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A Unifying Gravity Framework for Dispersal

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A unifying gravity framework for dispersal

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Abstract Most organisms disperse at some life-history stage, but different research traditions to study dispersal have evolved in botany, zoology, and epidemiology. In this paper, we synthesize concepts, principles, patterns, and processes in dispersal across organisms. We suggest a consistent conceptual framework for dispersal, which utilizes generalized gravity models. This framework will facilitate communication among research traditions, guide the development of dispersal models for theoretical and applied ecology, and enable common representation across taxonomic groups, encapsulating processes at the source and destination of movement, as well as during the intervening relocation process, while allowing each of these stages in the dispersal

process to be addressed separately and in relevant detail. For different research traditions, certain parts of the dispersal process are less studied than others (e.g., seed release processes in plants and termination of dispersal in terrestrial and aquatic animals). The generalized gravity model can serve as a unifying framework for such processes, because it captures the general conceptual and formal components of any dispersal process, no matter what the relevant biological timescale involved. We illustrate the use of the framework with examples of passive (a plant), active (an animal), and vectored (a fungus) dispersal, and point out promising applications, including studies of dispersal mechanisms, total dispersal kernels, and spatial population dynamics.

Keywords Conceptual framework · Dispersal patterns and processes · Empirical and mechanistic models · Migration · Movement · Serial and parallel processes

Introduction

Dispersal is a common biological phenomenon and an important aspect of the life-history strategies of most organisms (Stenseth and Lidicker 1992; Bullock et al. 2002; Smith et al. 2009; Clobert et al. 2012). Dispersal is recognized as a critical process in many theoretical and applied problems, such as population and community dynamics, evolution, conservation, invasion biology, disease control, and pest management (Hanski 1996; Shea et al. 1998; Dieckmann et al. 2000; Isard and Gage 2001; Hein and Gillooly 2011). However, different conceptual, empirical, and theoretical approaches to studying dispersal have evolved in the various biological subdisciplines and research traditions. There are an increasing number of studies on the dispersal of terrestrial animals and plants (Turchin 1998; Levin et al. 2003; Clobert et al. 2004; Schupp et al. 2010), airborne fungal and microbial pathogens (Isard and Gage 2001; Isard et al. 2011), and aquatic organisms (Bilton et al. 2001; Levin 2006). However, a synthesis of dispersal concepts, theory, and empirical work across organisms has lagged behind the progress within these subdisciplines (Nathan 2003; Hastings et al. 2005; Holden 2006; Nathan et al. 2008). Two possible reasons for this lag are the different uses of basic concepts in various research traditions and the fact that theoretical and empirical studies are often poorly integrated.

In this paper, we present a generalized gravity model as a unifying quantitative framework for dispersal. This framework is based on a simple conceptual model of dispersal processes that can be applied across organisms and research traditions. We broadly categorize the components of dispersal into three phases: (1) source, (2) relocation, and (3) destination processes (Fig. 1). In the gravity framework, these processes are represented by associated source, relocation, and destination functions, respectively. This framework leaves room for different timescales and the complexity and variability of dispersal processes across organisms, while paving the way for cross-fertilization among existing research

traditions. This synthetic approach may contribute to the further development of interdisciplinary fields of basic and applied research where dispersal plays a central role, such as the fields of landscape ecology (Forman and Gordon 1986; Skelsey et al. 2012), aerobiology (Isard and Gage 2001), and conservation and management (Jongejans et al. 2008; Dauer et al. 2009; Shea et al. 2010; Marchetto et al. 2014). We discuss several promising areas of research, including the quantification of dispersal processes, dispersal limitation, integration of multiple dispersal mechanisms and spatial population dynamics.

Conceptual framework

In order to identify generalities in dispersal, a consistent conceptual framework is necessary. While previous authors have elaborated on such frameworks, their focus has often been limited to particular taxonomic groups (e.g., plants; van der Pijl 1982), dispersal phenomena (e.g., migration; Dingle 1996), and physical mechanisms (e.g., atmospheric circulation; Isard and Gage 2001). The establishment of movement ecology as a research field (Nathan et al. 2008) underpins a need for simple, generally applicable frameworks to synthesize dispersal processes and patterns across research traditions. Below, we develop a unified cross-disciplinary conceptual framework with an explicit modeling formalization that generalizes and integrates aspects from these existing frameworks to the extent that they inform us about organismal dispersal. This allows us to deliberately highlight areas where critical information about the dispersal process is missing or understudied, which in turn will improve our understanding of dispersal of various types and in various taxa.

Following Nathan (2001), we define *dispersal* as the movement of dispersal units away from their source. A *dispersal unit* is an organism (in any life stage) or any part of an organism (e.g., a fragment of a modular organism, a gamete) that can depart from its source and can lead to gene flow across space (Bowler and Benton 2005; Ronce 2007). This definition of dispersal captures the wide range of definitions used in different research traditions in biology (Table 1). For instance, in botany, dispersal refers to the scattering of seeds or pollen away from mother plants (van der Pijl 1982), while in

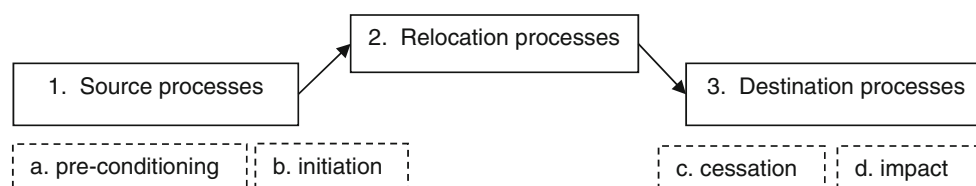


Fig. 1 A general conceptual dispersal process model. All dispersing organisms pass through three phases in dispersal: (1) source processes, (2) relocation processes, and (3) destination processes. Source processes include

(a) preconditioning (e.g., adaptations to dispersal) and (b) initiation (takeoff), and destination processes include (c) cessation (e.g., patch choice) and (d) impact (e.g., colonization) (adapted from Isard and Gage 2001)

Table 1 Examples of typical uses of dispersal-related concepts in different research traditions. Research traditions are interpreted widely: animal ecology includes zoology, behavioral ecology, and animal population ecology; plant ecology includes botany and plant population ecology;

disease ecology includes epidemiology of plants, animals, and humans; and macroecology includes metapopulation biology, landscape ecology, and biogeography

Type of movement	Terms used in different research traditions			
	Animal ecology	Plant ecology	Disease ecology	Macroecology
Individual movements				
Movement from one spatial unit to another	Migration ^a , dispersal ^b	Dispersal ^c	Dispersal ^d , (vector-borne) transmission	Migration
Movement away from a source	Emigration ^e	Dispersal ^f		
Movement not responsive to resources or home range	Migration ^g			
One-way extra home range movement	Migration ^h , dispersal ⁱ			
Round-trip traveling (usually seasonal)	Migration ^{h,i}			
Socially mediated infra-dispersal	Dispersal ^h , spacing behavior ⁱ			
Population (or species) movements				
Increase in the total area inhabited by the species	Range expansion, invasion	Migration ^j , range expansion, invasion ^k		Migration, dispersal
Movement into new areas without net change in range size	Range shift, invasion	Migration ^j , range shift		Migration

^a Baker (1978)

^b Clobert et al. (2012)

^c Berg (1983)

^d Campbell and Madden (1990)

^e Ims and Yoccoz (1996)

^f Nathan (2001)

^g Dingle (1996)

^h Taylor (1986)

ⁱ Stenseth and Lidicker (1992)

^j Pakeman (2001)

^k Clark et al. (2001)

zoology, dispersal means the movement of individuals away from a habitat, home range, or population (Stenseth and Lidicker 1992; Bilton et al. 2001). This movement between locations is often referred to as migration in population biology and landscape ecology (Ims and Yoccoz 1996; Bauer and Hoye 2014).

We discuss dispersal in terms of a modification of the general scale-independent movement model proposed by Isard and Gage (2001). Our conceptual model (Fig. 1) emphasizes that the biological concept broadly termed as “dispersal” is the result of multiple serial processes that occur prior to relocation, during relocation, and after relocation. This simple three-way division of the dispersal process (see also Yates and Boyce 2012) is appropriate for our presentation, but Isard and Gage (2001) further subdivide processes at the source into preconditioning and initiation, and at the destination into cessation and impact (Fig. 1). This suggests that there are multiple stages that any individual must pass through in the course of dispersal and that population-scale patterns are affected by variation among individuals at each of these many

stages. In addition, relocation processes may often also be subdivided into multiple mechanisms of relocation (passive, active, vectored), which may occur serially for any individual and in parallel across the population. Where serial processes require multiplication of gravity model components, addition is needed for parallel processes. Thus, the total dispersal pattern for any given population is likely to be a mixture of many individual dispersal processes (Nathan 2006, 2007).

The general conceptual dispersal model (Fig. 1) is useful for highlighting the differences and relationships among dispersal and related movement concepts that exist in different research traditions (Table 1). The types of movement differ with respect to the definitions of source and destination and the time frame of the movement. Whenever source and destination locations are different, the movement model describes dispersal. More specifically, when the source and destination in the dispersal process model (Fig. 1) differ in *habitat patches* or *populations*, the model describes *migration* in the meta-population sense (Table 1). In this case, the initiation of

movement is synonymous with *emigration* and the cessation of movement is synonymous with *immigration* (Ims and Yoccoz 1996; Ronce 2007). Also, when the source and destination change positions during the defined time frame (i.e., the destination becomes the new source and the old source becomes the destination within, for instance, a year or a generation), the movement model describes *cyclical migration* or *seasonal migration* (such as that of the monarch butterfly). However, when the source and destination locations are the same, the movement model describes some other kinds of non-dispersal *philopatric* movement, such as *spacing behavior* or *aggregation* (Stenseth and Lidicker 1992; Dingle 1996).

Different research traditions have focused on different phases of the dispersal process (Fig. 1). For instance, because of the interactions within the host immune system, the greatest barriers to pathogen dispersal (e.g., vector-borne transmission) are often the source (i.e., shedding) and destination (i.e., susceptibility and infection) processes. In contrast, for many other organisms, such as natal dispersal in deer, the focus of attention is on relocation processes (Turchin 1998). Furthermore, the first and last phases of the dispersal process at the source and destination, respectively, relate to the questions of why to start and why to stop dispersing; traditionally, these questions have been pursued mainly by behavioral and evolutionary ecologists (e.g., Armsworth 2008), while relocation has been pursued mainly by population ecologists. Because of this separation, the phases tend to be approached with different modeling techniques, and rarely is more than one phase of dispersal addressed directly within a single dispersal model (see the examples below as an illustration of studies in which dispersal phases were studied either separately or jointly). For example, mechanistic simulation models that are rich in detail and tailored to specific systems (e.g., plant pathogens; Aylor 2003; Isard et al. 2005) sometimes include all dispersal phases, which reduce the chance wherein important processes are overlooked, but such system-specific simulation models are not generally applicable. In the next section, we introduce a framework for treating the three phases of dispersal in a general quantitative framework and illustrate the framework with examples for different taxa and dispersal processes.

Generalized gravity models for dispersal

Inspired by the dispersal of an apple, Newton (1687) formulated his law of universal gravitation

$$F = G \frac{m_1 m_2}{d^2} \quad (1)$$

where F is the force between the masses, G is the gravitational constant, m_1 and m_2 are the masses of two objects, and d is

their distance apart. While Newton's law captures an important general physical relationship, many factors other than gravitation influence the timing, distance, and impact of the dispersal of apples, such as the drag forces of the wind on the desiccating connection with the tree, frugivores, collisions after falling, and light and pathogen conditions that influence the chance of establishing a seedling upon arrival. When applied to dispersal, in general, gravity models describe the rate (or number) of dispersal units relocating between sources and destinations in terms of source characteristics, destination characteristics, and the distance and conditions between source and destination. These three components are analogous to the three components of Newtonian gravity. In these models, characteristics of the source and destination are covariates that describe the propensity to initiate dispersal, e.g., the number of recreational boaters that can pick up zebra mussel larvae (Bossenbroek et al. 2001; Potapov et al. 2011). For the destination processes, it is also important to study the propensity to receive dispersers; e.g., large cities like London tend to get more visitors and thus are more likely to be visited by individuals infected with measles (Xia et al. 2004). Gravity studies in human migration date back to the nineteenth century (e.g., Ravenstein 1885; Thomas and Hugget 1980; Cohen et al. 2008). Since then, the gravity framework has also been applied to the study of trade and transportation (Black 2003), telecommunication (Krings et al. 2009), regional science (Roy 2004), invasion biology (Carrasco et al. 2010; Suttrave et al. 2012), and epidemiology (Bharti et al. 2008; Barrios et al. 2012; Maher et al. 2012).

Here, we present a general form of the gravity model and illustrate it using three case studies. We start by denoting the number of dispersal units (δ_{ij}) from the source (i) arriving at the destination (j) as

$$\delta_{ij} \propto g(\mathbf{c}_i, \mathbf{c}_j, \mathbf{c}_{ij}, d_{ij}) \quad (2)$$

where \mathbf{c} is the vector of conditions (external and/or internal to the organism) at the source (\mathbf{c}_i), destination (\mathbf{c}_j), and between the two (\mathbf{c}_{ij}), and d_{ij} is the distance between the source and the destination. We will use separate functions for source processes (S), relocation processes (R), and destination processes (D), so that

$$g(\mathbf{c}_i, \mathbf{c}_j, \mathbf{c}_{ij}, d_{ij}) = g(f_S(\mathbf{c}_i), f_R(\mathbf{c}_{ij}, d_{ij}), f_D(\mathbf{c}_j)). \quad (3)$$

This is a generalization of the classical Newtonian gravity model (Eq. 1) that retains the three main stages while giving sufficient flexibility to account for diverse source, relocation, and destination processes. The degree of independence of the three processes will vary from system to system. The classical Newtonian model is a special case of the general model with $f_S = m_1$, $f_R = d^{-2}$, and $f_D = m_2$ and a gravitational constant G of proportionality. The general model can be adapted to particular dispersal systems by choosing the appropriate process

functions. For instance, including both f_S and f_D as functions leads to a source-destination-mediated model (“production-attraction constrained” in the transportation literature; Black 2003), while setting f_D to a constant in cases where only source processes play a major role reduces the model to a source-mediated model (“production constrained”).

Examples

We present three examples to illustrate how the gravity framework can be used to highlight and integrate the different phases of dispersal for the full range of dispersal mechanisms from *passive* to *active* and *vectored* dispersal. The examples also cover different taxa (*plants*, *animals*, and *fungi*). There exist several examples in the literature of applications of gravity models to human-vectored dispersal (e.g., of invasive species and diseases; Bossenbroek et al. 2001; Xia et al. 2004; Muirhead et al. 2011; Leung et al. 2012); therefore, in order to illustrate the broad applicability of the gravity framework, we deliberately chose to focus on other examples here. Finally, the examples illustrate the conceptual dispersal process model and how the gravity framework may be useful at various stages of research from the formulation of hypotheses to model construction and hypothesis testing.

Example I: passive wind dispersal of thistle seeds

Passive dispersal of plant seeds is an example of a dispersal process where source processes play an important, but often overlooked role. We illustrate this using experimental results and models for musk thistle (*Carduus nutans*) dispersal. Wind dispersal of seeds of this species was measured in seed trapping studies in Pennsylvania, where the source was an artificially created patch of thistles and the destinations were sticky traps placed in sectors around the source (Skarpaas and Shea 2007). The distribution of dispersal distances seems to be well predicted by a mechanistic model of wind dispersal (the Wald analytical long-distance dispersal (WALD) model; Katul et al. 2005). We know from experimental studies that seed release is affected by several factors, including wind speed (Skarpaas et al. 2006; Jongejans et al. 2007). In the original analyses, this source process was accounted for by weighting the wind frequency in the integrated WALD model by wind speed (Skarpaas and Shea 2007). Here, to put this in the context of the generalized gravity model and separate the source and relocation processes, we use the integrated WALD model as the relocation function (Skarpaas and Shea 2007) and make a separate source function in which seed release depends linearly on the horizontal wind speed (U). Additionally, the source function accounts for the numbers of dispersal units released (Q_i), i.e., $f_S = \beta U Q_i$, where β is the linear wind release slope. The destination function is simply the trap width, $f_D = w$. The

total gravity model for thistle seed dispersal by wind is the product of the source, relocation, and destination functions

$$\begin{aligned} \delta_{ij} &= f_S(c_i) f_R(c_{ij}, d_{ij}) f_D(c_j) \\ &= \beta U Q_i \left(\iint \left(\frac{\lambda'}{2\pi d_{ij}^3} \right)^{\frac{1}{2}} \exp \left(-\frac{\lambda' (d_{ij} - \mu')^2}{2\mu'^2 d_{ij}} \right) p(F) p(U) dF dU \right) w \end{aligned} \quad (4)$$

where μ' and λ' are related to environmental and species traits (see Skarpaas and Shea 2007 for details). To account for variability in seed terminal velocity (F) and hourly mean horizontal wind velocity (U), the WALD model was integrated over these variables to obtain the seasonal relocation function (f_R) (Skarpaas and Shea 2007).

Equation 4 is an example of a source-mediated model since the destination function (f_D) is constant. Equation 4 could be seen as a traditional way of multiplying a probability density function by the number of propagules. The innovation, however, is that it is very explicit about all phases of dispersal and also that the source and relocation functions have mechanistically and biologically meaningful parameters. The model parameters were all obtained from measurements independent from dispersal distances (Skarpaas et al. 2006; Skarpaas and Shea 2007). Using these independent estimates, it is clear that our knowledge of the seed release process contributes substantially to our ability to predict dispersal: the model including the seed release function (f_S) fits the empirical data much better than a model without f_S (Fig. 2; see also Skarpaas et al. 2011). The source function can be further extended to include

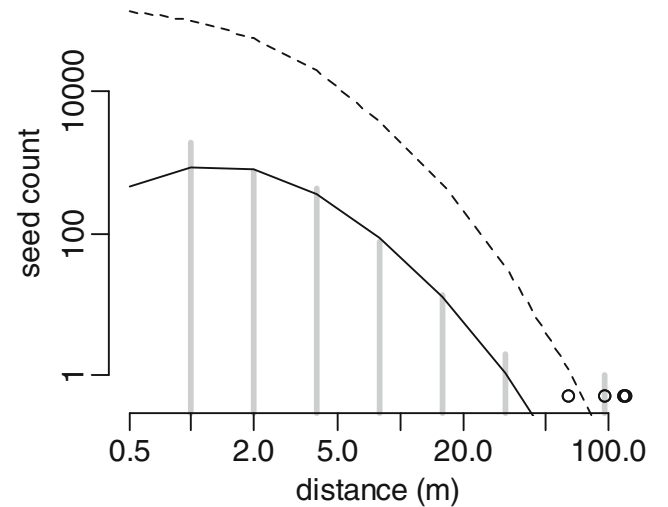


Fig. 2 Observed (gray bars; circles indicate empty traps) and predicted dispersal distances for musk thistle (*Carduus nutans*) using the generalized gravity model with components describing all parts (source, relocation, and destination; solid line) and with the source component left out (dashed line) (adapted from Skarpaas and Shea 2007). The expected seed count at a destination (j) (i.e., a seed trap) is the sum over sources (i). In this case, there is only one source, so the expected seed count is given by Eq. 4, with and without the source component, $f_S = \beta U Q_i$

factors such as turbulence, drying, and herbivory, which have been shown to influence seed release (Jongejans et al. 2007; Marchetto et al. 2012, 2014).

Example II: active natal dispersal of white-tailed deer

Natal dispersal (i.e., dispersal away from the birthplace) of animals is an example of a dispersal process where source, relocation, and destination processes may all play important roles. Here, we show how the gravity framework may help to highlight important missing components in our understanding of the dispersal of subadult male white-tailed deer (*Odocoileus virginianus*) and to suggest ways to address them.

Relevant source processes for dispersal include two complementary life-history strategies: avoidance of inbreeding and reduction of mate competition. Both of these could be considered sex-specific, density-dependent processes. The reduced adult female density seems to decrease the dispersal of subadult males due to a reduced need to avoid inbreeding, whereas the increased adult male density increases the dispersal of subadult male deer because of mate competition (Long et al. 2008). Relocation processes seem to be influenced primarily by landscape and age (Skuldt et al. 2008). With increasing forest cover, average dispersal distance decreases (Long et al. 2005), but the relocation function seems to retain the shape of a lognormal distribution (Diefenbach et al. 2008). Landscape features such as mountains, roads, and rivers influence dispersal direction (Fig. 3; Long et al. 2010) and spatial genetic structure (Robinson et al. 2012). Deer may terminate dispersal early due to hesitation when crossing roads (hereafter referred to as the stopping rule; Long et al. 2010).

Apart from this, little is known about why dispersing deer stop where they do.

Thus, by separating source, relocation, and destination processes in deer dispersal, it becomes clear that the destination processes are presently the least well known. Given that inbreeding avoidance and mate competition seem to drive the initiation of dispersal, one might hypothesize that the settlement of subadult male deer would also be density dependent and would respond differently to differing densities of males and females. Gravity models could help disentangle these hypotheses with different competing models for settlement on the basis of the alternative mechanisms. For example, the mate competition hypothesis would suggest a destination function declining with male density at the destination.

By integrating all this information, a full gravity model of dispersal would include an appropriate destination function (discussed above), a source function to account for dispersal initiation in response to female and male densities in the source patch (e.g., a linear relationship), and a relocation function to account for distance between sources and destinations (a lognormal distribution) and environmental conditions during relocation (effects of landscape configuration on dispersal distances). This source-destination-mediated gravity model would predict that for similar source and relocation conditions, a destination with lower male densities would receive more dispersers. The null model, a source-mediated gravity model with no destination effect, would predict no differences among destinations with different male densities. While these predictions could be tested directly by comparing observations from different destinations, the gravity model would greatly increase the power to detect destination effects by controlling for dissimilar source and relocation conditions

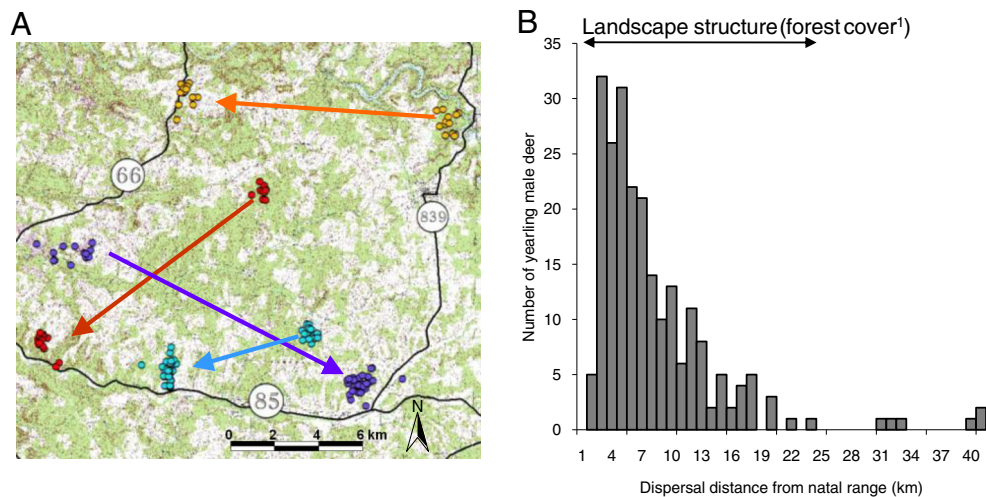


Fig. 3 a Map of the movement of four yearling male white-tailed deer from their natal home range to their breeding range in Pennsylvania, USA, showing the role of roads as barriers to dispersal (Long 2005). Roads/highways are indicated by numbers. b Dispersal distances of 228 radio-collared yearling male white-tailed deer in Pennsylvania. Meta-

analysis of ten populations of white-tailed deer indicated the percentage of forest cover-predicted mean dispersal distance (as indicated by the range of distances from the source that are most likely forested; Long et al. 2005), but roads limited relocation movements (Long et al. 2010)

in the surrounding landscape. Although it is a very complicated exercise to describe the dispersal phases accurately and mechanistically in this case study, defining a gravity model allows us to identify and prioritize which missing information would be most useful to gather next.

Because deer are active dispersers, the stopping rule may be a relocation process and a destination process (i.e., habitat selection); this is an example where the processes are not fully independent. This insight may apply to active dispersers in general: the way active dispersers move may be more of a function of how resources and other conditions are distributed (i.e., what options are available) than how far they choose to travel. This suggests that failing to consider the destination component of the stopping rule may severely bias the applicability of results from one organism or setting to another.

Example III: vectored dispersal of anther smut disease

Disease transmission is fundamentally a dispersal process. Infectious spores, bacteria, or other infectious agents must disperse from one host to another before establishing and initiating a disease response in the new host. For vector-borne pathogens, the steps that result in transmission can be described in terms of (a) characteristics that increase the likelihood of a vector feeding and acquiring spores (source processes), (b) the movement behavior of the vector (relocation processes), and (c) characteristics that increase the likelihood of a vector feeding and depositing spores on a susceptible host (destination processes).

Ferrari et al. (2006) showed that the spatial and temporal distribution of infection by the pollinator-borne fungus, *Microbotryum violaceum*, was best characterized using a gravity model of spore dispersal. *M. violaceum* is a fungal pathogen that causes anther smut disease and commonly infects members of the Caryophyllaceae such as *Silene latifolia* (white campion). The infection is dispersed by pollinators such as bumblebees and various moth species (Altizer et al. 1998) in the course of foraging. Building on the vast theoretical work on optimal foraging theory, Ferrari et al. (2006) developed a mechanistic model for the rate of spore movement from infected to healthy plants that necessarily results in a probability of infection that depends on the three components of the gravity framework.

Consider the probability of a movement between two plants in a distance (d_{ij}) apart; the simplest assumption for pollinator movement is random walk. Broadbend and Kendall (1953) showed that if the probability of encountering a plant during the random walk in a short interval (∂t) is $\lambda \partial t$, then the probability of a movement between a source (here an infected plant) and destination (a healthy plant) is a decreasing function of their distance apart and depends on both the diffusion rate of the pollinator's random walk and the density of plants.

Ohashi and Yahara (1999), building on Charnov's (1976) marginal value theorem, showed that the optimal number of

flowers to visit on a plant should increase linearly with the total number of flowers on that plant, with a slope determined by the relative cost of a movement within versus between plants. Ferrari et al. (2006) showed that, if a pollinator acquires spores at some rate during the course of foraging and the duration of a foraging bout increases with the number of flowers, i.e., the foraging reward in the models of Ohashi and Yahara (1999) and Charnov (1976), then the total spores acquired (and thus possible to disperse) should increase with the number of flowers at the source plant. By a similar argument, the number of spores deposited at a destination plant should be an increasing function of the number of flowers. Thus, conditional on a movement between two plants, the total number of spores transferred is expected to be an increasing function of the number of flowers at both the source and the destination. Since the probability of a movement is a decaying function of distance, then the expected number of spores dispersed and, thus, the probability of infection depends on the number of flowers at the source, the number at the destination, and their distance apart, leading to a gravity model.

Very simple qualitative predictions emerge from this gravity model: *M. violaceum* infection should be more likely in plants that are larger and closer to large, infected source plants. Ferrari et al. (2006) showed that in over three experimental populations of 64 equally spaced plants, infection (i.e., pathogen dispersal) was strongly biased toward individuals that were larger than average and closer to large source plants than expected by chance (Fig. 4). Further, they showed that the full gravity model, incorporating the number of flowers of infected

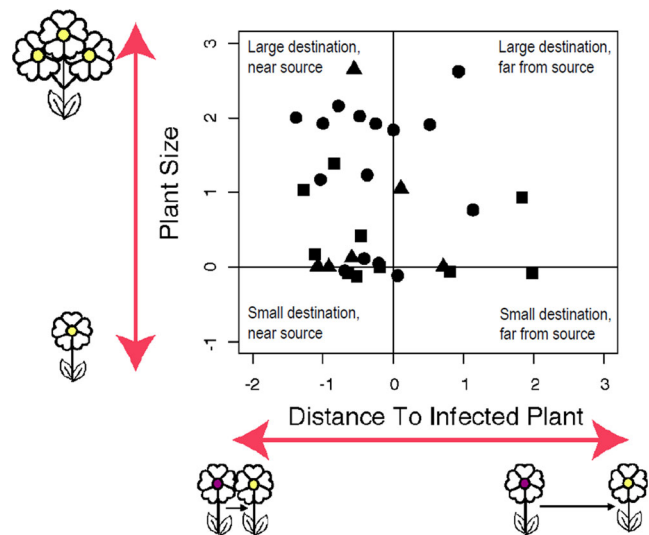


Fig. 4 Relative floral display size and distance to infected sources for *Silene latifolia* individuals that became infected with *Microbotryum violaceum*. Each point gives the distances of each susceptible plant to all infected sources (X-axis) and the number of flowers (Y-axis) per plant. Values are standardized relative to the median and variance at the time of observation. The symbols indicate three different experimental replicates (adapted from Ferrari et al. 2006)

plants, the number of flowers of healthy plants, and their distances, was more predictive (measured by AIC) than the sub-models that incorporated only some of these covariates (Ferrari et al. 2006).

While this model was formulated specifically for a pollinator-borne pathogen, several general predictions emerge from this mechanistic formulation that may be relevant for vectored dispersal in general. The relocation model depends on both the diffusion rate (i.e., the movement rate of the vector) and the plant density. Thus, in populations where vectors are highly mobile or suitable habitat is common, then the observed pattern of dispersal may be better predicted by the distribution of characteristics at the source and destination than by separation in space. In contrast, if suitable resources are limiting, such that the cost to the vector of passing over a marginal location is high, then the observed pattern of dispersal may be more spatially limited. Thus, despite the same underlying process, the gravity model implies that the observation of vector-borne dispersal phenomena may change depending on the landscape-level pattern of resource distribution.

Discussion

Why are we interested in dispersal and how can we most effectively advance a dispersal research agenda? Dispersal fundamentally determines how organisms move in a manner that affects their ecology. We want to know not only how far organisms move but also whether they will survive and reproduce at their destination and why they started dispersing in the first place. In the case of endangered or pest species, or diseases, this information has direct implications for management. The gravity framework can assist spatial ecological research in two main ways. First of all, modeling the entire dispersal pathway, from source to destination, enables us to highlight the dispersal phases that are poorly understood. Second, the gravity framework can also be used to investigate how management efforts should be allocated.

Although dispersal researchers have made great progress in many areas, challenges remain for many organisms (see, e.g., Cousens et al. 2008). For certain groups of organisms, such as invertebrates and fungi, incomplete taxonomic information contributes to the difficulty in identifying and detecting those species and their propagules. Even though their poor detectability hinders dispersal research for some groups, indirect approaches have been proven to be useful, as in the employment of chronosequences to study the primary assembly of soil communities in recently emerged glacier-free land (Ingimarsdóttir et al. 2012). For other organisms, particularly species of economic importance (e.g., trees, game animals, diseases, and some invasive species), a complete

understanding of the entire dispersal process is within reach (e.g., white-tailed deer). Model organisms, such as *Drosophila* and *Arabidopsis*, have played important roles in other biological disciplines and may also improve our understanding of dispersal. The vast collective knowledge of the genetics, physiology, and behavior of these organisms should provide substantial insight into source, relocation, and destination processes.

From an applied point of view, a gravity framework can allow us to target management efforts. For example, we can assess if the management of the relocation phase is likely to be the most efficient or whether management should target the initiation of dispersal at the source or its cessation at the destination. For instance, in the case of the spread of rabid raccoons, gravity models can be used to see whether it is more efficient to bait-trap raccoons before or after they cross a river that forms a semipermeable barrier (Smith et al. 2002; Côté et al. 2012). Similarly, the gravity framework can be used to study when it is best to exchange ballast water in order to minimize the risk of introducing invasive species (MacIsaac et al. 2002). While national biosecurity agencies (like APHIS/AQIS) mainly focus on preventing the arrival of invaders, new trade treaties force exporting countries to take better measures to prevent invasions at the source (Burgiel et al. 2006; Hulme et al. 2008). This interfaces into a growing body of research on source-destination management (Epanchin-Niell and Hastings 2010; Epanchin-Niell and Wilen 2012; Leung et al. 2012).

In the following sections, we discuss four promising areas for research using our gravity framework and modeling approach: (1) a conceptual and formal reconciliation of knowledge about dispersal, (2) the quantification of dispersal processes, (3) the analysis of limiting dispersal processes in general gravity models, and (4) the link between dispersal processes and spatial population dynamics. All have both basic and applied ramifications.

Promising direction 1: conceptual and formal reconciliation of knowledge about dispersal

The gravity framework we present allows for both conceptual (qualitative) and formal (quantitative) reconciliations of dispersal-related research. Synthesis of existing dispersal information will permit us to clearly delineate what we know and do not know about dispersal, immediately highlighting useful avenues of research. A unifying framework is useful because data from various organisms and ecological systems are often collected at different stages of the dispersal process (Fig. 1) and the meanings of basic dispersal concepts vary across disciplines (Table 1). This reflects differences in the types of movement of ecological interest underlying biological questions and, importantly, differences in what can and cannot easily be measured. For instance, (seasonal) migration is a conspicuous phenomenon in many birds, bats, and insects

(Bauer and Hoye 2014) but is obviously not important in plants. Although the gravity model is, in its basic form, a time-implicit two-patch model, conceptually, it can be straightforwardly extended to represent migration with multiple stopovers and various timescales. In studies on species that rely on external vectors for long-distance dispersal, the focus might be more on source processes, while in invasion ecology, an interest in destination processes may dominate (although preventing transport is also important; Leung et al. 2012). The sessile habit of plants, and the release of many small dispersal units (pollen and seeds), lends itself to studies of dispersal patterns from point sources (e.g., Johansson et al. 2014, but see Kelly et al. 2013 for realistic distributions of release locations). In epidemics, the impacts of dispersal are typically observed, i.e., infection, and not the organism itself.

However, underlying all of these differences are key commonalities. General empirical patterns, such as right-skewed (and leptokurtic) distributions of dispersal distances, do emerge (Willson 1993; Greene and Calogeropoulos 2002; Allen 2007; Petrovskii and Morozov 2009; Petrovskii et al. 2011). Allometric patterns also seem to be quite general (Sutherland et al. 2000; Thomson et al. 2011), although these patterns may be different from central tendencies (mean, median) and extreme long-distance dispersal (e.g., 99.9 %) because median and long-distance dispersal are not necessarily well correlated (Greene and Johnson 1989). Generalities are also evident within specific phases of dispersal. For instance, during the relocation phase, air, water, and (or) humans seem to be responsible for long-distance dispersal in many organisms (e.g., Isard and Gage 2001; Finlay 2002; Nathan 2006; Evans and Oszako 2007; Shea et al. 2008; Leuven et al. 2009). Another commonality that arises from the deer and smut examples above is the potential role that the landscape plays in shaping the pattern that is observed: habitat distribution, dispersal costs in non-habitat, and attractiveness of destination patches can affect all aspects of dispersal. These commonalities and differences can only be explored within a general framework. Our examples demonstrate how a unifying gravity framework for dispersal facilitates the comparison of studies from different research traditions to gain insights from other disciplines.

Comparisons across dispersal disciplines also highlight the importance of considering the entire dispersal process, not one phase (e.g., relocation only). The gravity framework is the simplest possible framework that captures the three major components of dispersal common to most organisms. It also provides a conceptual synthesis and contributes to a rigorous formalization of the dispersal process. This provides flexibility in applications across organisms. For instance, gravity models for vector-borne pathogen dispersal (e.g., smut example; Ferrari et al. 2006) are extremely similar to gravity models for floral visitor-pollen dispersal (Yang et al. 2011). Such models can now be applied to study, for instance, the

vector-borne transmission of malaria by mosquitos. Recent research has shown that mosquitoes are more attracted to malaria-infected mice, reflecting a manipulation of the source characteristics by the parasite (De Moraes et al. 2014), while odor cues also affect the choice of destinations of mosquitoes (Takken and Knols 1999). Taken together, this work could result in a more complete model of vector movement and vector-borne transmission risk that includes source and destination characteristics. Also in other cases, mathematical (theoretical) models may adequately represent multiple processes depending on how particular variables and parameters are interpreted. For example, different biological mechanisms (e.g., wind dispersal and water dispersal) may be reduced to the same mathematical mechanism (e.g., fluid mechanics models).

A mechanistic rather than merely descriptive understanding of dispersal, as provided by our framework, is also essential to project how organisms (at both the species and individual level) will move in response to global changes such as increased habitat patchiness due to human landscape manipulation, changes in source/destination characteristics, increased global movement, loss or introduction of vector species, and climate change (Zhang et al. 2011; Bullock et al. 2012; Caplat et al. 2013). Spatial changes in climate envelopes may, for instance, not be matched by the dispersal capability of species (Urban et al. 2013). The key to predicting how well species will “keep up” with moving climate envelopes is to know how individuals disperse in realistic landscapes and how dispersal processes themselves are affected by changing conditions (Zhang et al. 2011).

Promising direction 2: quantifying dispersal: source-relocation-destination

Our synthesis has highlighted potentially important missing information at all stages of the dispersal process. For example, data on dispersal remain relatively scarce for many species (e.g., fungi, aquatic and terrestrial invertebrates). This is partly due to the highly stochastic nature of dispersal processes and due to difficulties in marking and then recapturing sufficient numbers of individuals, which for some groups requires extraordinary efforts (see Jackson et al. 1999 who marked >100,000 caddisfly larvae). Recapturing sufficient numbers of individuals may be nearly impossible in some uncommon, but potentially biologically important dispersal events such as hurricanes and flash floods. Inadequate sampling designs can also be problematic (Koenig et al. 1996; Skarpaas et al. 2005, 2011). On the other hand, technological advances are providing a wealth of new opportunities for studies of dispersal, further increasing the need for a general conceptual framework. Examples include the use of remote sensing instrumentation to monitor pest movement and environmental variables (e.g., weather and land cover) in pest management systems,

increasingly small radio transmitters and geolocators for studying dispersal and migration patterns (Bubb et al. 2004; Mueller et al. 2011; Lisovski et al. 2012; Kavathekar et al. 2013), the use of camera traps for the quantification of animal and animal-vectored dispersal (Jansen et al. 2012), large-scale observation networks of citizen scientists, internet-based tools for data collection and immediate global data sharing, and high-speed computation for spatial modeling and forecasting (Isard et al. 2011; M.D. Visser et al., unpublished manuscript).

Still, because of difficulties in observing relocation, researchers frequently use indirect measures such as genetic patterns to infer dispersal (i.e., similar genetics suggests frequent dispersal and genetic mixing, whereas genetic differences suggest little dispersal; Ouborg et al. 1999; Bilton et al. 2001). Similarly, isotope signatures of ear bones of fish can be used for reconstruction where adult fish grew up, allowing for estimation of dispersal kernels (Huijbers et al. 2013). For pathogens, difficulties may arise because the disease symptoms are observed rather than the relocation of the organism itself (but see Lowen et al. 2007; Noti et al. 2013); thus, asymptomatic carriers may bias the observed distribution and inference about dispersal processes. In studies of tree seed dispersal using seed traps, we observe the primary destination distribution without knowing from which trees (and over what distance) the seeds came. When the adult tree density of a particular tree species is low, as in highly diverse tropical forests, inverse modeling can be used to estimate probable dispersal distances, directional bias, and size-dependent seed production (Ribbens et al. 1994; Muller-Landau et al. 2008; van Putten et al. 2012).

If the patterns we observe (such as seed rain, genetic patterns, colonization, and disease symptoms) are the results of not only relocation but also source and destination processes, it is essential to consider the variability in all these processes. As illustrated by the thistle example above, source processes can markedly affect dispersal distances of passively dispersed organisms (see also Schippers and Jongejans 2005; Soons and Bullock 2008; Marchetto et al. 2010; Pazos et al. 2013; Teller et al. 2014). Processes resulting in takeoff therefore need to be better investigated. For actively dispersing organisms, both initiation and cessation of dispersal are affected by multiple factors and represent a challenge to researchers (Clobert et al. 2004). Incorporating multiple factors (e.g., density dependence and resource quality), which act in concert on dispersal, should be central in the modeling process, because the outcome of dispersal, which is what concerns spatial and applied ecology most, is the product of all consecutive phases. The gravity framework highlights that distribution patterns may be the result of processes in series; i.e., the observed pattern of dispersal of seeds might be the consequence of human impacts on movement and on the distribution of available destination habitat. Failing to recognize and address these intertwined processes could lead to significant errors in projections of spatial dynamics.

The smut example shows how multiple factors may be tested using the gravity framework (Ferrari et al. 2006). Similarly, the deer example suggests that a gravity approach may be helpful in formulating alternative models of dispersal patterns for different hypothetical destination processes, while controlling for variability in source and relocation processes. Estimating small-scale deer population densities is critical for testing competing hypotheses (models) and for our understanding of dispersal processes in actively moving organisms such as deer. Indeed, density-dependent destination processes seem to be poorly known in many species: Matthysen (2005), who reviewed density-dependent dispersal in birds and mammals, concentrated on source processes because few studies report destination densities.

The gravity framework may also be used to test alternative relocation functions. A wide range of mathematical functions have been used to model the variety of empirical dispersal curves (Turchin 1998; Bullock et al. 2006; Jongejans et al. 2008; Nathan et al. 2012), and only some of which are derived from dispersal mechanisms. In general, we commend Turchin's (1998) advice for linking patterns and processes: use empirical dispersal models derived from theory (e.g., Tufto et al. 1997; Okubo et al. 2001; Gaylord et al. 2002; Stockmarr 2002; Katul et al. 2005; Morales et al. 2010), as in the thistle and smut examples above, rather than arbitrary functions. Exploration of alternative models may still be necessary and useful when theoretically derived kernels for the process in question are not available or do not fit the data, suggesting that the theoretical representation of the dispersal mechanism is incomplete, such as in the deer example. For some major dispersal mechanisms, considerable progress has been made in modeling relocation. Powerful mechanistic models have been developed for dispersal by wind (Kuparinen 2006; Nathan et al. 2011) and water (Gaylord et al. 2002), and various models exist for different types of active movement (Turchin 1998), which may be further refined based on increasing knowledge of movement behavior (Morales et al. 2010). However, not enough mechanistic modeling has been done which incorporates animal behavior in vector-mediated dispersal of plants, animals, and microorganisms. This applies to animal vectors in general and to humans in particular (but see Brockmann et al. 2006; Wichmann et al. 2009; von der Lippe et al. 2013).

Promising direction 3: using different types of gravity model to study dispersal limitation

Generalization of the classical gravity model is needed to capture the complexities of dispersal. For instance, in the classical Newtonian model, the interaction between source and destination is inversely related to the square of distance. As mentioned, different relocation functions may be

appropriate for different organisms (see also, e.g., Gaylord et al. 2002; Kuparinen 2006; Jongejans et al. 2008), and these may need to be combined with source and destination functions in different ways, including stochasticity (Potapov et al. 2011), allowing for subsequent model selection (Muirhead and MacIsaac 2011; Maher et al. 2012) and validation with independent distribution data (Rothlisberger and Lodge 2011). Gravity models thus have great flexibility in incorporating important details, while at the same time, using the same general framework may lead to fruitful generalizations, such as the development of general classes of dispersal models (i.e., source-, relocation-, and destination-mediated gravity models).

Consider the example of disease transmission by vectors. The relative importance of source, relocation, and destination processes to effective transmission depends strongly on the life history of the pathogen. The dispersal of pathogens that are transmitted via direct or venereal contact may be dominated by source (i.e., duration of infection and spore shedding rate) and destination processes (i.e., contact rate and behavior; e.g., Snäll et al. 2008), while the transmission of airborne pathogens is likely to be dominated by relocation processes. The abstractions of these processes are source-destination-mediated and relocation-mediated models. Identifying the relative importance of each component (i.e., indicating where bottlenecks occur) might allow targeting of management based on which component most limits dispersal. In a review of studies that combined spread dynamics with monetary costs of invasion damages and control options, Epanchin-Niell and Hastings (2010) found that optimal control options were very context dependent.

Mechanistic insights gained by applying the gravity framework to ecological questions may shed new light on long-standing debates such as dispersal versus recruitment limitation in plant ecology. The classical framing of this problem is whether plant establishment is limited by the arrival of dispersal units at a destination or by subsequent destination processes (germination and/or seedling establishment; Münzbergová and Herben 2005). The gravity framework adds at least two new perspectives. First, the arrival of dispersal units may be source mediated or relocation mediated. Although these types of dispersal limitation may produce the same net arrival of dispersal units at a particular location, it is vital to understand their relative importance to predict the degree of dispersal limitation in different landscapes with varying source and relocation conditions. Second, as for vector-borne disease transmission (above) and freshwater organisms (Shurin et al. 2009), the type and degree of dispersal limitation in plants may be related to the dispersal mechanism. Wind- and water-dispersed plants may be strongly source mediated and/or relocation mediated, whereas plants dispersed by animal vectors such as squirrels (Vander Wall 1992) and sheep (Fischer et al. 1996) tend to be transported

to other suitable habitats and may therefore be less limited by relocation and destination processes (dispersal or recruitment) than passively dispersed species. This also applies to dispersal by humans. In many systems, humans are arguably the most efficient dispersal vectors; our power as dispersal vectors has increased with the parallel development of our population size and our technological innovations for transportation (e.g., boats, cars, and airplanes) and habitat modification (Leung et al. 2012). For example, in heavily glaciated countries like Norway and New Zealand, humans may have assisted the post-glacial dispersal and colonization of more than 50 % of the plant species in the present-day flora (Elven 2005). Many of these species were brought with agriculture, which provided a wealth of both relocation opportunities and suitable destinations.

Promising direction 4: spatial population dynamics and total dispersal kernels

Although our main focus here is dispersal, the gravity model framework can easily be extended to include population processes such as survival and reproduction at the destination (Järemo 2009). When repeated over time and space, the model can thus represent spatial population dynamics (e.g., Xia et al. 2004; Carrasco et al. 2010) and is also useful for metapopulation models and individual-based analyses of the effects of landscape fragmentation (Hanski and Ovaskainen 2000; Bonte et al. 2010; van Noordwijk et al. 2014).

When moving from dispersal to spatial population dynamics, such as spread (Table 1), it is important to acknowledge that many species are dispersed by several mechanisms (with the possible exception of large active dispersers). In the plant literature, species are often classified as wind dispersed (anemochorous), water dispersed (hydrochorous), or animal dispersed (zoochorous), according to presumed adaptations to dispersal (van der Pijl 1982). However, these assumptions are sometimes incorrect (Jongejans and Telenius 2001) and the main dispersal mechanism may be less strongly related to morphological traits than frequently assumed (Hughes et al. 1994). For instance, *C. nutans* is putatively wind dispersed, but its longest distance dispersal is human-mediated (Jongejans et al. 2011). Because many organisms disperse by multiple mechanisms and dispersal mechanisms often apply to multiple organisms, there is a need to map the many-to-many relationships among organisms and their dispersal mechanisms (Stiles and White 1986; Fischer et al. 1996; Higgins et al. 2003; Nathan 2007). For each particular organism, it is clearly important to capture all the mechanisms by which the organism disperses (total dispersal kernels; Nathan 2006, 2007) and the proportions of propagules dispersing by different vectors. Thus, the key to determining total dispersal kernels is to understand and quantify source processes that sort propagules over various dispersal vectors and to integrate

these pathways fully. For instance, contrasting propagule types (which can be produced at different rates) with contrasting dispersal kernels can be included in Neubert-Caswell models of invasion speed (Le Corff and Horvitz 2005; Marchetto et al. 2014). However, with these parallel dispersal kernels, serial dispersal (Redbo-Torstensson and Telenius 1995; Jansen et al. 2012) can occur. After reaching a destination, organisms can disperse again, potentially by a different vector, as is the case with seeds that are dragged by wind along the ground surface (Schurr et al. 2005) or wind-dispersed seeds that are subsequently moved by animals (Alba-Lynn and Henk 2010; Jongejans et al. 2015). This emphasizes the need to assess all consecutive processes of dispersal.

The gravity framework becomes even more inclusive if not only parallel and serial dispersal events are considered but also the entire process of gene flow. Jordano and colleagues (Jordano et al. 2007; García et al. 2007), for instance, have studied almost all vectors involved with pollen and seed dispersal for the tree *Prunus mahaleb* (reviewed in Shea 2007). Extending the thistle example introduced above to an all-inclusive gene flow framework would mean combining gravity models for pollen dispersal, in which plant distributions and densities at both the source and destination, as well as flying insect vectors, are important (Yang et al. 2011), with seed dispersal models that include seed release dynamics (Marchetto et al. 2014), effects of local environment on dispersal characteristics (Teller et al. 2014), wind dispersal (Dauer et al. 2007; Skarpaas and Shea 2007), human transport (e.g., hay bales or contaminated crop seeds; Jongejans et al. 2011), secondary dispersal by ground-dwelling insects (Alba-Lynn and Henk 2010), and habitat-specific establishment rates (Peterson-Smith and Shea 2010).

A key pattern in need of further investigation is the tail of dispersal distributions, because the shape of the tail and the factors that determine the shape have important implications for large-scale ecological and evolutionary questions (Portnoy and Willson 1993; Kot et al. 1996; Clark et al. 2001). Determining the shape of the tail in total dispersal kernels is particularly challenging because of the multiple mechanisms involved. Multiphase dispersal modeling may aid in this regard and can be done by linking several empirical models (Higgins et al. 2003; Bullock et al. 2006), preferably derived from dispersal mechanisms. In practice, fitting empirical models to total dispersal patterns may be challenging, because some or all of the underlying processes are unobserved. One way to improve parameter estimates is by hierarchical modeling of the observation process and the unobservable phases of the dispersal process (Jonsen et al. 2006; Snäll et al. 2007). However, modeling should not replace direct measurements of the underlying processes, whenever such measurements are possible. Ultimately, quantification of the mechanisms that govern source, relocation, and destination processes will

give the best understanding of how dispersal contributes to spatial dynamics.

Conclusions

There is a need to break down and to synthesize the dispersal process. The general gravity framework we espouse here will facilitate both of these research approaches, as we have illustrated with examples from our own research. Our framework allows for synthesis and common representation across taxonomic groups and encapsulates the processes at the source and destination of movement as well as during the intervening relocation process. This framework allows us to discern commonalities in the dispersal process and also to address each stage of the dispersal process separately and in relevant detail. All dispersal stages can be important in determining the outcome of dispersal, i.e., its impact, which is of ecological, demographic, and evolutionary relevance (Travis et al. 2012). Furthermore, the gravity framework can be used to highlight areas where additional research is needed, such as initiation of dispersal (e.g., seed release/source processes in plants) and termination of dispersal (e.g., larval settling/destination processes in aquatic organisms). Areas in need of additional research, and their relative importance, will vary across disciplines. The gravity model will allow us to think explicitly about what affects/motivates individuals that move, and how they perceive their environments (e.g., chemical cues) at an array of organizational levels, and hence, to integrate these individual movements into population-level outcomes. The gravity model suggests that naive fitting of dispersal kernels may be misleading as they may depend on the local spatial context with respect to source and destination characteristics; i.e., the portability of dispersal inference from system to system requires the local context.

We therefore encourage dispersal researchers to look for inspiration across traditional disciplinary boundaries both within and outside biology. Cross-fertilization of different research traditions is likely to become a major source of progress in dispersal research if we can place information in a common structure. We intend for the generalized gravity model to serve as just such a unifying framework, as it is able to capture the general conceptual and formal components of any dispersal process.

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