to adult recruitment. Unfortunately, predissemination and postdissemination stages of seed dispersal are rarely considered in a unified framework that facilitates analysis of the 'immediate' quantitative effects and the 'delayed' qualitative effects of dispersers. Demographic models provide a promising integrative tool for doing this and quantifying the SDE of dispersal agents (Godínez-Alvarez *et al.*, 2002; Howe & Miriti, 2004). The approach of Godínez-Alvarez & Jordano (2007) combines a detailed assessment of seed dispersal for each disperser (predissemination and postdissemination stages) with projection matrices that model population growth resulting from each dispersal agent. Briefly, the approach is based on four probabilities: the probability of seed removal; the probability of seed deposition in particular patches; the probability of germination after gut passage; and the seed-to-recruit transition probability in each patch. Incorporating these probabilities into the projection matrix, we can estimate population growth rate resulting from each disperser. Alternatively, stochastic simulation modeling can estimate SDE for individual dispersers, especially when the entire demographic loop is not connected, as Calviño-Cancela & Martín-Herrero (2009) did. Few researchers have taken such demographic approaches to date, but they have potential, especially given they could be expanded to incorporate statistical tests of differences among disperser species in SDE.

## V. How are disperser assemblages distributed on the SDE landscape?

We know little about where seed disperser assemblages lie on the SDE landscape. The answer has implications for the overall SDE a plant receives, the contributions of individual dispersal agents to that overall SDE, and the resiliency of
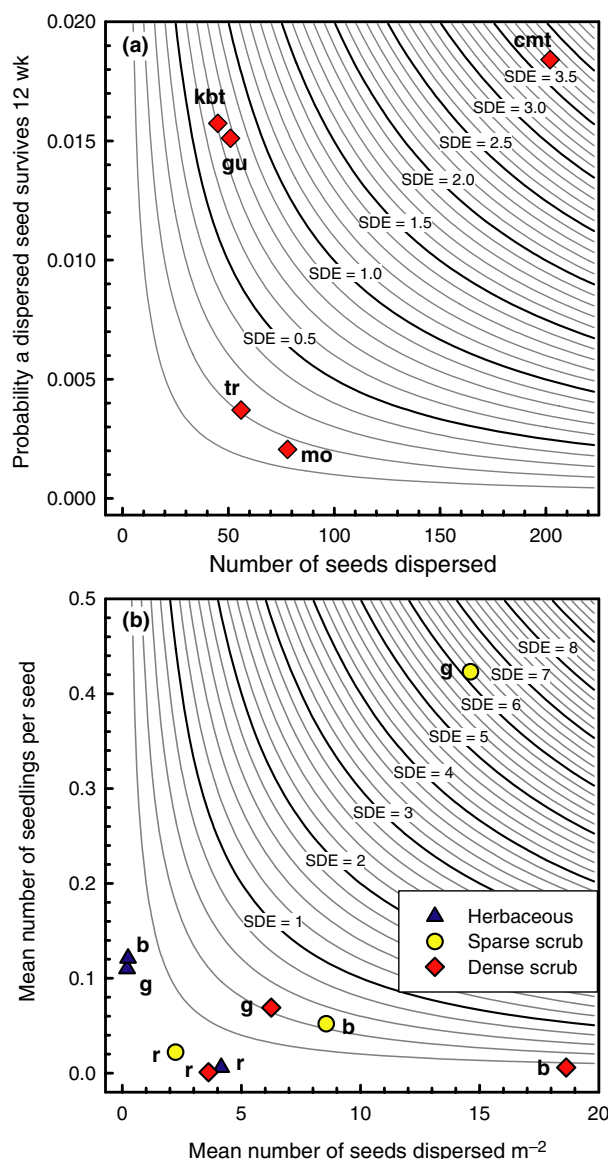
seed dispersal systems. For example, is there only a single dispersal agent providing highly effective dispersal to a given plant population or is there redundancy, with multiple effective dispersal agents?

Three hypothetical disperser assemblages are shown in Fig. 3a. Diamonds represent a disperser assemblage composed of species clustering with relatively high values of quantity and quality – a disperser assemblage in which species providing high SDE are quite redundant. Circles represent an assemblage that is much more variable in SDE and with quantity and quality positively correlated – the most effective dispersers are both quantitatively and qualitatively superior to less effective ones. Lastly, triangles represent a disperser assemblage composed of species varying greatly in the quantity of seeds dispersed but with all species having relatively low quality scores. Note that these alternatives are not exhaustive.

Few real assemblages can be plotted on the SDE landscape, largely because of a paucity of good information on the quality of dispersal past the seedling stage. Thus, generalities are elusive at this point. However, based on preliminary but incomplete analyses it appears that a very wide variety of SDE landscape distributions exist. In addition, patterns in Figs 4 and 5 suggest that most assemblages will vary widely across the quantitative axis, unlike the hypothetical assemblage represented by diamonds in Fig. 3a.

For 11 waterfowl species dispersing *Ruppia maritima* grass seeds, the quantity (number of seeds per dropping) and quality (proportion of seeds passing through the gut intact and proportion of intact seeds germinating) of SDE were positively correlated (Figuerola *et al.*, 2002). By contrast, based on our analysis, the quantity and quality of SDE for five bird species dispersing *Virola surinamensis* were not correlated (Fig. 6a; Pearson $r = 0.078$; quantity from Howe & Vande Kerckhove (1981); quality calculated as estimated 12-wk survival of a dispersed seed using the distribution of distances seeds were dispersed by each species, from Howe (1986), and probability of surviving as a function of distance, from Howe *et al.* (1985)). This assemblage forms three groups on the SDE landscape. Chestnut-mandibled toucans had the greatest SDE because of relatively high quality and quantity of dispersal. Although providing only slightly lower-quality



**Fig. 6** Tentative examples of seed dispersal effectiveness (SDE) landscapes for two relatively well-studied systems. (a) Five birds dispersing *Virola surinamensis* in Panama constructed with data we extracted or calculated from Howe & Vande Kerckhove (1981), Howe *et al.* (1985) and Howe (1986). The quantity of dispersal is the estimated number of seeds dispersed by a species during defined watches at focal trees while the quality of dispersal is the estimated probability of a dispersed seed surviving 12 wk (6 wk as a seed and 6 wk as a seedling) based on the distribution of dispersal distances from the parent and the survival of experimental seeds and seedlings at different distances from parents. Dispersal agents are: gu, the crested guan *Penelope purpurascens*; tr, the slaty-tailed trogon, *Trogon massena*; mo, the rufous motmot *Baryphthengus martii*; cmt, the chestnut-mandibled toucan, *Ramphastos swainsonii*; and kbt, the keel-billed toucan, *Ramphastos sulfuratus*. (b) *Corema album* in three adjacent habitats in northeastern Spain, herbaceous vegetation (triangles), sparse scrub vegetation (circles), and dense scrub vegetation (diamonds), constructed with data from Calviño-Cancela & Martín-Herrero (2009). The quantity of dispersal is the mean number of seeds dispersed m$^{-2}$ by a dispersal agent in a given habitat while the quality of dispersal is the mean number of seedlings produced per seed by the activities of a dispersal agent in a given habitat. Dispersal agents are: r, the European rabbit, *Oryctolagus cuniculus*; b, the blackbird, *Turdus merula*; and g, the herring gull, *Larus michaelis*. Note the extreme context dependence of SDE because all dispersers differ among habitats, in some cases dramatically, in both the quantitative and qualitative components of SDE. In addition, the relationship between quantity and quality differed depending on the habitat.

dispersal than chestnut-mandibled toucans, keel-billed toucans and crested guans had intermediate SDE because they dispersed fewer seeds. Lastly, rufous motmots and slaty-tailed trogons had low SDEs because they dispersed relatively few seeds and provided low-quality dispersal because of short dispersal distances.

In another different pattern, the European badger (*Meles meles*) only infrequently fed on *Pyrus bourgaeana* fruits but provided the greatest SDE because of high-quality dispersal (based on treatment in gut and microhabitat of destination), while the quantitatively important *Cervus elaphus* and *Oryctolagus cuniculus* had low SDEs because of very low-quality dispersal (Fedriani & Delibes, 2009). Thus, at a gross level, quantity and quality were inversely related. Interestingly, evidence from Costa Rica suggests that the positions of six bird species on the SDE landscape differed depending on which of four Melastomataceae was being dispersed (Loiselle & Blake, 1999); for some plant species the quantity (based on numbers of seeds in defecations) and quality (based on habitat selection) of dispersal appeared to be positively correlated across dispersers while for other species quantity and quality appeared to be negatively correlated across the same disperser assemblage.

A preliminary SDE landscape for *Corema album* dispersed by rabbits (*O. cuniculus*), herring gulls (*Larus michaelis*), and blackbirds (*Turdus merula*) in three habitats in northeastern Spain (Calviño-Cancela & Martín-Herrero, 2009) gives further insight into real assemblages (Fig. 6b). Quantity is the number of seeds dispersed $m^{-2}$, quality is the number of seedlings produced per seed and SDE is the number of seedlings emerging $m^{-2}$. Quantity, quality and SDE of dispersal agents varied with habitat (see also Figueroa-Esquivel *et al.*, 2009). For example, *L. michaelis* SDE was 14 times greater in sparse than in dense scrub as a result of greater quantity and quality of dispersal. In addition, the relationship between quantity and quality depended on habitat. In sparse scrub, quantity and quality increased together, resulting in *L. michaelis* having a substantially greater SDE than the other species, while in herbaceous vegetation quantity and quality were negatively related, resulting in all three dispersers having basically equivalent SDE.

One lesson is that highly frugivorous species are not necessarily more effective dispersers of fleshy-fruited plants than incidental frugivores; much the same as frequent visitors are not necessarily contributing the highest proportion of dispersal in quantitative terms (Fig. 3a). In most situations *L. michaelis*, seldom viewed as a frugivore, is a far more effective disperser of *C. album* than is the highly frugivorous *T. merula* (Calviño-Cancela, 2002; Calviño-Cancela & Martín-Herrero, 2009). Although this is an unusual dispersal system, this decoupling of degree of frugivory and effectiveness is unlikely to be unique.

In summary, there are important unanswered questions related to the distribution of assemblages on SDE landscapes.

Does quantity or quality better explain SDE? Does the relative importance of quantity and quality change in predictable ways, for example, with environmental conditions? How much redundancy is there in the most effective seed dispersers of assemblages (that is, how dependent is a plant on one or a few highly effective dispersers, and therefore how vulnerable is it to changes in the abundances of those species)? These are fundamental questions that remain largely unaddressed in studies of seed dispersal.

## VI. Composite seed shadows and SDE: are there advantages to being dispersed by multiple dispersal agents?

The primary focus of this point was on the SDE of individual disperser agents, especially factors determining SDE and variability in SDE among dispersers. We must also consider the combined effect of the entire suite of dispersal agents on the SDE a plant population receives. In particular, are their SDE advantages to being dispersed by multiple dispersers, even if this includes dispersers providing low-quality dispersal? First, we discuss SDE consequences of being dispersed by multiple dispersers during Phase I dispersal (initial dispersal from the parent, Chambers & MacMahon, 1994). That is, the SDE consequences of the composite seed shadow created by the activities of all dispersal agents. We then discuss the case of diplochory, where different dispersal agents contribute to Phase I and Phase II (secondary seed movement) dispersal. In both cases the key question is: are multiple dispersers better than one?

### 1. Composite seed shadows in Phase I dispersal

Studying the shrub *Ochradenus baccatus*, Spiegel & Nathan (2007) reported that grackles (*Onychognathus tristramii*) mostly provided longer-distance dispersal among subpopulations while bulbuls (*Pycnonotus xanthopygos*) dispersed seeds within subpopulations. They also argued that because the two species had equal SDE based on quantity and quality of dispersal, they provided complementary dispersal; contribution of bulbuls to local population dynamics were complemented by contribution of grackles to metapopulation dynamics. They further suggested that such complementary dispersal is widespread. In fact, complementary dispersal is a foundation of the idea of Total Dispersal Kernels (Nathan, 2007).

Such 'complementary' dispersal long has been recognized; in western North American piñon pines (*Pinus* spp.), rodents and several jays provide local seed dispersal and population growth while other corvids disperse seeds longer distances to found new subpopulations (Chambers *et al.*, 1999). Many species produce heteromorphic seeds that result in some seeds being dispersed relatively far and others being dispersed only short distances; *Heterosperma pinnatum*

produces achenes with adhesive awns that disperse well and achenes without sticky awns that disperse poorly (Venable *et al.*, 1998). Such complementary dispersal may be even more important for population spread and persistence than Spiegel & Nathan (2007) suggested in that local and meta-population dispersal are likely synergistic (Clark *et al.*, 1998). Effective local dispersal leads to local population growth and increased population-level seed production, which in turn is expected to increase the number of seed dispersal events occurring. No matter how low the probability of metapopulation dispersal, an increase in the number of seed dispersal events should increase the number of rare long-distance dispersal events, leading to more frequent dispersal among subpopulations and founding of new subpopulations. Thus, the more effective the local dispersal, the more likely metapopulation dispersal will be effective.

Spiegel & Nathan (2007) imply that if some seeds receive local dispersal and others receive metapopulation dispersal SDE will be greater than if all seeds are dispersed locally or all are dispersed at the metapopulation scale, although this need not be true (see scenarios at end of this section, and Section VIII). Complicating the determination, species dispersing seeds different distances almost always differ in other ways. Consider two systems Spiegel & Nathan (2007) mention. Many corvids disperse seeds much further than do rodents (Chambers *et al.*, 1999; Gómez, 2003; Gómez *et al.*, 2008), but their dispersal differs in other ways as well. In *Quercus ilex*, jays move acorns longer distances than do rodents, but they also are more likely to disperse acorns to pine woodlands or shrubs where seed predation by wild boars (*Sus scrofa*) is less and establishment is relatively high (Gómez, 2003, 2004; Gómez *et al.*, 2008). *Prunus mahaleb* is dispersed 'long distances' by carnivores (e.g. *Vulpes vulpes*) and large birds, 'intermediate distances' by mid-sized birds (e.g. *Turdus viscivorus*), and 'short distances' by small birds (e.g. warblers) (Jordano *et al.*, 2007). Carnivores and large corvids also deposit many seeds in piles in open interspaces, while medium-sized birds deposit a few seeds together beneath pines and in the open, and small birds deposit seeds singly beneath shrubs (Schupp, 1993; Jordano & Schupp, 2000; Jordano *et al.*, 2007). These dispersal agents even differ in small-scale patterns of genetic relatedness created (García *et al.*, 2009). While the number of seeds in a deposition has unknown consequences, microhabitat of deposition is critical, with the greatest chance of recruitment beneath low shrubs and virtually no chance in the open (Schupp, 1995; E. W. Schupp & P. Jordano, unpublished). Consequently, these dispersers likely differ greatly in the SDE they provide plants independent of whether they disperse seeds within a local population or among subpopulations.

Even within local populations, multiple dispersal agents create complex composite seed shadows by using the habitat differently and contributing to seed rain in different parts of the population (e.g. different distances from parents), and these composite shadows can have consequences for SDE. Considering *P. mahaleb* further (Jordano & Schupp, 2000), seed dispersal to low shrubs was mostly by *Sylvia communis*, *T. merula*, and *Erithacus rubecula*, but all dispersal to rock outcrops was by *Phoenicurus ochruros* and *T. viscivorus*. The combination of species disperses seeds over more of the habitat than can be reached by any one species or group of similar species, but what are the overall consequences for SDE? One perspective, implicit from the origination of the SDE framework (Schupp, 1993), assumes plant population growth is limited primarily by activities of the species providing the highest quality of SDE. If more seeds were dispersed by the highest quality disperser and fewer by other species, overall SDE received by the plant would be greater. In this view, multispecies dispersal is detrimental, better viewed as 'competitive' dispersal (Vander Wall & Longland, 2005). Population growth and the SDE the plant receives are limited because seeds dispersed by lower-quality dispersers are unavailable to be dispersed by higher-quality dispersers. However, this assumption need not always hold; under some scenarios a suite of dispersers that includes lower-quality dispersers can provide greater SDE to a plant than can a single high-quality seed disperser, and thus be beneficial to the plant.

Consider five scenarios where multiple species are better than one and selection should favor generalized rather than specialized dispersal systems. Scenario 1: if multiple dispersal agents result in seeds reaching a wider variety of locations there are more chances to land in unpredictably suitable sites (Murray, 1988), which is especially valuable for disturbance-dependent species (colonization hypothesis; Howe & Smallwood, 1982). Scenario 2: if the number of seeds dispersed by the highest-quality disperser is limited by something other than seed availability or competition with other dispersers, the presence of lower-quality dispersers will increase overall SDE as long as the seeds they disperse have some chance of recruiting. For example, if breeding season territoriality (Bas *et al.*, 2006) limits population size of the highest-quality disperser such that they are satiated (Hampe, 2008), other lower-quality dispersers are dispersing 'excess' seeds that would not be dispersed otherwise (see Calviño-Cancela & Martín-Herrero, 2009). Scenario 3: if increased dispersal by the highest-quality disperser results in higher seed densities in the most suitable recruitment sites, density dependence might reduce the quality of that dispersal to the point that overall SDE the plant receives might be higher if fewer seeds were dispersed to these sites and more were dispersed to apparently less suitable sites that can still result in recruitment (see also Spiegel & Nathan, 2010). The 'suitability' of a site in this scenario is not constant, but varies with the density of arriving seeds – a form of context-dependent SDE (see Section VII). Scenario 4:

similarly, the quality of dispersal can vary from year to year with environmental fluctuations such that the highest-quality dispersal is provided by species A under some conditions and by species B under other conditions, a different form of context-dependent SDE (see Section VII). Scenario 5: as discussed earlier, complementary dispersal might provide metapopulation benefits by promoting colonization of new patches and maintaining connectivity among subpopulations while maintaining effective local dispersal and local population growth (i.e. population persistence), resulting in more recruits and thus higher SDE for the plant population. Note that with all scenarios, if multispecies dispersal is advantageous it would favor the evolution of diversified interactions with multiple dispersers rather than specialization on the most effective disperser, no matter how superior it is as an individual species.

### 2. Diplochory and SDE

Vander Wall & Longland (2004, 2005) highlight the importance of diplochory, which they define as seed dispersal in two sequential phases with different dispersal agents involved in initial dispersal away from the parent (Phase I) and in subsequent secondary dispersal (Phase II). They identified five syndromes: wind-dispersed seeds secondarily scatter-hoarded by rodents or corvids; ballistically dispersed seeds secondarily dispersed by ants; endozoochorously-dispersed seeds moved and buried in feces by dung beetles; endozoochorously-dispersed seeds scatter-hoarded by rodents; and endozoochorously-dispersed seeds secondarily dispersed by ants.

The sequential combination of two dispersal mechanisms can yield greater SDE for a plant than can any single mechanism (Vander Wall & Longland, 2004, 2005). Phase I dispersal mostly benefits plants by moving seeds away from parents and scattering them in lower densities, reducing distance- and density-dependent mortality. Phase II dispersal can add further benefits by moving dispersed seeds to more suitable sites for recruitment through burial or directed dispersal (Howe & Smallwood, 1982; Wenny, 2001; Briggs *et al.*, 2009).

Although the second stage of diplochory likely is advantageous for the plant in many cases, we lack studies quantifying the SDE attributable to each phase, which is necessary to know whether two dispersers are better than one – and if they are, how much better. Perhaps the most controversial diplochory syndrome is endozoochory combined with scatter hoarding. Although rodent harvesting of endozoochorously dispersed seeds is often assumed to equal predation, we seldom know the fate of harvested seeds and some fraction might be cached and successfully recruit (Vander Wall & Longland, 2004, 2005; Vander Wall *et al.*, 2005a). Some defecated and regurgitated seeds are harvested and cached by rodents, and survive (Fragoso, 1997; Wenny,

1999; Feer & Forget, 2002; Vander Wall *et al.*, 2005b; Forget & Cuiljpers, 2008); seed burial can reduce desiccation, heat stress and predation by non-dispersing granivores, and increase hydration and germination (Vander Wall, 2001). However, these benefits come at a very high cost in consumed seeds (Hulme & Kollmann, 2005; Vander Wall & Longland, 2005). We know little about the balance between benefits and costs in such systems where benefits of endozoochorous Phase I dispersal have already been gained. Our understanding is further clouded by the realization that seed predation may not always limit population growth, as when recruitment is microsite-limited rather than seed-limited (Hulme & Kollmann, 2005).

We suggest the addition of scatter-hoarding Phase II dispersal is most likely to result in greater SDE for plants than would be achieved solely by Phase I endozoochorous dispersal when seeds are larger and therefore more likely to be harvested by rodents, less likely to work into the soil on their own and more likely to benefit from burial (Chambers & MacMahon, 1994; Vander Wall, 2001; Vander Wall *et al.*, 2005b). However, confounding interactions affect the likelihood and benefits of burial. Movement of seeds into the soil is affected by soil texture, slope, wind conditions, precipitation and soil surface stability (Chambers & MacMahon, 1994; Chambers, 2000), germination benefits of burial vary with the environment (Sork, 1985), and rodents may or may not direct dispersal to highly suitable sites (Vander Wall, 2002).

Although Vander Wall & Longland (2004) and Vander Wall *et al.* (2005b) only considered diplochorous systems where the second agent was an animal, secondary dispersal by abiotic means also occurs. In the small montane riparian forest tree *Frangula alnus*, seeds initially dispersed by birds are redistributed by water during winter storms (Hampe, 2004). Benefits, if any, accruing from this second phase of dispersal are unclear, but it seems improbable that hydrochory preferentially moves seeds to more suitable sites. As with other forms of diplochory, Phase II dispersal might improve survival of dispersed seeds by lowering local seed densities or moving more seeds outside the parent canopy (Beaumont *et al.*, 2009). In summary, the effects of diplochory in all its forms on the SDE plants receive is a potentially important theme ripe for further research to gain better generalizations as to when and where two seed dispersers are better than one.

## VII. The context dependence of SDE

Understanding the context dependence of species interactions across scales is a key gap in ecology (Agrawal *et al.*, 2007). In this light, there is growing evidence that SDE is context-dependent across a range of spatial and temporal scales, whether considering the relative SDEs provided by different dispersal agents or the overall SDE plants receive

from their assemblage (Schupp, 2007). However, evidence is essentially anecdotal with little systematic consideration of SDE context dependence. A major goal of ecology is to quantify the effects of species interactions on population dynamics and community structure, and a key knowledge gap is an understanding of how the strengths and signs of species interactions are affected by biotic and abiotic contexts (Agrawal *et al.*, 2007). This lack of knowledge is perhaps greater for species interactions involved in SDE than for many other species interactions. Developing a predictive understanding of SDE ultimately requires embracing context dependence, not as a collection of idiosyncratic results, but in a systematic, experimental search for generalities. The first step forward is acknowledging the breadth of context-dependent SDE. Here we present an overview of the context dependence of the quantitative component and implications for SDE. We then highlight a recent insight from this form of context dependence: spatially explicit plant–frugivore networks. Lastly, we discuss the context dependence of the quantitative component of SDE.

## 1. The quantitative component of SDE is context-dependent

Disperser assemblages can vary among geographic regions, populations within a region and individuals within a population (Wang & Smith, 2002). The composition of ant assemblages dispersing *Helleborus foetidus* differed between geographic regions of Spain and to a lesser extent among populations within regions (Manzaneda *et al.*, 2007; Rey & Manzaneda, 2007). Bird assemblages dispersing *P. mahaleb* varied among regions (Jordano, 1994), nearby habitats in the same area (Guitián *et al.*, 1992) and individuals within populations (Jordano & Schupp, 2000; Fuentes *et al.*, 2001). Frugivorous bird assemblages in Europe differed within a plant species across sites as much as they did among plant species within a site (Fuentes, 1995). Similarly, disperser assemblages vary across years (Jordano, 1994; Herrera, 1998; Manzaneda *et al.*, 2007). These variations in disperser assemblages can lead to variation in the quantitative component of SDE (Guitián *et al.*, 1992; Jordano, 1994; Jordano & Schupp, 2000; García *et al.*, 2001; Rey & Manzaneda, 2007), but see Luck & Daily (2003).

Both extrinsic and intrinsic factors drive spatial and temporal variation in the quantitative component of SDE. Extrinsic drivers include the composition of the assemblage, local habitat structure and fruiting neighborhoods (Jordano, 1994; Fuentes *et al.*, 2001; García *et al.*, 2001; Saracco *et al.*, 2005; Carlo *et al.*, 2007; Rey & Manzaneda, 2007). Intrinsic factors include diaspore traits and crop sizes (Jordano, 1995; Saracco *et al.*, 2005; Carlo *et al.*, 2007; Rey & Manzaneda, 2007). Importantly, these drivers can interact in complex and unpredictable ways, as with *H.

*foetidus* where major determinants of seed dispersal varied geographically and temporally (Rey & Manzaneda, 2007).

Spatially and temporally changing disperser assemblages affect SDE directly by altering the quantity of seeds dispersed and indirectly by altering the overall quality of dispersal as different dispersers almost always treat seeds differently (Schupp, 1993). Thus, SDE could be sensitive to context dependence of the quantity of dispersal. However, the true extent to which context dependence alters SDE has received little attention; for example, to what degree do known between-year changes in disperser abundances and interaction strengths with plants result in variation in seed shadows and plant recruitment? More well-replicated studies across spatial scales as with *H. foetidus* would be invaluable in a search for patterns.

## 2. Spatially explicit plant–frugivore networks: nodes, patterns of dispersal and SDE

Variation among individual plants in the quantity of dispersal can be so extreme as to create spatial networks of plant 'hubs' capturing the majority of dispersal services and plant 'nonhubs' receiving few if any visits (Clark *et al.*, 2004a; Carlo *et al.*, 2007). Hubs might be individuals, species or heterospecific neighborhoods that are disproportionately visited (Lázaro *et al.*, 2005). In this view, most disperser movement is from hub to hub and when nonhubs are visited, dispersers move quickly back to a hub. Modeling suggests the development of hub–nonhub systems is affected strongly by local fruiting neighborhood density and disperser abundance and more weakly by landscape-level plant aggregation; these same variables influence seed dispersal distances (Carlo & Morales, 2008) and, potentially, local genetic structure (Jordano & Godoy, 2002).

Spatial networks have two major consequences for SDE (Carlo *et al.*, 2007). First, hubs create patchily-distributed seed dispersal limitation; while some individuals or neighborhoods have high quantities of seeds dispersed, many have very few seeds dispersed. Although nonhubs always have few seeds dispersed, proximity to a hub can increase or decrease the number dispersed depending on how dispersers respond to the pattern and qualities of overall resources. Effects of these structured spatial patterns of dispersal on the genetic composition of the seed rain have only recently begun to be studied (García *et al.*, 2009).

Second, frugivory hubs result in nested directional patterns of seed rain, creating a form of spatially contagious seed dispersal (*sensu* Schupp *et al.*, 2002), or dispersal resulting in many seeds arriving in some sites and few in others. Seeds from nonhubs are dispersed almost exclusively to hubs while seeds from hubs are dispersed largely to hubs, but also widely across the landscape. Thus, most seeds fall beneath or near hubs, within higher-density seed patches than expected in the absence of such networks. If density dependence is important,

such dispersal will result in reduced dispersal quality overall, but more for nonhubs, whose seeds are almost solely dispersed to higher-density patches, than for hubs, who also have seeds dispersed widely. In addition, multispecies hubs likely result in suites of species being dispersed together, which can affect seed survival; identities of seeds in a neighborhood can alter seed predator foraging such that the presence of one seed species can increase or decrease harvest of another seed species (Veech, 2001; García *et al.*, 2007). Further, predictable dispersal of suites of plant species together can have longer-term consequences for SDE by creating nested patches of co-occurring fruiting species (Lázaro *et al.*, 2005). Because fruiting neighborhood is an important driver of variation in the quantity of seed dispersed (see Section VII, Subsection 1, the quantitative component of SDE is context-dependent), such networks can create spatial structure in the fruiting plant community that amplifies facilitative or competitive effects on dispersal, depending on species interactions. Networks can also affect local genetic structure and patterns of relatedness among adult trees (Jordano & Godoy, 2002; García *et al.*, 2009). As a consequence, spatially explicit frugivory networks can have large consequences for SDE by affecting both quantitative and qualitative components of effectiveness.

### 3. The qualitative component of SDE is also directly context-dependent

The qualitative component of seed dispersal can be context-dependent in many ways (Schupp, 2007). Whether dispersal of *Quercus ilex* to pine woodlands is of higher quality than dispersal to shrubs depends on whether wild boars (*S. scrofa*) are present (Gómez & Hódar, 2008). Fruiting *Cestrum diurnum* neighbors resulted in *Solanum americanum* seeds being dispersed in more 'packets' of fewer seeds each without affecting the quantity dispersed (Carlo, 2005), increasing the number of sites reached and reducing possible density dependence. The quality of dispersal *Ateles paniscus* provided *Virola calophylla* varied with the time of day seeds were deposited; diurnally-deposited seeds were more widely-scattered and had greater survival and seedling recruitment than were nocturnally-deposited seeds accumulating beneath sleeping trees (Russo, 2005).

More complex forms of context-dependent dispersal quality are likely widespread. Of particular interest are two concepts whose importance is increasingly appreciated: the balance between interference and facilitation; and life-stage conflicts (Schupp, 2007).

While existing plants can interfere with recruitment through competition or allelopathy, they can simultaneously facilitate recruitment by ameliorating the biotic (e.g. reduce browsing) or abiotic (e.g. improve water status) environment; we see the net effect (Bertness & Callaway, 1994; Brooker *et al.*, 2008). Bertness & Callaway (1994)

proposed that the frequency and net strength of facilitation increase with physical stress and consumer pressure. Under the stress gradient hypothesis (SGH, Brooker *et al.*, 2008) existing plants exert net interference on recruits in low-stress environments, but with increasing stress facilitation increases and net interference decreases until there is a switch to net facilitation whose strength increases with stress. Support for the SGH is mixed, but even studies failing to support it show that the net effect varies with the environment (Brooker *et al.*, 2008).

Because stress varies spatially and temporally, plants, as both populations and individuals, occupy zones of a gradient rather than specific points on a gradient (Schupp, 2007). That is, the degree of environmental stress plants face is not constant, but varies among individuals within a population (e.g. on ridge vs slope bottom) and within individuals across years (e.g. wet vs dry years). Consequently, the relative quality of seed dispersal to a shrub as opposed to an open interspace can vary spatially and temporally. In many cases, the net effect likely varies in strength while remaining positive or negative. However, in some portion of the gradient we expect the net effect to switch between facilitation and interference depending on environmental conditions (Ibáñez & Schupp, 2001; Lloret *et al.*, 2005).

Recently, the evolutionarily dynamics of plant–plant interactions has gained interest. On a shorter time scale, the net strength of facilitation can depend on local adaptation of recruit populations to stress (Espeland & Rice, 2007). On a longer time scale, increasing phylogenetic relatedness between facilitator and recruit appears to increase the likelihood that the interaction switches from facilitation at the seedling stage to interference later while phylogenetically distant interactions are more likely to remain facilitative (Valiente-Banuet & Verdú, 2008). While these results are compatible with the long-standing expectation that more closely related species compete more strongly among themselves than with more distantly related species, such a relationship between phylogenetic relatedness and competition is not universal (e.g. Cahill *et al.*, 2008).

Although it is uncertain how widespread a positive competition-relatedness relationship is, in cases where more closely related species compete with each other more intensely as recruits, the tendency of related plant species to share disperser assemblages (Rezende *et al.*, 2007) has negative implications for SDE. Related plant species dispersed largely by the same disperser assemblage should have seeds dispersed together, resulting in phylogenetically related seedling neighborhoods suffering greater competition during establishment and reduced SDE for the plants relative to the expectation when unrelated species are dispersed together. This highlights the far-reaching consequences that context-dependent SDE can have for establishment and vegetation assembly in communities dominated by animal-mediated dispersal.

Life-stage conflicts also can lead to context-dependent seed dispersal quality (Schupp, 2007). Conflicts exist when a site that is more suitable for some developmental stages (e.g. seed survival) is less suitable for others (e.g. sapling survival). When life-stage conflicts exist, the overall quality of dispersal to a given site depends not just on the quality of the site for germination and initial establishment, which are the most frequently studied aspects of quality, but rather on the sum of a series of benefits and detriments associated with that site throughout the regeneration process. As with the balance between interference and facilitation, a spatially and temporally variable environment can result in spatial and temporal variation in the relative quality of dispersal to distinct microhabitats as the strengths of the effects of seed predators, seedling pathogens, sapling browsers, drought stress, and more vary. Life-stage conflicts and the balance between interference and facilitation may frequently be intertwined; a shift from facilitation of seedlings to interference with older recruits is a life-stage conflict (Schupp, 2007).

Overall, context dependence of the qualitative component of SDE has received little attention, but implications are potentially great. Although context dependence makes the study of SDE more difficult, its existence does not mean that variation in the quality of dispersal is so case specific that deterministic patterns and processes are unknowable. By explicitly incorporating context dependence into empirical studies we can begin to develop a predictive understanding of variation in SDE. This can be accomplished through careful replication of studies across a natural range of environments and through experimental manipulations of the environment (Schupp, 2007).

### 4. Dynamic SDE landscapes

Context-dependent SDE results in dynamic SDE landscapes. If we compare a tree population in 2 yr, or two populations in a single year, we expect shifts in the disperser assemblage along both axes of SDE. Some species disperse more seeds, others fewer; some species drop out, others enter, and unchanged patterns of dispersal increase the quality of dispersal in some cases and decrease it in others (Fig. 3b). The *C. album* example (Calviño-Cancela & Martín-Herrero, 2009; Fig. 6b) clearly shows a spatially shifting landscape.

Thus, both the SDE that a plant population receives and the relative contributions of different dispersers to that SDE likely vary spatially and temporally. However, we do not know how much variation in SDE landscapes to expect at what spatial and temporal scales, how important it is for understanding the consequences of seed dispersal, and what the evolutionary consequences are. For example, the degree to which frugivorous birds spatially and temporally track variable fruit crops (Herrera, 1998; García & Ortiz-Pulido, 2004; Hampe, 2008; Tellería *et al.*, 2008; Lehouck *et al.*, 2009) will affect how variable assemblages are on the

quantitative axis of the SDE landscape. However, context-dependent SDE likely constrains the evolution of specialized seed dispersal systems (Schupp, 2007). Although positive effects of mutualistic interactions have been detected for mutualisms with marked context dependence (e.g. ant–plant interactions; Chamberlain & Holland, 2009), we might expect pervasive context dependence in plant-disperser interactions to favor generalization and weak patterns of pairwise dependence, as documented for diversified plant–animal mutualisms (Bascompte & Jordano, 2007). These in turn would favor the emergence of multispecies dispersal assemblages with species differing in dispersal patterns.

## VIII. 'Distance-dependent SDE'

Perhaps the most innovative attempt to revise the SDE framework was by Spiegel & Nathan (2007) who stressed the need to integrate what they refer to as 'distance-dependent SDE' into the traditional SDE framework. For *Ochradenus*, although bulbuls and grackles had equivalent traditional SDE based on recruitment of seedlings, they suggested that because longer distance dispersal by grackles was mostly responsible for metapopulation dynamics the grackle had a greater distance-dependent SDE based on survival and spread of populations.

But what is their distance-dependent SDE? It is clearly not based on traditional within-population distance-based process such as Janzen–Connell. Although not explicitly defined, distance-dependent SDE appears to be a synonym of long-distance dispersal (LDD) with more LDD equaling greater 'distance-dependent SDE'. Given the traditional within-population focus of distance dependence in recruitment studies it is not clear this is the best terminology to use, but it is a potentially important idea. However, the path to incorporating 'distance-dependent SDE' into the traditional framework is unclear given that there is neither a functional definition nor a quantitative framework provided. Without a quantitative framework predicting a contribution to fitness it is unclear how to compare a dispersal agent's 'distance-dependent SDE' with its traditional SDE.

In addition, although LDD is important for plant dynamics, contributing to population spread, subpopulation persistence, recolonization and gene flow (e.g. Bohrer *et al.*, 2005; Nathan, 2006; Levey *et al.*, 2008), we seldom know how important it is. The challenges to incorporating distance-dependent SDE into the traditional SDE framework are the same facing LDD in general: a biologically relevant definition and an empirical framework for quantifying consequences of LDD. Long-distance dispersal can lead to colonization, but what is the likelihood of successful establishment following LDD compared with local dispersal? It can contribute to gene flow in heterogeneous landscapes, but how important is that relative to gene flow

by pollen? It can promote subpopulation persistence, but what is the likelihood of subpopulation extinction without LDD? These questions and more are relevant and difficult to answer. Indeed, it is proving surprisingly difficult to link patterns of dispersal to patterns of recruitment even in very well-studied systems (Steele *et al.*, 2007).

While 'distance-dependent SDE' is a potentially ground-breaking concept, barriers to incorporating it quantitatively into the traditional SDE framework are great. A potential avenue could be through its relation with multispecies dispersal, and with the fact that frugivores differentially contributing to LDD events (Jordano *et al.*, 2007) show quantifiable differences in SDE. Ongoing theoretical and empirical research on LDD should begin to breach the barriers.

## IX. Emerging issues

### 1. Spatially explicit approaches

As noted, the most widely-used ways to assess where seeds are dispersed have been quantifying arrival in distinct habitats or microhabitats (e.g. Jordano & Schupp, 2000) and modeling dispersal kernels to reveal the distance distribution of dispersal (e.g. Soons & Bullock, 2008), neither of which reflect the true, spatially heterogeneous patterns of dispersal (Schupp *et al.*, 2002). Although the microhabitat of destination is frequently important for SDE, whether a single seed is dispersed to each of 100 different shrubs or 100 seeds are dispersed to the same shrub likely has a large impact on SDE. Thus, more spatially explicit approaches to seed dispersal will improve our understanding of SDE.

Recently, a number of authors have developed spatially explicit seed dispersal models based on animal behavior to investigate spatial heterogeneity of seed dispersal (Russo *et al.*, 2006; Levey *et al.*, 2008), effects of fruiting tree spatial structure on the quantity and patterns of seed dispersal (Carlo & Morales, 2008), and consequences of spatially contagious seed dispersal and overlapping seed shadows of co-occurring fruiting trees on spatial structuring of the seed rain (Kwit *et al.*, 2007). Such models can improve linkage with the consequences of dispersal because they can model landscape-level patterns of seed removal and seed dispersal, including patch type of destination and spatial clumping of seeds, and implicitly incorporate seed fates. Although this modeling approach is promising, Muller-Landau *et al.* (2008) identify a number of difficulties in developing truly 'effective' mechanistic models for seed dispersal by animals.

Spatial analyses of actual seed rain also promise improved understanding of spatial patterns of seed dispersal and their SDE consequences. Spatial point pattern analysis revealed that rodents dispersed and cached *Q. ilex* acorns in a less clumped pattern in a year of low acorn availability than in a year of higher availability (Puerta-Piñero *et al.*, 2010). This

is compatible with the hypothesis that rodents increase spacing of caches to reduce pilfering in years when resources are more valuable (Moore *et al.*, 2007), potentially increasing acorn survival. Using a similar approach, Fedriani *et al.* (2009) conducted spatial point pattern analysis of *P. bourgaeana* adults and of dispersed seeds and determined that seeds dispersed by wild boars were mostly randomly distributed with respect to other seeds but had a strong tendency to be deposited in the vicinity of adults; thus, they concluded boars likely contribute mostly to maintenance of existing tree clumps. By contrast, seeds dispersed by badgers were tightly clumped with respect to each other (scale < 10 m) but independent of adults; thus they concluded that badgers likely contribute mostly to founding new clumps. Use of explicit spatial analyses of mapped dispersed seeds will hopefully increase along with the expanding suite of spatial analytical tools (Schiffers *et al.*, 2008) that are becoming available.

### 2. Hotspots of initial recruitment?

Contagious seed dispersal, such as found in the high-density seed fall beneath primate sleeping trees, results in high densities of seedlings and saplings (e.g. Julliot, 1997; Russo & Augspurger, 2004); that is, greater amounts of seed fall carry through to greater overall levels of sapling recruitment, even with reduced survival per seed (Russo & Augspurger, 2004). Recent analysis of multiyear data from five fleshy-fruited tree populations of three species in three ecosystems has shed new insight on the potential creation of sites with disproportionately high recruitment, in particular the temporal component of recruitment (Hampe *et al.*, 2008). Across all populations, sites with the most long-term seed input and seedling recruitment across years also had the greatest year-to-year consistency in input and recruitment. These sites were referred to as 'hotspots' of initial plant recruitment. The key is not simply that some sites accumulate more recruits than other sites, but that the sites that accumulate more recruits are sites that consistently receive greater amounts of seed input and recruitment over time. The existence of sites that consistently receive high numbers of seeds and recruits has implications for spatial patterns of recruitment, SDE, and genetic structure (García *et al.*, 2009). Whether consistent hotspots of seed arrival improve or diminish SDE relative to less consistent patterns likely depends on the degree of long-term consistency in site quality and the degree of concordance between patterns of seed arrival and site quality; it matters whether 'hotspots' are the result of directed dispersal (Wenny, 2001) to highly suitable recruitment sites. Other evidence for hotspots of recruitment has been reported (Wiegand *et al.*, 2009), but at this point much remains to be learned about the breadth, strength, and SDE consequences of hotspots of recruitment.

### 3. Secondary chemistry and the directed deterrence hypothesis

Plants might be able to 'choose' higher-quality dispersers and discourage lower-quality ones. The directed deterrence hypothesis (*sensu* Cipollini & Levey, 1997) proposed that fruit secondary compounds have evolved to discourage damaging vertebrates such as seed predators while not inhibiting helpful frugivores such as seed dispersers. For example, capsaicinoids in chilies deter seed-eating rodents but not seed-dispersing birds (Tewksbury & Nabhan, 2001; Levey *et al.*, 2006). Directed toxicity could also discourage lower-quality dispersers, not just predators. The wild chili *Capsicum annum* benefits from facilitation by other fruiting plants and birds tend to disperse seeds to appropriate microhabitats (Tewksbury *et al.*, 1999). As mammals frequently disperse seeds to open, less suitable sites (Martinez *et al.*, 2008), deterrence of mammals by capsaicin might discourage legitimate dispersers such as lagomorphs and carnivores that would provide lower-quality dispersal. However, many larger mammals apparently swallow chilies whole, which likely decreases the impact of capsaicinoids (JJ Tewksbury, pers. comm.). Further, effects of capsaicin – and other secondary compounds – can be complex, affecting gut retention time, seed germination and presumably dispersal distances (Tewksbury *et al.*, 2008). Given abundant within-population variation in concentrations of secondary compounds and covariation among secondary compounds and nutrients (Izhaki *et al.*, 2002), these compounds might be playing extremely important roles in both quantitative and qualitative aspects of SDE.

## X. Conclusions

Seed dispersal effectiveness provides a conceptual tool for quantifying the effects of seed dispersers on plant population recruitment as well as a more general framework for organizing thinking on how seed dispersers influence the ecology and evolution of the plants. In the last 17 yr, tremendous progress has been made in understanding causes and consequences of SDE. However, as in almost all fields of research, the more we learn, the more questions arise. A fundamental issue is where seed disperser assemblages lie on the SDE landscape. With multiple factors contributing to both the quantitative and qualitative axes there is substantial potential for variation across dispersal agents in SDE. It is likely that some assemblages vary more on the quantitative axis while others vary more on the qualitative axis, and that this variation is in some manner related to species richness or functional diversity of assemblages. However, understanding the distribution of real assemblages is inhibited by a lack of complete studies on the quality of dispersal. Given the diversity of SDEs in assemblages, there is extensive opportunity for multispecies dispersal, including

diplochory, to influence the overall SDE a plant population receives. This is especially true in light of the growing evidence for the context dependence of both the quantity and quality of dispersal. It is important to develop a better understanding of when or where multispecies dispersal increases rather than decreases overall SDE. Further, it is critical to directly address context-dependent SDE, including its extent and amplitude, ecological and evolutionary consequences, and predictability in order to develop generalities in the face of context dependence. Lastly, 'distance-dependent SDE' is a ground-breaking concept but it is still unclear how to incorporate this into the original SDE concept. There is tremendous diversity and complexity in plant–seed disperser interactions. We have made significant progress in disentangling these complexities, but much remains to be discovered.

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