

# Manuscript Draft

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

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Sevilla, June 23, 2016

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**Key words:** \*\*\*

**Manuscript information:** \*\* Words; \*\* Chars; \*\* Pages, \* Figures; \* Tables.

## 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-

182 ulation, originating local long-distance ( $LDD_{loc}$ ) dispersal events (Table 1, Fig.  
 183 2A). Actual short-distance dispersal would then involve those situations where the  
 184 propagule is disseminated within *both* the population limits and the genetic neigh-  
 185 borhood boundary ( $SDD_{loc}$ ). Along a similar reasoning, dispersal events outside  
 186 the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this is  
 187 expected in cases where the genetic neighborhoods are extensive, going beyond the  
 188 geographic limits of local populations, as in fig trees (Nason *et al.*, 1998), generat-  
 189 ing LDD events within the genetic neighborhood ( $LDD_{neigh}$ ). Finally, strict-sense  
 190 LDD events would involve dissemination outside *both* the population limits and  
 191 the genetic neighborhood boundary ( $LDD_{ss}$ ) (Table 1, Fig. 2A).

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

## 197 Individual and Population Neighborhoods as Reference

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

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



where  $\sigma^2$  is the variance of the dispersal distance and  $\delta$  is the density of individuals. 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 size can affect  $N_e$  (highly clumped populations will have reduced  $N_e$ ).

$$N_b = 4p\sigma^{2d} \quad (2)$$

where  $d$  is the density of adults per unit area and  $\sigma$  is the variance in distance between birth and breeding sites. 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) :

$$N_b = 4p(\sigma_s^2 + \frac{t\sigma_p^2}{2})d(1+t) \quad (3)$$

where  $\sigma_s^2$  is the variance in seed dispersal,  $\sigma_p^2$  is the variance in pollen dispersal and  $d$  is the density of potential parents.

Neighborhood size in plants can be estimated by marking pollen and seeds with fluorescent dyes, tags, or marks. However, these methods do not measure effective pollen or seed movement, but they may be combined with genetic analysis to do so. Individuals with a unique allele in a stand can provide valuable insight on seed movement (Eguiarte *et al.*, 1993).

## Empirical Studies of Seed Dispersal

## 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

*Acknowledgements.* I am indebted to Cristina García, José A. Godoy, Manolo Carrión, Juan Luis García-Castaño, Jesús Rodríguez and, especially, Juan Miguel Arroyo for generous help with field and laboratory work and making possible this study. I appreciate the help and advice of Cristina García and Etienne Klein during the final stages of the manuscript. The study was supported by a Junta de Andalucía Excellence Grant (RNM-5731), as well as a Severo Ochoa Excellence Award from the Ministerio de Economía y Competitividad (SEV-2012-0262). The Agencia de Medio Ambiente, Junta de Andalucía, provided generous facilities that made possible this study in the Andalusian natural parks (Sierra de Cazorla, Alcornocales) and authorized my work there.

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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
	Outside
Within	Local, short-distance dispersal, $SDD_{loc}$ Within neighborhood, long-distance dispersal, $LDD_{neigh}$
Outside	Local, long-distance dispersal, $LDD_{loc}$ 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-



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

288

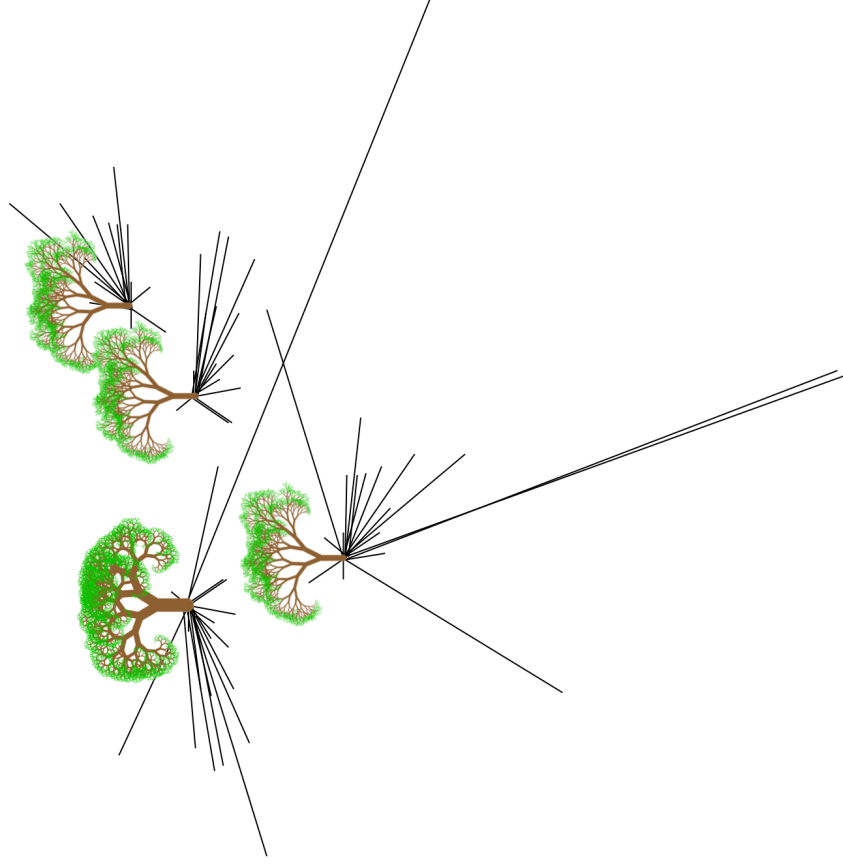
289 **Figure 4.** Differential contributions of functional groups of frugivores to the four  
290 combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1. These  
291 result from dissemination within (yellow) or outside (blue) the population geo-  
292 graphic limits ( $SDD_{loc}$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

294

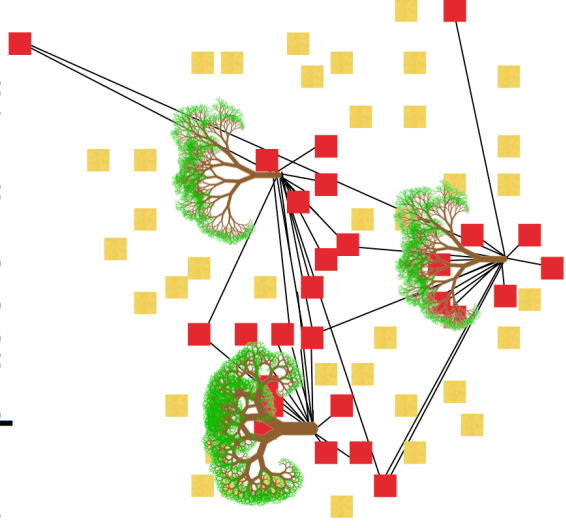
## 295 **Online Support Material and data accessibility**

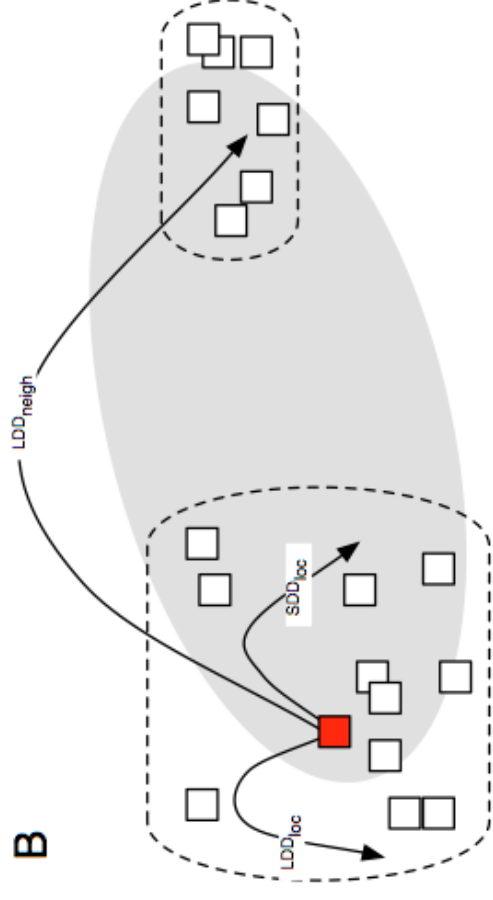
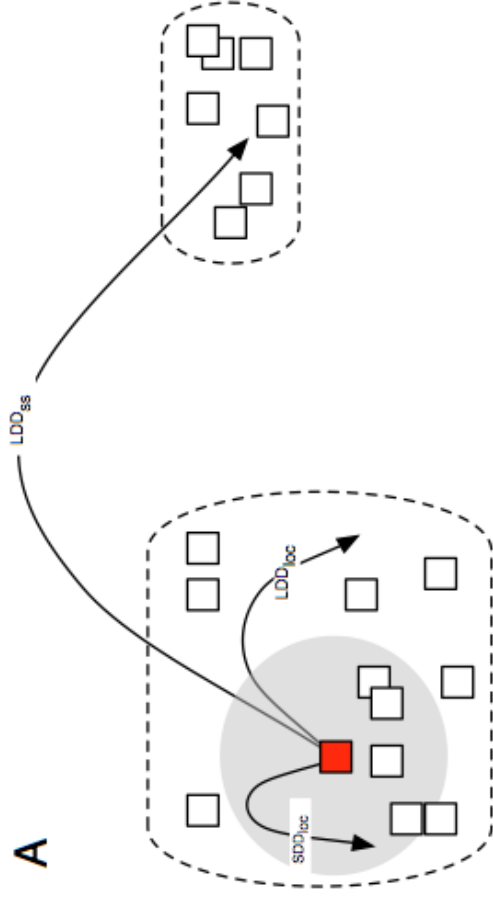
296 This review does not use new raw data, but includes some re-analyses of pre-  
297 viously published material. All the original data supporting the paper, R code,  
298 supplementary figures, and summaries of analytical protocols is available at the  
299 author's GitHub repository ([https://github.com/pedroj/MS\\_LDD](https://github.com/pedroj/MS_LDD)), with DOI:  
300 `#/zenodo.#`.

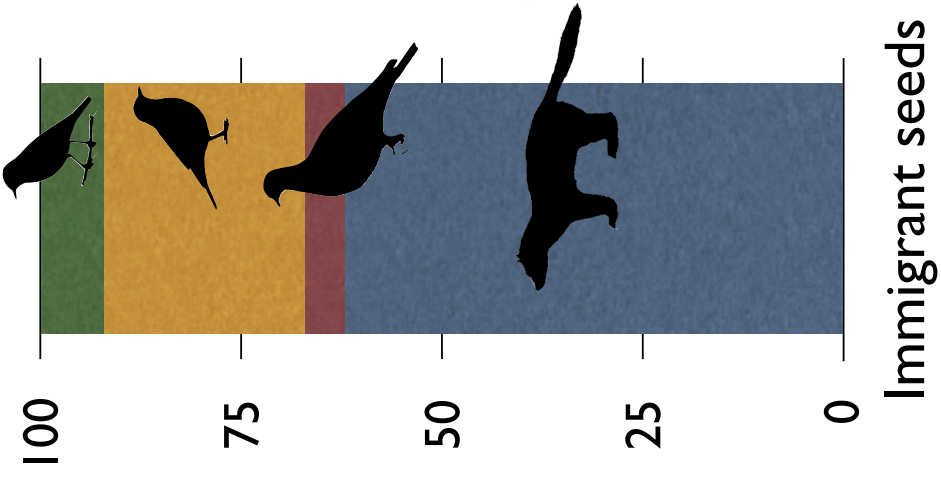
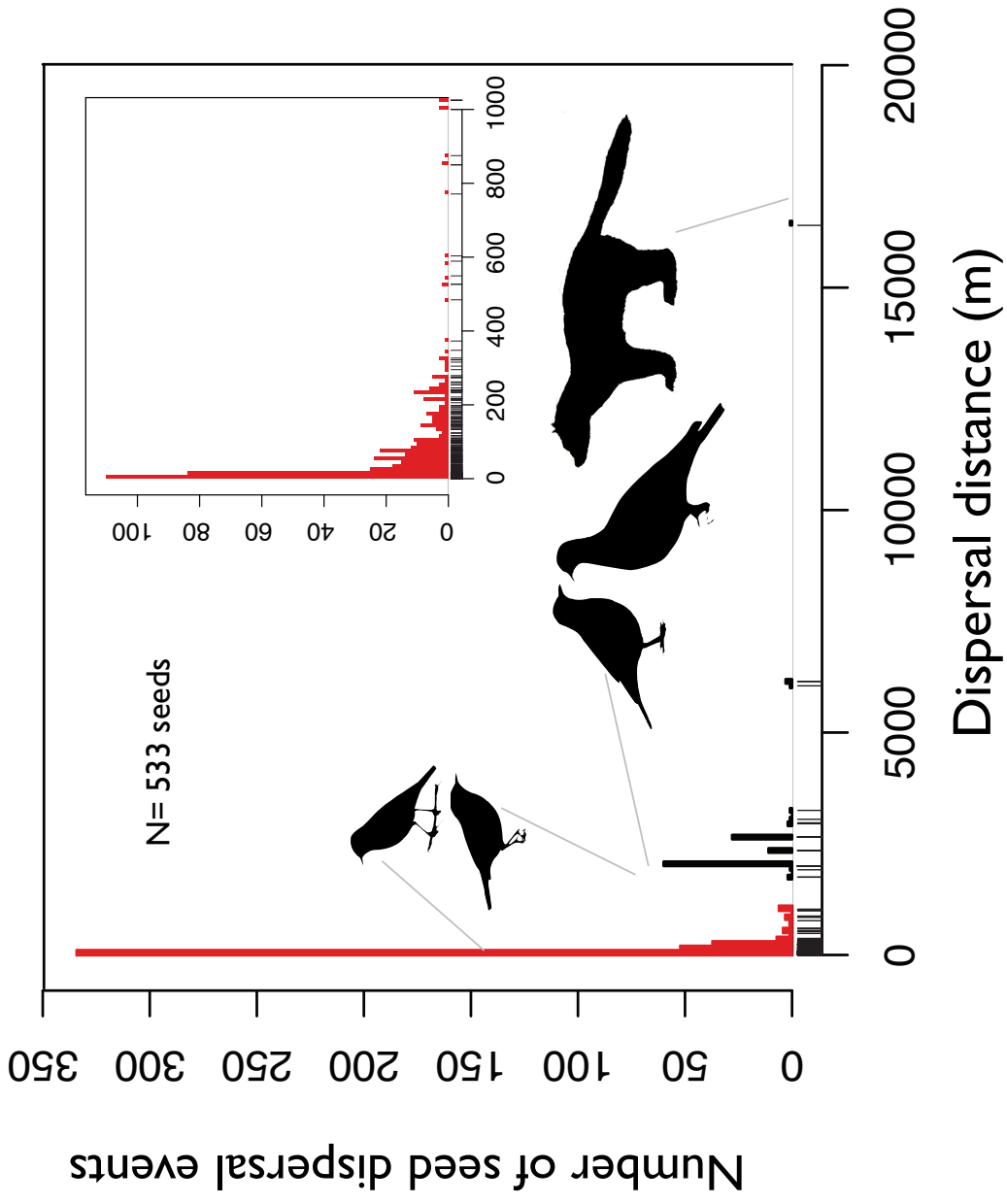
A. Emphasis on dispersal



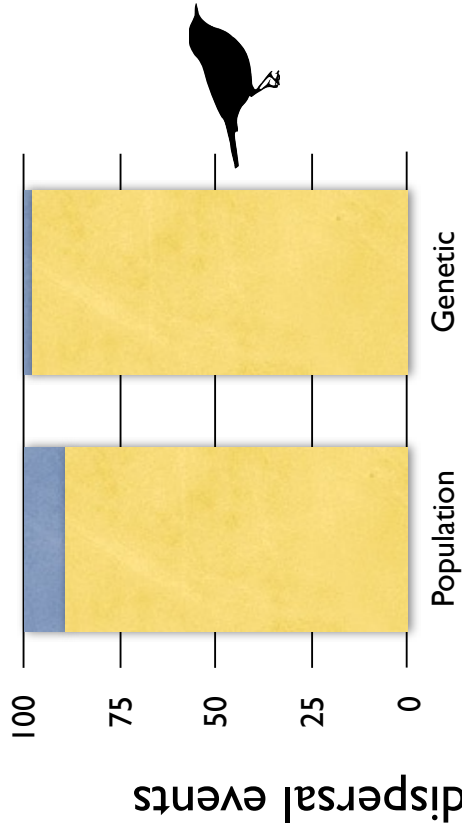
B. Emphasis on arrival



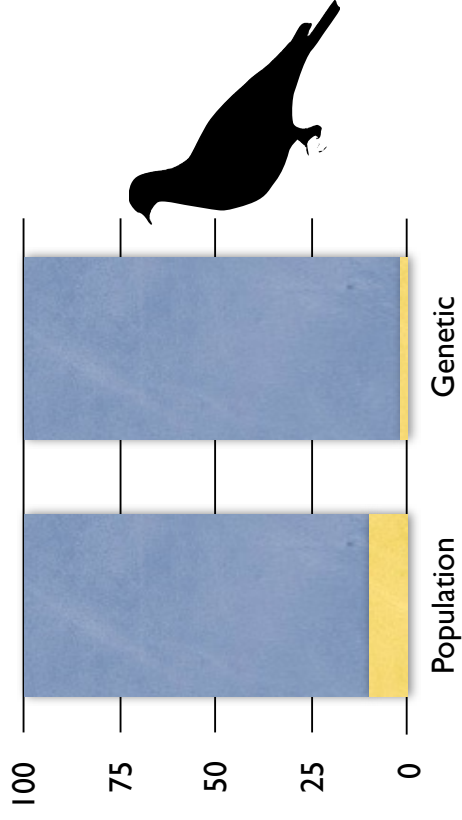




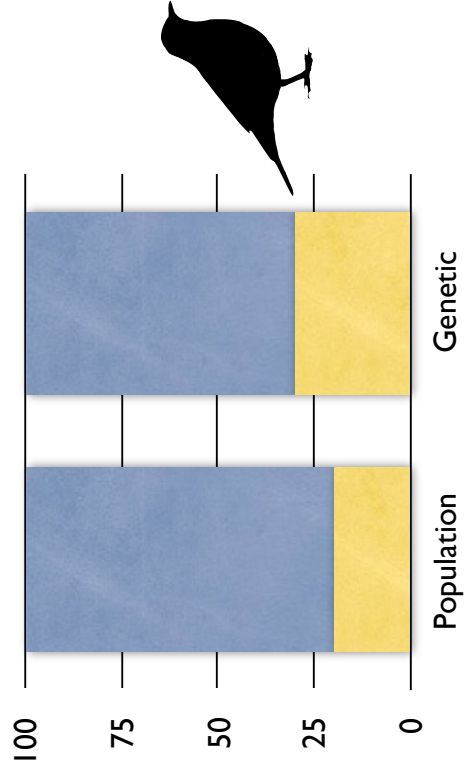
Within Outside



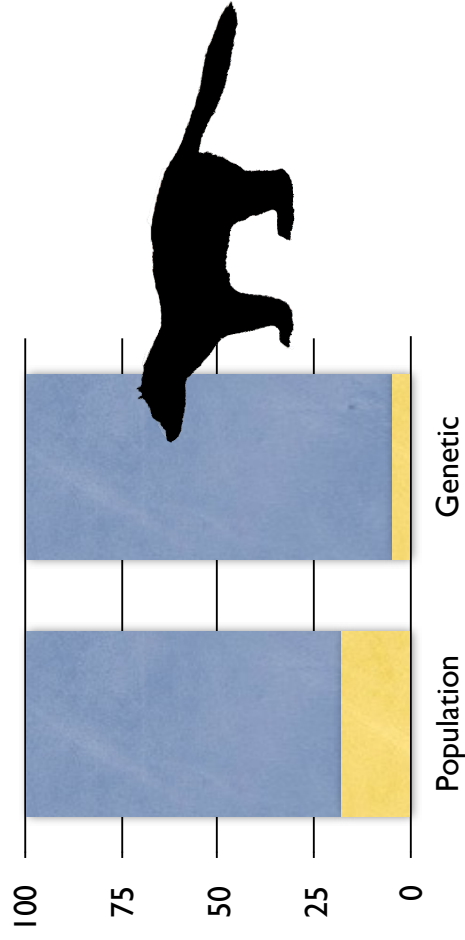
Small birds



Large birds



*Turdus*



Mammals