

# 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

<sup>23</sup> events helps to assess, for example, how the ongoing defaunation of large-bodied  
<sup>24</sup> frugivores pervasively entails the loss of crucial LDD functions.

## <sup>25</sup> Introduction

<sup>26</sup> Dispersal is a key individual-based process influencing many life-history attributes  
<sup>27</sup> and scaling up to population-level properties (e.g., metapopulation connectivity,  
<sup>28</sup> Cousens *et al.* 2008). In the specific case of plants, largely sessile organisms,  
<sup>29</sup> dispersal has three basic components: 1) a distinct (sessile) source, the maternal  
<sup>30</sup> plant producing the fruits or the paternal tree acting as a source of pollen; 2) a  
<sup>31</sup> distance component between source and target locations; and 3) a vector actually  
<sup>32</sup> performing the movement entailing the dispersal event. While realized dispersal  
<sup>33</sup> also depends upon stages subsequent to dissemination (e.g., successful germination  
<sup>34</sup> and seedling establishment) Schupp (1995), the three previous components fully  
<sup>35</sup> characterize the dispersal process per se. Therefore, plant movement differs in  
<sup>36</sup> important natural history details from animal dispersal, yet both can be assessed  
<sup>37</sup> within a common conceptual framework (e.g., Nathan, 2006). Characteristically,  
<sup>38</sup> animal-assisted plant dispersal has three distinct, highly integrated, components  
<sup>39</sup> missing in the process of animal dispersal: the properties of the source (parental)  
<sup>40</sup> plant, that mediate in the foraging of the animal vector (pollinator or frugivore),  
<sup>41</sup> the intrinsic properties of the propagule, and the functional characteristics of the  
<sup>42</sup> animal vector who performs the movement (Nathan *et al.*, 2008a).

<sup>43</sup> The movement of pollen and seeds by animals and its consequences have intrigued  
<sup>44</sup> population geneticists and field ecologists since the infancy of both research dis-  
<sup>45</sup> ciplines. Each has generated an impressive body of theoretical and empirical  
<sup>46</sup> 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, especially those involving movement over long-distances (long-distance dispersal, LDD). LDD is a characteristically extreme event of propagule movement in any plant population, typically occurring with an extremely low probability but potentially reaching an extremely long distance. Some progress has recently been made through the fast-paced implementation of molecular tools in ecological research labs and the availability of cutting-edge technology for biotelemetry applications [REF]. But much of the population geneticist and ecologist communities remains unaware of the state of the art in each other and likely under-appreciates their potential to validate and enrich dispersal studies (Jones & Muller-Landau, 2008). In particular, LDD events remain difficult to assess, both technically- with serious methodological problems for its reliable estimation- and conceptually. Our aim here is to review the LDD concept with a specific emphasis on dispersal of plant propagules (seeds and pollen), providing an extended definition that might be helpful in the robust quantification of LDD events.

Two main conceptual approaches have been used to assess dispersal (Fig. 1). 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 (Fig. 1A). This is the main approach used in the movement ecology framework (Nathan *et al.*, 2008a), with extensive application to animal movement based on the use of advanced biotelemetry. 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 (Fig. 1B), i.e., by using an inverse modeling approach. The main technical challenge in Fig. 1A is to sample enough dispersal events away from the source to be able to fully characterize the tail (LDD events) of the dispersal function. In Fig. 1B, 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. Both approaches are limited logically by the difficulties to sample the vast areas required to assess LDD events from the focal source population.

No explicit definition of what constitutes an LDD event exists. Previous approaches (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

93 definition of LDD. This leaves the consideration of LDD as an extreme form of  
94 context-dependent phenomenon, strongly dependent upon the scale of the biological  
95 process studied (Kinlan *et al.*, 2005). For example, Kinlan *et al.* (2005) used  
96 a spatial reference frame to characterize LDD events of marine organisms, where  
97 sedentary adults and larvae differ enormously in the spatial scales of their dispersal  
98 (D'Aloia *et al.*, 2013). Therefore, any measure of extent and reach of LDD events  
99 requires reference to an explicit spatial frame or "local" scale (Kinlan *et al.*, 2005).

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

110 Long-distance dispersal is currently one of the most debated topics in dispersal  
111 ecology; it defines the connectedness within the network of local populations and  
112 the possibilities for range expansion and successful colonization events. We pro-  
113 pose a first demogenetically-based, operational definition of what a long-distance  
114 dispersal event actually is, and review existing empirical literature on distance  
115 thresholds from population and genetic perspectives. We also show how molecular

116 tools have been used to identify the respective contributions of different animal  
117 species to the LDD portion of dispersal kernels of pollen and seeds by setting  
118 empirically-derived distance thresholds. Finally, we highlight potential applica-  
119 tions 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 propag-  
133 ules 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).

150 Two important components of plant dispersal ecology concern the movement of  
151 propagules away from the source population, a type of dispersal relevant to col-  
152 onization ability and range expansion (Howe & Miriti, 2004), and the movement  
153 away from the location of close relatives, i.e., a movement away from the genetic  
154 neighborhood (Hardesty *et al.*, 2006; Jones & Muller-Landau, 2008). If we classify  
155 dispersal events according to these two spatial frameworks (Table 1) we end up  
156 with four distinct types of events depending on whether or not dispersed propagules  
157 are disseminated within these reference areas. Setting the limits of a population  
158 can be problematic (Waples & Gaggiotti, 2006) yet we can identify with relative  
159 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 population, 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  $SDD_{loc}$  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

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:

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

where  $\delta$  is the density of adults per unit area and  $\sigma$  is the standard deviation of the 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  $N_e^b$  (highly clumped populations will have reduced  $N_e^b$ ). 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). With enough distance separating them, two plant individuals have a low probability of mating and can be considered members of distinct genetic populations even if they are not located in geographically distinct populations.

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,

224 neighborhood size can be defined with the following equation (Crawford 1984) :

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

225 where  $\sigma_s$  is the standard deviation of seed dispersal distance,  $\sigma_p$  is the standard  
226 deviation of pollen dispersal distance, and  $\delta$  is the density of potential parents.

227 Neighborhood size in plants can be estimated by marking pollen and seeds with  
228 fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,  
229 these methods do not measure effective pollen or seed movement, but they may  
230 be combined with genetic analysis to assess genetic identity and relatedness with  
231 hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,  
232 2001) to achieve reliable estimates of both effective population size and neighbor-  
233 hood area.

234 The extent of neighborhood area in plants can be extremely variable, depending  
235 on life-history attributes such as life-span, spacing patterns, mating system, etc.

236 Even a limited sample of available information (Table S1) highlights the fact that  
237 the size of neighborhood areas can in some cases exceed the geographic limits of  
238 local populations (Nason *et al.*, 1998). The size of neighborhood areas may en-  
239 compass at least four orders of magnitude,  $10^{-2} – 10^2$  km in radius, and include  
240 many individuals. Therefore, reference to this "genetic/evolutionary" paradigm  
241 and reference to the geographic boundaries (*sensu* Waples & Gaggiotti, 2006) may  
242 be instrumental to understand the actual role of LDD events in shaping the struc-  
243 turing of genetic pools and contributing to gene dispersal.

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

## 249 Empirical analysis of contributions to LDD

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

259 We inferred the frugivore groups contributing dispersal events by visually iden-  
260 tifying scats and regurgitations in seed traps and line transects (see Jordano  
261 *et al.*, 2007, and Suppl. Mat. for additional details of methods). These frugivore  
262 functional groups include up to 38 bird and 4 mammal species feeding on *P. ma-*  
263 *haleb* fruits (Jordano & Schupp, 2000). Here, we differentiate four major frugivore  
264 groups: large carnivorous mammals (such as foxes, badgers, and stone martens);

265 two species of medium-sized frugivorous birds, mistle thrushes (*T. viscivorus*),  
 266 and carrion crows (*Corvus corone*); and a pool of small-sized frugivorous birds,  
 267 including warblers, redstarts, and robins (Jordano *et al.*, 2007).

268 To a large extent, short-distance dispersal events (strict-sense,  $SDD_{loc}$  events)  
 269 are contributed by small- and medium-sized (*Turdus*) frugivorous birds (Table 2).  
 270 Given the relatively reduced  $N_e^b$  area of *P. mahaleb* (Suppl. Mat. Table S1),  
 271  $< 1km^2$ , well below the extent of the local study population (Garcia *et al.*, 2007,  
 272 2005), we cannot estimate  $LDD_{neigh}$  events (Table 2), as all LDD events outside the  
 273 reference population occur, by definition, outside the  $N_e^b$  area. Larger frugivores  
 274 such as corvids and the pigeon *Columba palumbus* contribute most LDD events,  
 275 and most immigrant seeds potentially dispersed from other populations. Notably,  
 276 strict-sense long-distance dispersal ( $LDD_{ss}$ ) appears consistently associated with  
 277 large-bodied frugivores (Table 2), most likely associated with a greater frequency  
 278 of movements outside the local population (Fig. 4).

## 279 Long-Distance Dispersal: the ecology of extreme events

280 Long-distance dispersal (LDD) is a major component of the population dynamics,  
 281 genetic structure, and biogeographic history of plant species. It determines the  
 282 colonization ability of new habitats and the possibilities for fragmented populations  
 283 to sustain a cohesive metapopulation by immigration-emigration dynamics that  
 284 rely on LDD events (Nathan *et al.*, 2008b; Schurr *et al.*, 2009). Yet our current  
 285 understanding of the extent, frequency, and consequences of LDD is very limited.

286 On one hand, theoretical models fail to predict accurately the behavior of the tail  
287 of the dispersal functions, and thus fail to predict very basic properties of LDD. On  
288 the other hand, we still have very limited documentation of actual LDD events in  
289 natural populations and we still see LDD as a sporadic, rarely far-reaching process  
290 still marked with the stamp of natural history curiosity.

291 Combining spatially-explicit references to the geographic population limits and the  
292 genetic neighborhood area extent ( $N_e^b$ ) helps avoiding some imprecision in setting  
293 distance thresholds to characterize LDD events (Jones & Muller-Landau, 2008).

294 In addition, the framework outlined in Table 1 bridges the combined demographic  
295 and genetic effects of LDD events. When methods available to assign frugivore  
296 taxa to the analyzed dispersal events, as in the study case with *P. mahaleb*, a  
297 classification in the four categories of events is possible.

298 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal  
299 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect  
300 that this extreme variation translates in an ample pattern of foraging modes, move-  
301 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results  
302 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the  
303 functional roles of frugivore species in terms of contributions to LDD events are  
304 structured in two distinct groups: small-bodied frugivores, with substantial con-  
305 tributions to SDD events, and large-bodied species with a disproportionate contri-  
306 bution to LDD events. Both components of this sort of diplochorous (vander Wall  
307 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with  
308 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied

309 frugivores largely contribute the short-distance dispersal key to support *in situ*  
310 recruitment and population persistence. Yet the large-bodied frugivores distinctly  
311 contribute LDD events that sustain the connectivity of metapopulation scenarios  
312 (Urban & Keitt, 2001). Yet, as shown in Table 1, SDD and LDD events can be  
313 more complex when we consider the contributions to gene flow via seed and the  
314 consequences in terms of structure and spatial distributions of the genetic pools.

315 A number of classic studies have demonstrated that the activity of large furgivores  
316 may also significantly contribute to SDD events and inefficient dispersal: i.e., ter-  
317 ritorial defence, short gut retention times relative to on-tree foraging, frequent  
318 revisititation of same trees and perches, etc., resulting in substantial SDD events  
319 (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright, 1991).

320 Yet these large-bodied frugivores are crucial for both  $LDD_{loc}$  and  $LDD_{ss}$ , given  
321 that extensive movement patterns and extremely large foraging ranges may fre-  
322 quently contribute dissemination beyond distance thresholds defined with either  
323 spatial landscape or genetic references. Recent analyses of the movement ecology  
324 of large frugivores, coupled with results of their seed dispersal services emphasize  
325 that LDD are by no means exceptional, either in terms of frequency and extent  
326 (Westcott *et al.*, 2005; ?).

327 As defined in our framework (Table 1), LDD, and in particular  $LDD_{ss}$  events are  
328 a specific case of extreme events (García & Borda-de Água, 2017) consistently  
329 associated with large-sized frugivores, yet including also medium-sized and highly  
330 efficient frugivorous bird species.

331 - Large-bodied frugivores and LDD. Discuss lb frugivores not always contributing  
332 LDD events: Pratt, tapirs - Loss of large-bodied frugivores, consequences.

333 **Challenges and future avenues for research**

334 Pollen and seed dispersal in plants are essentially spatially-structured processes  
335 for which the outcomes of interactions with dispersal vectors is intimately linked  
336 to landscape features. Given this mechanistic link between the features of the  
337 vector and the environments where its displacement occurs (Nathan *et al.*, 2008a),  
338 consideration of landscape is key to understand the consequences of LDD events.  
339 Yet these consequences hit two central aspects of plant life-histories: the demo-  
340 graphic recruitment process (Harper, 1977), and the genetic signatures of pollen-  
341 and seed-mediated gene flow .

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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.

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

**Table 2:** Relative 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.  $N = 655$  seeds (see Table 1 in Jordano *et al.*, 2007). Given that the estimated neighborhood size is smaller than population area,  $LDD_{neigh}$  would be zero.

Frugivore group	Within-population, within-neighborhood $SDD_{loc}$	Within-population, long-distance $LDD_{loc}$	Outside-population, within-neighborhood $LDD_{neigh}$	Strict-sense long-distance $LDD_{ss}$	$N$ seeds
Small-birds	0.7842	0.0171	0.00	0.1986	292
<i>Turdus</i>	0.2370	0.5549	0.00	0.2081	173
Large-birds	0.0435	0.3913	0.00	0.5652	23
Mammals	0.0120	0.2455	0.00	0.7425	167

## Figures

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

364

365   **Figure 2.** Schematic representation of different types of long-distance dispersal  
366   events in relation to the geographical limits of local populations (dashed lines)  
367   and the genetic neighborhood area  $N_e^b$  (grey area) of specific individual plants  
368   (squares). Dispersal events (arrows) can be classified depending on their actual  
369   incidence on propagule movement outside these spatially-explicit reference areas  
370   (Table 1). Strict-sense long-distance dispersal events ( $LDD_{ss}$ ) just include the  
371   LDD events that disseminate propagules out of *both* the population and genetic  
372   neighborhood boundaries. A, the neighborhood area is included within the geo-

373 graphic limits of the population, with some dispersal events potentially contribut-  
374 ing local LDD; B, the neighborhood area is much larger than the geographic limits  
375 of the population.

376

377 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function  
378 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In  
379 red, left (inset), frequencies of within-population dispersal events inferred from di-  
380 rect assignment based on seed endocarp genotypes and maternal trees genotypes.  
381 Larger frame, left, contributions of four functional frugivore groups (small birds,  
382 medium- and large-sized birds, and mammals) to seed dissemination and propor-  
383 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,  
384 those not matching any maternal tree in the study population) (Jordano *et al.*,  
385 2007).

386

387 **Figure 4.** Differential contributions of functional groups of frugivores to the  
388 four combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1.  
389 These result from dissemination within (yellow) or outside (blue) the population  
390 geographic limits; within-population dispersal events can either be short-distance  
391 ( $SDD_{loc}$ ) or local LDD ( $LDD_{loc}$ ) depending on the size of the genetic neigborhood.  
392 Dispersal outside the local population can entail short-distance dispersal, if within  
393 the genetic neighborhood area limits ( $SDD_{neigh}$ ) (yellow) or represent strict-sense  
394 LDD ( $LDD_{ss}$ ) (blue).

395

396 **Online Support Material and data accessibility**

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







