

Manuscript Draft

What is long-distance dispersal? And a taxonomy of dispersal events

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Abstract

1 Dispersal is a key individual-based process influencing many life-history attributes,
2 scaling up to population-level properties (e.g., metapopulation connectivity). A
3 persistent challenge in dispersal ecology has been the robust characterization of
4 dispersal functions (kernels), a fundamental tool to predict how dispersal processes
5 respond under global change scenarios. Especially the rightmost tail of these func-
6 tions, i.e. the long-distance dispersal (LDD) events, are difficult to characterize
7 empirically and to model in realistic ways. But, when is it a LDD event? In the
8 specific case of plants, dispersal has three basic components: 1) a distinct (sessile)
9 source, the maternal plant producing the fruits or the paternal tree acting as a
10 source of pollen; 2) a distance component between source and target locations;
11 and 3) a vector actually performing the movement entailing the dispersal event.
12 Here we discuss operative definitions of LDD based on their intrinsic properties: 1)
13 events crossing geographic boundaries among stands; and 2) events contributing
14 to effective gene flow and propagule migration. Strict-sense long distance disper-
15 sal involves movement both outside the stand geographic limits and outside the
16 genetic neighborhood area of individuals. Combinations of propagule movements
17 within/outside these two spatial reference frames results in four distinct modes
18 of LDD. Beyond traditional statistical approaches to characterize distributions,
19 Extreme Value Analysis (EVA) can be used to properly and explicitly evaluate
20 the properties of frequency and extent of LDD events. We discuss conditions
21 where global change scenarios truncate dispersal processes, leading to the loss of
22 key dispersal services in natural populations. Proper characterization of the LDD
23 events helps to assess, for example, how the ongoing defaunation of large-bodied
24 frugivores pervasively entails the loss of crucial LDD functions.

Introduction

Dispersal is a key individual-based process influencing many life-history attributes and scaling up to population-level properties (e.g., metapopulation connectivity, Cousens *et al.* 2008). In the specific case of plants, largely sessile organisms, dispersal has three basic components: 1) a distinct (sessile) source, the maternal plant producing the fruits or the paternal tree acting as a source of pollen; 2) a distance component between source and target locations; and 3) a vector actually performing the movement entailing the dispersal event. While realized dispersal also depends upon stages subsequent to dissemination (e.g., successful germination and seedling establishment) Schupp (1995), the three previous components fully characterize the dispersal process *per se*. Therefore, plant movement differs in important natural history details from animal dispersal, yet both can be assessed within a common conceptual framework (e.g., Nathan, 2006). Characteristically, animal-assisted plant dispersal has three distinct, highly integrated, components missing in the process of animal dispersal: the properties of the source (parental) plant, that mediate in the foraging of the animal vector (pollinator or frugivore), the intrinsic properties of the propagule, and the functional characteristics of the animal vector who performs the movement (Nathan *et al.*, 2008a).

The movement of pollen and seeds by animals and its consequences have intrigued population geneticists and field ecologists since the infancy of both research disciplines. Each has generated an impressive body of theoretical and empirical research through the past decades, yet advances have long been co-existing in ‘parallel worlds’ and the great synergistic potential of population genetics and demography for the study of plant dispersal by animals remains little explored. Knowledge gaps still having the imprint of this conceptual disconnection include the idea of long distance dispersal, and the paradoxes of forest fragmentation effects on genetic diversity (Kramer *et al.*, 2008), survival and persistence of relict tree species (Hampe & Jump, 2011), rapid post-Pleistocene recolonization of vast continental areas in response to climate modification (Clark *et al.*, 1998; Clark, 1998), among other persisting issues. This conceptual isolation has been exacerbated by technical difficulties for the robust characterization of dispersal events,

56 especially those involving movement over long-distances (long-distance dispersal,
 57 LDD). LDD is a characteristically extreme event of propagule movement in any
 58 plant population, typically occurring with an extremely low probability but poten-
 59 tially reaching an extremely long distance. Some progress has recently been made
 60 through the fast-paced implementation of molecular tools in ecological research
 61 labs and the availability of cutting-edge technology for biotelemetry applications
 62 [REF]. But much of the population geneticist and ecologist communities remains
 63 unaware of the state of the art in each other and likely under-appreciates their
 64 potential to validate and enrich dispersal studies (Jones & Muller-Landau, 2008).
 65 In particular, LDD events remain difficult to assess, both technically- with seri-
 66 ous methodological problems for its reliable estimation- and conceptually. Our
 67 aim here is to review the LDD concept with a specific emphasis on dispersal of
 68 plant propagules (seeds and pollen), providing an extended definition that might
 69 be helpful in the robust quantification of LDD events.

70 Two main conceptual approaches have been used to assess dispersal (Fig. 1).
 71 The “forward” approach attempts to track the dispersal events away from the
 72 known sources, e.g., by tracking the movement patterns of frugivores as they leave
 73 fruiting plants after feeding (Fig. 1A). This is the main approach used in the
 74 movement ecology framework (Nathan *et al.*, 2008a), with extensive application
 75 to animal movement based on the use of advanced biotelemetry. The “backward”
 76 approach attempts to reconstruct the most likely source of a dispersed propagule
 77 by inferring the sources given the propagule delivery pattern, the fecundity of
 78 potential sources, and the dispersal function (Fig. 1B), i.e., by using an inverse
 79 modeling approach. The main technical challenge in Fig. 1A is to sample enough
 80 dispersal events away from the source to be able to fully characterize the tail
 81 (LDD events) of the dispersal function. In Fig. 1B, the main challenge is to have
 82 a robust sampling scheme with propagule collectors (e.g., seed traps) and a good
 83 characterization of the potential sources to derive robust estimates of the actual
 84 sources. Both approaches are limited logistically by the difficulties to sample the
 85 vast areas required to assess LDD events from the focal source population.

86 No explicit definition of what constitutes an LDD event exists. Previous ap-
 87 proaches (e.g., Nathan, 2006; Schurr *et al.*, 2009) include both absolute and

proportional definitions to characterize LDD events. This means providing information about the absolute distances moved by a given percentile of the events and/or providing data on the proportion of events exceeding a given distance threshold (Nathan *et al.*, 2008b). The exact proportional or absolute thresholds selected remain arbitrary, as no reference spatial frame is provided within the definition of LDD. This leaves the consideration of LDD as an extreme form of context-dependent phenomenon, strongly dependent upon the scale of the biological process studied (Kinlan *et al.*, 2005). For example, Kinlan *et al.* (2005) used a spatial reference frame to characterize LDD events of marine organisms, where sedentary adults and larvae differ enormously in the spatial scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent and reach of LDD events requires reference to an explicit spatial frame or "local" scale (Kinlan *et al.*, 2005).

We aim at providing a general framework for the quantitative analysis of LDD events so that estimates of its frequency and extent could be comparable across different study systems. We argue that both demographic and genetic elements are needed for this framework, most likely requiring a combination of field-based movement data and genetic analyses. These elements can be overlaid on previous definitions based on absolute and proportional characterizations of LDD. We start with a definition of LDD events within a spatially-explicit mechanistic framework allowing an unambiguous meaning for setting long-distance thresholds. We then use a case study to assess differential contributions of animal frugivores performing LDD.

Long-distance dispersal is currently one of the most debated topics in dispersal ecology; it defines the connectedness within the network of local populations and the possibilities for range expansion and successful colonization events. We propose a first demogenetically-based, operational definition of what a long-distance dispersal event actually is, and review existing empirical literature on distance thresholds from population and genetic perspectives. We also show how molecular tools have been used to identify the respective contributions of different animal species to the LDD portion of dispersal kernels of pollen and seeds by setting empirically-derived distance thresholds. Finally, we highlight potential applications of molecular markers beyond the quantification of just the dispersal distances

120 that prevails in current studies, e.g., experimental approaches to assess dispersal
121 limitation and Janzen-Connell effects.

122 **LDD within a demo-genetic perspective: a taxonomy of dis-** 123 **persal events**

124 Here we propose an explicit definition of LDD and what constitutes a LDD event.
125 Previous definitions of dispersal patterns emphasized only their distance compo-
126 nents and characterized LDD events basically in terms of geographic distance be-
127 tween a dispersed propagule (or an established early seedling) and its most likely
128 maternal or paternal (in case of pollen) source. Absolute and proportional defini-
129 tions for the LDD events have been proposed depending on arbitrary thresholds
130 of either the distance beyond which a dispersal event is LDD or the proportion of
131 events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).
132 Thus, two key biological aspects of LDD events involve the transport of propa-
133 gules outside a reference area: moving away from the source stand or population,
134 and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These
135 two movements do not necessarily concur: a propagule may move over a very
136 long distance yet still be disseminated within the reach of the neighborhood where
137 parental individuals mate. Within a demo-genetic framework it is easy to envision
138 a combination of situations concerning the spatial scale of the dispersal processes
139 (Table 1) and unambiguously define different types of LDD events. The idea that
140 dispersal occurs in reference to these two spatial reference frames, i.e., the popu-
141 lation or stand and the genetic neighborhood area, is motivated by the fact that
142 dispersal entails the movement of both an individual propagule (i.e., a pollen grain
143 or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or
144 a seed genotype). Thus, dispersal entails simultaneous demographic and genetic
145 effects through recruitment of new individuals in the population and through con-
146 tributions to gene flow (Harper, 1977). When considered its combined influence
147 on demography and population genetics, the concept of LDD nicely bridges these
148 two paradigms embedded in the biological definition of population (Waples &
149 Gaggiotti, 2006).

Two important components of plant dispersal ecology concern the movement of propagules away from the source population, a type of dispersal relevant to colonization ability and range expansion (Howe & Miriti, 2004), and the movement away from the location of close relatives, i.e., a movement away from the genetic neighborhood (Hardesty *et al.*, 2006; Jones & Muller-Landau, 2008). If we classify dispersal events according to these two spatial frameworks (Table 1) we end up with four distinct types of events depending on whether or not dispersed propagules are disseminated within these reference areas. Setting the limits of a population can be problematic (Waples & Gaggiotti, 2006) yet we can identify with relative ease the geographical limits of plant stands, patches, habitat spots or other types of habitat or microhabitat discontinuities that determine landmark boundaries of biological significance (see Kinlan *et al.*, 2005, for further discussion of boundaries for dispersal). These "frontiers" set biological limits to what a LDD event is in relation to the geographic limits of the source population. Most plants are distributed as clumped patches, discrete stands, or relatively isolated populations, so we may distinguish between short-distance and long-distance dispersal events that end up with dissemination within or beyond, respectively, the stand or population geographic boundaries (Table 1, SSD_{loc} or LDD_{loc}) (Figure 2).

A second consideration in terms of spatial boundaries, with effects on dispersal patterns, is the genetic neighborhood area N_b , i.e., the spatial extent including a subset of panmictic individuals within a population (Wright, 1943, 1946). Thus, the N_b area can be equal to the whole extent of the population whenever the population is unstructured and there is evidence for random mating events among all the individuals. However, most populations and stands of long-lived trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006), where relatively long distances may separate groups of individuals within the same population. In these cases we might expect N_b area to be substantially smaller than the total population area. Therefore, at least four possible scenarios exist with distinct implications in terms of consequences for dispersal (Table 1). In the case of dispersal events not extending beyond the geographic limits of the population or reference area, actual LDD events may involve dissemination beyond a reduced neighborhood area that is smaller than the geographic extent of the pop-

ulation, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig. 2A). Actual short-distance dispersal would then involve those situations where the propagule is disseminated within *both* the population limits and the genetic neighborhood boundary (SDD_{loc}). Along a similar reasoning, dispersal events outside the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this is expected in cases where the genetic neighborhoods are extensive, going beyond the geographic limits of local populations, as in fig trees (Nason *et al.*, 1998), generating LDD events within the genetic neighborhood (LDD_{neigh}). Finally, strict-sense LDD events would involve dissemination outside *both* the population limits and the genetic neighborhood boundary (LDD_{ss}) (Table 1, Fig. 2A).

While both SSD_{loc} and LDD_{loc} can be crucial for assuring the local persistence of populations, LDD_{neigh} and LDD_{ss} would be extremely important contributors to the structuring of genetic pools, realized gene flow, and maintaining connectivity in metapopulation scenarios. We argue that both the demographic and the genetic references are relevant for a proper definition of LDD.

Individual and Population Neighborhoods as Reference

Continuous populations can be modeled with the concepts of isolation by distance and neighborhood size (Wright, 1943, 1946). The former refers to the case that limited gene dispersal in continuous populations produces demes that are panmictic internally, but are isolated to some extent from adjacent demes. Each group of reproducing individuals is the neighborhood, defined as the population of a region in a continuum, from which the parents of individuals born near the center may be treated as if drawn at random (Wright, 1969). The importance and influence of the dispersal process in determining the size of the neighborhood is given by this equation, which shows how the spatial dispersion (pattern of spatial distribution) of the population influences the effective population size. This influence on the effective size is given by:

$$N_b = 4\pi\sigma^2\delta \quad (1)$$

where δ is the density of adults per unit area and σ is the variance in distance between birth and breeding sites. This formulation is often called the neighborhood size and assumes a normal distribution of distances between parents and offspring (out in a perfect circular shape from the source). Thus, changes in the variance of dispersal distance can affect N_e (highly clumped populations will have reduced N_e). This is the basic model of "Isolation by Distance" proposed by Wright (1943, 1946). Under this type of model, migration (gene flow) is given by the variance in dispersal, and not by the proportion of the population that is composed of migrants (denoted m), as is the case with island models (Slatkin, 1985).

For plants, gene flow may be accomplished by both seeds and pollen, so the variance may be decomposed to account for different patterns of seed and pollen dispersal, and to take into account the mating system (outcrossing rate, t). Thus, neighborhood size can be defined with the following equation (Crawford 1984) :

$$N_b = 4\pi(\sigma_s^2 + \frac{t\sigma_p^2}{2})\delta(1 + t) \quad (2)$$

where σ_s^2 is the variance in seed dispersal, σ_p^2 is the variance in pollen dispersal and δ is the density of potential parents.

Neighborhood size in plants can be estimated by marking pollen and seeds with fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However, these methods do not measure effective pollen or seed movement, but they may be combined with genetic analysis to assess genetic identity and relatedness with hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano, 2001) to achieve reliable estimates of both effective population size and neighborhood area.

The extent of neighborhood area in plants can be extremely variable, depending on life-history attributes such as life-span, spacing patterns, mating system, etc. Even a limited sample of available information (Table S1) highlights the fact that the size of neighborhood areas can in some cases exceed the geographic limits of local populations (Nason *et al.*, 1998). The size of neighborhood areas may encompass at least four orders of magnitude, $10^{-2} - 10^2$ km in radius, and include

many individuals. Therefore, reference to this "genetic/evolutionary" paradigm and reference (sensu Waples & Gaggiotti, 2006) may be instrumental to understand the actual role of LDD events in shaping the structuring of genetic pools and contributing to gene dispersal.

Whenever there is a large discrepancy between population area extent and N_b we might expect the frequency of LDD_{loc} and LDD_{neigh} differ enormously. For example, relatively small N_b may rise the importance of LDD_{loc} in preserving scenarios of panmixia within a local population, as most distant dispersal events will disseminate seeds outside the neighborhood of maternal plants.

Empirical analysis of contributions to LDD

Empirical evaluation of differential contributions to the different forms of LDD events outlined in Table 1 requires identification of source trees as well as assignment of the dispersed propagules to specific vectors or functional groups of vectors (Jordano *et al.*, 2007). Recently, DNA-barcoding techniques have been developed and successfully applied to the identification of frugivore species contributing to specific seed dispersal events whose source can be identified with genetic, direct assignment techniques (González-Varo *et al.*, 2014). Otherwise, visual identification can reliably assign the genotyped seeds to frugivore species groups based on specific characteristics of scats and regurgitations (Jordano, 2007).

Long-Distance Dispersal: the ecology of extreme events

Long-distance dispersal (LDD) is a major component of the population dynamics, genetic structure, and biogeographic history of plant species. It determines the colonization ability of new habitats and the possibilities for fragmented populations to sustain a cohesive metapopulation by immigration-emigration dynamics that rely on LDD events. Yet our current understanding of the extent, frequency, and consequences of LDD is very limited. On one hand, theoretical models fail to predict accurately the behavior of the tail of the dispersal functions, and thus fail

to predict very basic properties of LDD. On the other hand, we still have very limited documentation of actual LDD events in natural populations and we still see LDD as a sporadic, rarely far-reaching process still marked with the stamp of natural history curiosity.

As defined in our framework (Table 1), LDD, and in particular LDD_{ss} events are a particular case of extreme events (García & Borda-de Água, 2017).

Challenges and Promising Avenues for Research

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Table 1: Types of dispersal as a function of population area limits and genetic neighborhood limits. See Fig. 2 for a graphical representation of the four scenarios.

Population geographic limit	
Genetic neighborhood limit	
	Within
Within	Local, short-distance dispersal, SDD_{loc}
Outside	Local, long-distance dispersal, LDD_{loc}
	Outside
	Within neighborhood, long-distance dispersal, LDD_{neigh}
	Strict sense long-distance dispersal, LDD_{ss}

Table 2: Frequencies of *Prunus mahaleb* seed dispersal events for different frugivore groups according to population area limits and genetic neighborhood limits. See Fig. 2 for a graphical representation of the four scenarios.

Frugivore group	Within- population, within- neighborhood SSD_{loc}	Within- population, long-distance LDD_{loc}	Outside- population, within- neighborhood LDD_{neigh}	Strict-sense long-distance LDD_{ss}
Small birds	?	?	?	?
<i>Turdus</i>	?	?	?	?
Large birds	?	?	?	?
Mammals	?	?	?	?

Figures

Figure 1. The two approaches used in analyses of dispersal processes in plants. A, the “forward” approach attempts to track the dispersal events away from the known sources, e.g., by tracking the movement patterns of frugivores as they leave fruiting plants after feeding. B, the “backward” approach attempts to reconstruct the most likely source of a dispersed propagule by inferring the sources given the propagule delivery pattern, the fecundity of potential sources, and the dispersal function. The main technical challenge in A is to sample enough dispersal events away from the source to be able to fully characterize the tail (long-distance dispersal, LDD, events) of the dispersal function. In B, the main challenge is to have a robust sampling scheme with propagule collectors (e.g., seed traps) and a good characterization of the potential sources to derive robust estimates of the actual sources with inverse-modeling techniques.

Figure 2. Schematic representation of different types of long-distance dispersal events in relation to the geographical limits of local populations (dashed lines) and the genetic neighborhood area N_b (grey area) of specific individual plants (squares). Dispersal events (arrows) can be classified depending on their actual incidence on propagule movement outside these spatially-explicit reference areas (Table 1). Strict-sense long-distance dispersal events (LDD_{ss}) just include the LDD events that disseminate propagules out of *both* the population and genetic neighborhood boundaries. A, the neighborhood area is included within the geographic limits of the population; B, the neighborhood area is much larger than the geographic limits of the population.

Figure 3. Empirical frequency distributions of seed dispersal events as a function of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In red, left (inset), frequencies of within-populations dispersal events inferred from direct assignment based on seed endocarp genotypes and maternal trees genotypes. Larger frame, left, contributions of four functional frugivore groups (small birds, medium- and large-sized birds, and mammals) to seed dissemination and propor-

311 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,
312 those not matching any maternal tree in the study population).

313

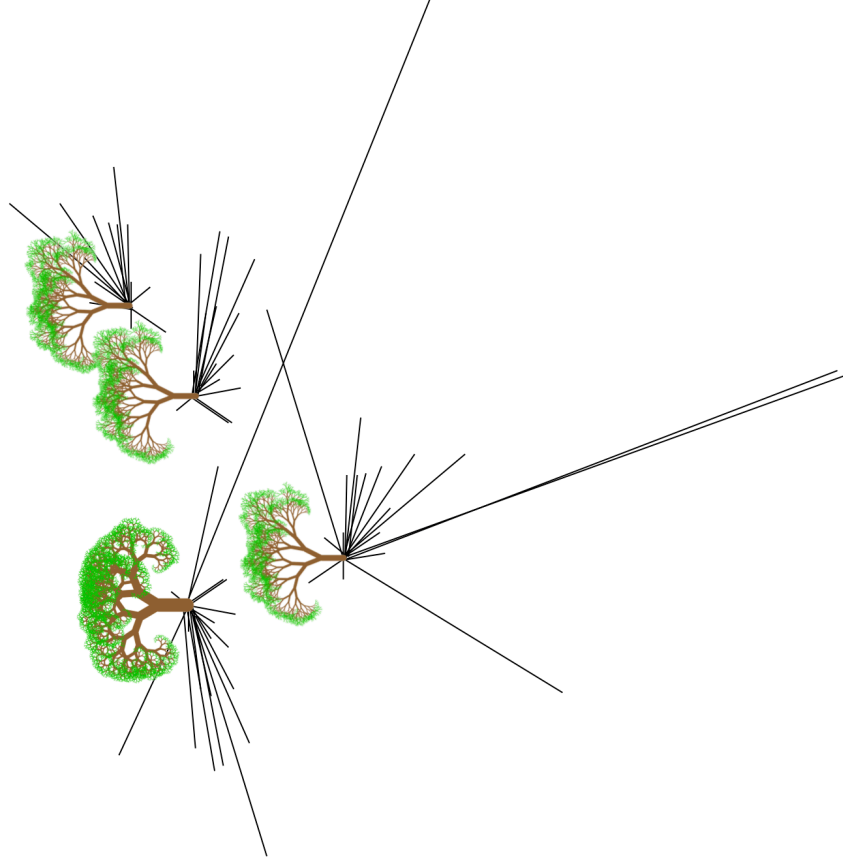
314 **Figure 4.** Differential contributions of functional groups of frugivores to the four
315 combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1. These
316 result from dissemination within (yellow) or outside (blue) the population geo-
317 graphic limits (SDD_{loc} , LDD_{loc} , respectively) and within or outside the genetic
318 neighborhood area limits (SDD_{neigh} , LDD_{ss} , respectively).

319

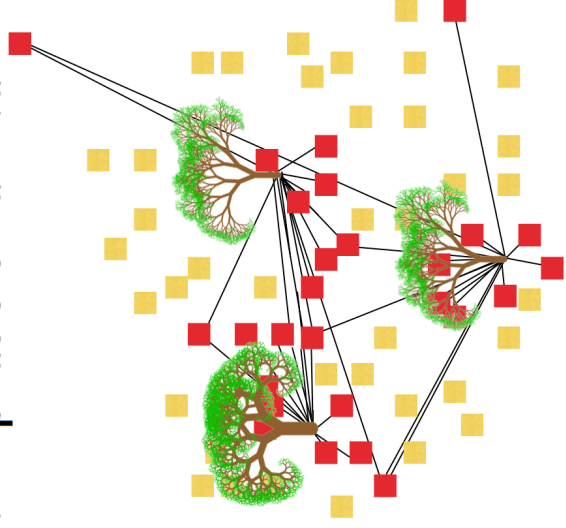
320 **Online Support Material and data accessibility**

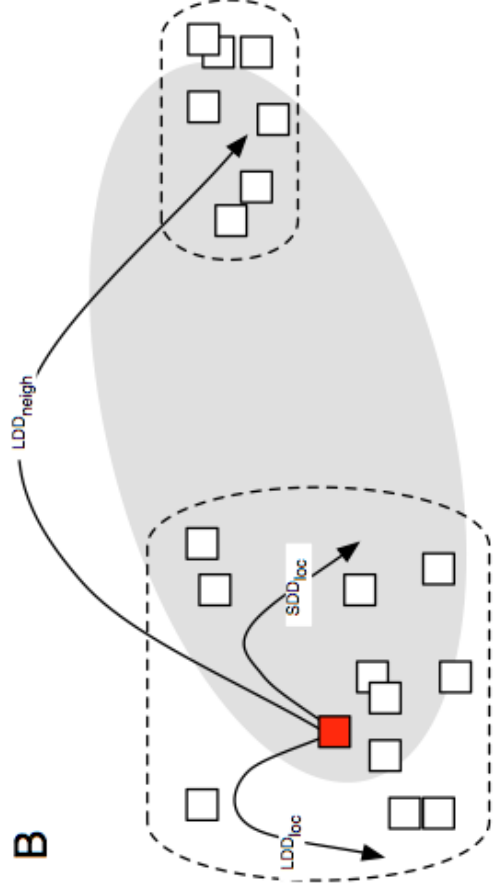
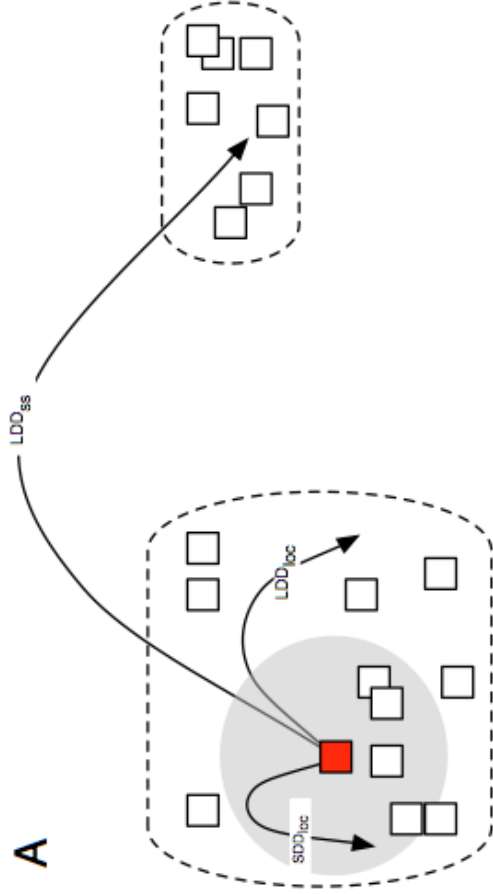
321 This review does not use new raw data, but includes some re-analyses of pre-
322 viously published material. All the original data supporting the paper, R code,
323 supplementary figures, and summaries of analytical protocols is available at the
324 author's GitHub repository (https://github.com/pedroj/MS_LDD), with DOI:
325 [#/zenodo.11](#).

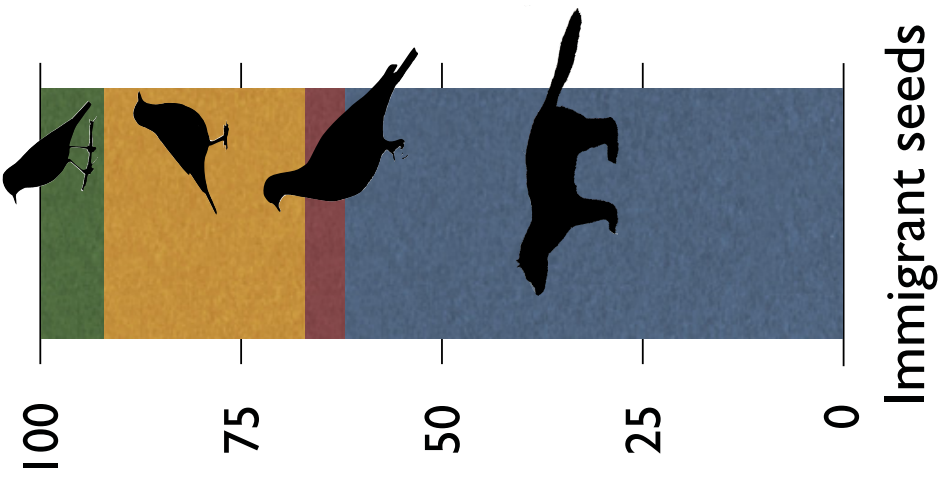
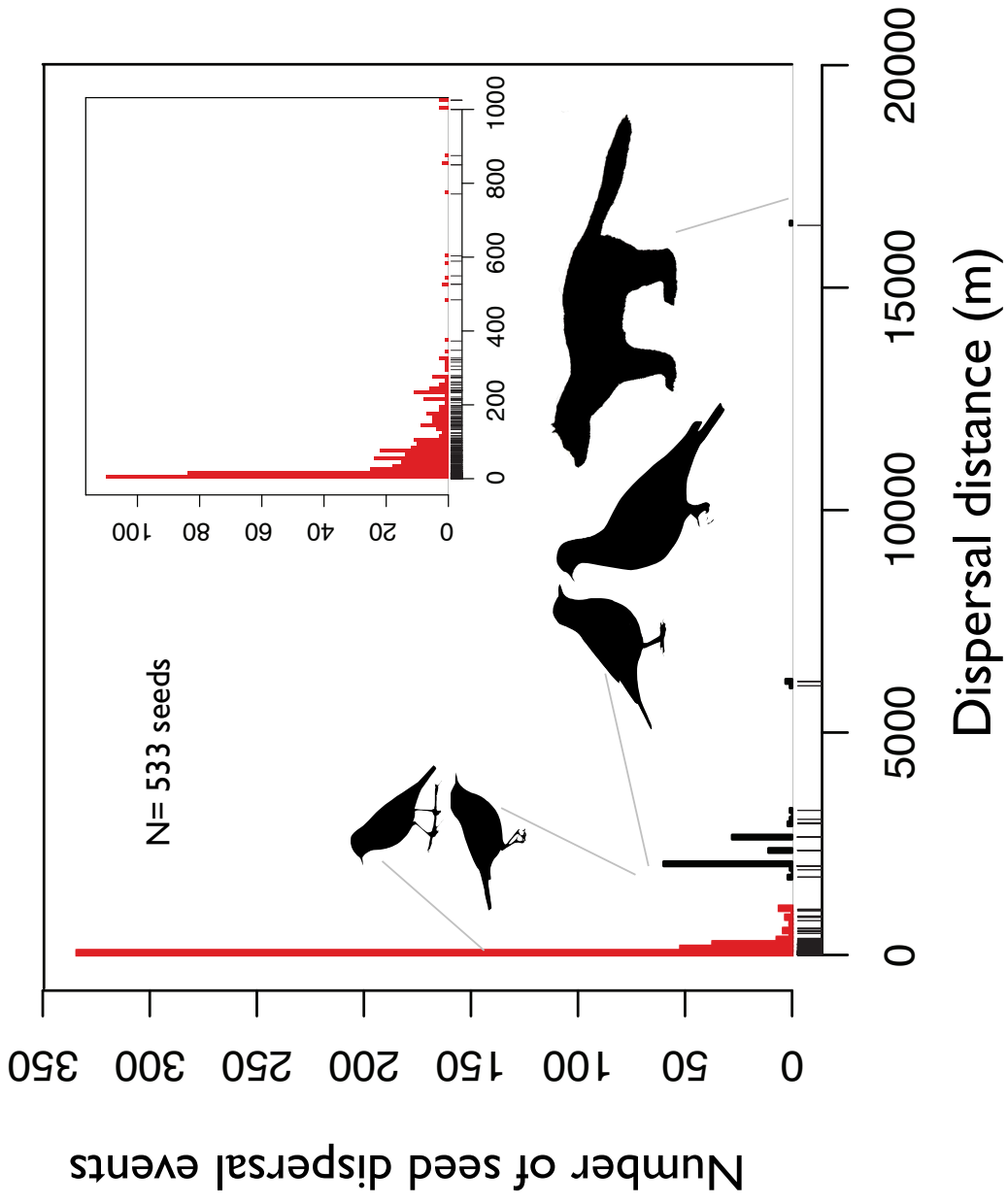
A. Emphasis on dispersal



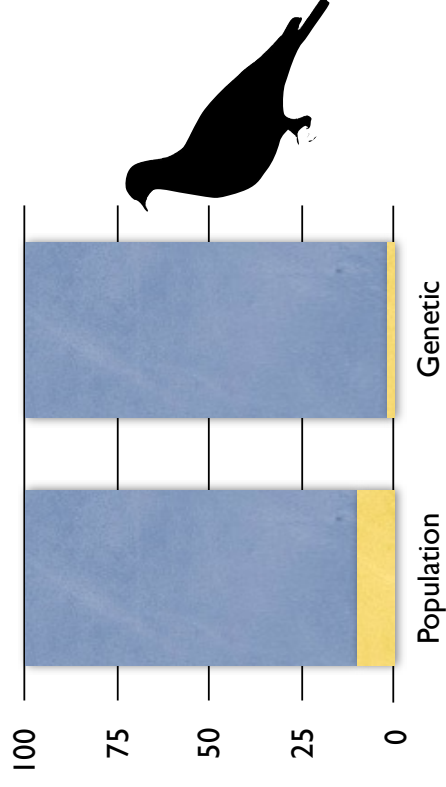
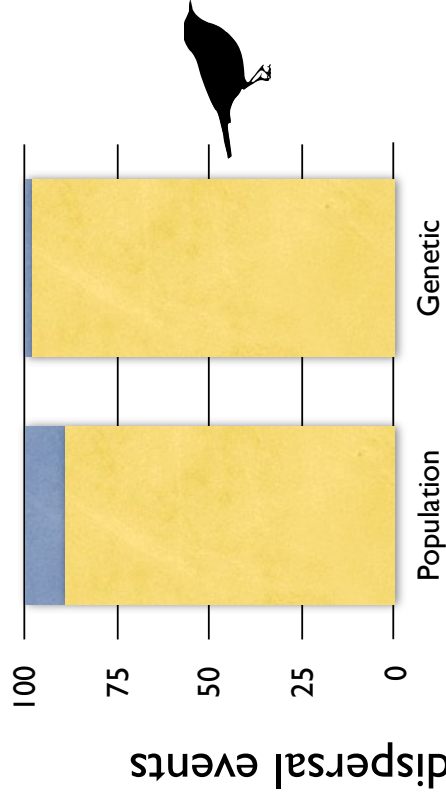
B. Emphasis on arrival





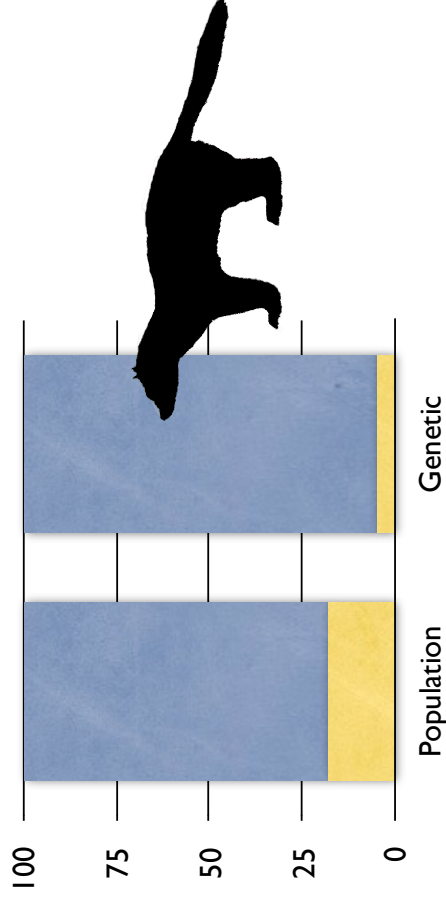
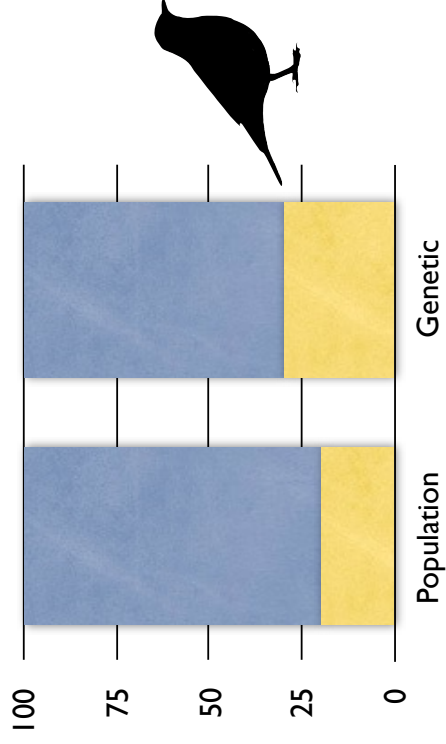


Within Outside



Small birds

Large birds



Turdus

Mammals