

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

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## Abstract

- 1    1. Dispersal is a key individual-based process influencing many life-history at-  
2 tributes, scaling up to population-level properties (e.g., metapopulation connec-  
3 tivity). A persistent challenge in dispersal ecology has been the robust characteri-  
4 zation of dispersal functions (kernels), a fundamental tool to predict how dispersal  
5 processes respond under global change scenarios. Especially the rightmost tail  
6 of these functions, i.e. the long-distance dispersal (LDD) events, are difficult to  
7 characterize empirically and to model in realistic ways.
- 8    2. But, when is it a LDD event? In the specific case of plants, dispersal has three  
9 basic components: 1) a distinct (sessile) source, the maternal plant producing  
10 the fruits or the paternal tree acting as a source of pollen; 2) a distance compo-  
11 nent between source and target locations; and 3) a vector actually performing the  
12 movement entailing the dispersal event. Here we discuss operative definitions of  
13 LDD based on their intrinsic properties: 1) events crossing geographic boundaries  
14 among stands; and 2) events contributing to effective gene flow and propagule  
15 migration.
- 16    3. Strict-sense long distance dispersal involves movement both outside the stand  
17 geographic limits and outside the genetic neighborhood area of individuals. Combi-  
18 nations of propagule movements within/outside these two spatial reference frames  
19 results in four distinct modes of LDD.
- 20    4. *Synthesis.* We discuss conditions where global change scenarios truncate disper-  
21 sal processes, leading to the loss of key dispersal services in natural populations.  
22 Proper characterization of the LDD events helps to assess, for example, how the

<sup>23</sup> ongoing defaunation of large-bodied frugivores pervasively entails the loss of cru-  
<sup>24</sup> cial LDD functions.

<sup>25</sup>

## 26 Introduction

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

44 The movement of pollen and seeds by animals and its consequences have intrigued  
45 population geneticists and field ecologists since the infancy of both research disci-  
46 plines. Each has generated an impressive body of theoretical and empirical research  
47 through the past decades, yet advances have long been co-existing in ‘parallel

48 worlds' and the great synergistic potential of population genetics and demography  
49 for the study of plant dispersal by animals remains little explored. Knowledge  
50 gaps still having the imprint of this conceptual disconnection include the idea of  
51 long distance dispersal, and the paradoxes of forest fragmentation effects on ge-  
52 netic diversity (Kramer *et al.*, 2008), survival and persistence of relict tree species  
53 (Hampe & Jump, 2011), rapid post-Pleistocene recolonization of vast continental  
54 areas in response to climate modification (Clark *et al.*, 1998; Clark, 1998), among  
55 other persisting issues. This conceptual isolation has been exacerbated by techni-  
56 cal difficulties for the robust characterization of dispersal events, especially those  
57 involving movement over long-distances (long-distance dispersal, LDD). LDD is a  
58 characteristically extreme event of propagule movement in any plant population,  
59 typically occurring with an extremely low probability but potentially reaching  
60 an extremely long distance. Some progress has recently been made through the  
61 fast-paced implementation of molecular tools in ecological research labs and the  
62 availability of cutting-edge technology for biotelemetry applications. But much of  
63 the population geneticist and ecologist communities remains unaware of the state  
64 of the art in each other and likely under-appreciates their potential to validate  
65 and enrich dispersal studies (Jones & Muller-Landau, 2008). In particular, LDD  
66 events remain difficult to assess, both technically- with serious methodological  
67 problems for its reliable estimation- and conceptually. Our aim here is to review  
68 the LDD concept with a specific emphasis on dispersal of plant propagules (seeds  
69 and pollen), providing an extended definition that might be helpful in the robust  
70 quantification of LDD events.

71 Two main conceptual approaches have been used to assess dispersal (Fig. 1).  
72 The “forward” approach attempts to track the dispersal events away from the  
73 known sources, e.g., by tracking the movement patterns of frugivores as they leave  
74 fruiting plants after feeding (Fig. 1A). This is the main approach used in the  
75 movement ecology framework (Nathan *et al.*, 2008a), with extensive application  
76 to animal movement based on the use of advanced biotelemetry. The “backward”  
77 approach attempts to reconstruct the most likely source of a dispersed propagule  
78 by inferring the sources given the propagule delivery pattern, the fecundity of  
79 potential sources, and the dispersal function (Fig. 1B), i.e., by using an inverse  
80 modeling approach. The main technical challenge in Fig. 1A is to sample enough  
81 dispersal events away from the source to be able to fully characterize the tail  
82 (LDD events) of the dispersal function. In Fig. 1B, the main challenge is to have  
83 a robust sampling scheme with propagule collectors (e.g., seed traps) and a good  
84 characterization of the potential sources to derive robust estimates of the actual  
85 sources. Both approaches are limited logically by the difficulties to sample the  
86 vast areas required to assess LDD events from the focal source population.  
  
87 No explicit definition of what constitutes an LDD event exists. Previous ap-  
88 proaches (e.g., Nathan, 2006; Schurr *et al.*, 2009) include both absolute and  
89 proportional definitions to characterize LDD events. This means providing in-  
90 formation about the absolute distances moved by a given percentile of the events  
91 and/or providing data on the proportion of events exceeding a given distance  
92 threshold (Nathan *et al.*, 2008b). The exact proportional or absolute thresholds  
93 selected remain arbitrary, as no reference spatial frame is provided within the

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

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

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

117 thresholds from population and genetic perspectives. We also show how molecular  
118 tools have been used to identify the respective contributions of different animal  
119 species to the LDD portion of dispersal kernels of pollen and seeds by setting  
120 empirically-derived distance thresholds. Finally, we highlight potential applica-  
121 tions of molecular markers beyond the quantification of just the dispersal distances  
122 that prevails in current studies, e.g., experimental approaches to assess dispersal  
123 limitation and Janzen-Connell effects.

124 **LDD within a demo-genetic perspective: a taxonomy of dis-  
125 persal events**

126 Here we propose an explicit definition of LDD and what constitutes a LDD event.  
127 Previous definitions of dispersal patterns emphasized only their distance compo-  
128 nents and characterized LDD events basically in terms of geographic distance be-  
129 tween a dispersed propagule (or an established early seedling) and its most likely  
130 maternal or paternal (in case of pollen) source. Absolute and proportional defini-  
131 tions for the LDD events have been proposed depending on arbitrary thresholds  
132 of either the distance beyond which a dispersal event is LDD or the proportion of  
133 events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).  
134 Thus, two key biological aspects of LDD events involve the transport of propag-  
135 ules outside a reference area: moving away from the source stand or population,  
136 and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These  
137 two movements do not necessarily concur: a propagule may move over a very

long distance yet still be disseminated within the reach of the neighborhood where parental individuals mate. Within a demo-genetic framework it is easy to envision a combination of situations concerning the spatial scale of the dispersal processes (Table 1) and unambiguously define different types of LDD events. The idea that dispersal occurs in reference to these two spatial reference frames, i.e., the population or stand and the genetic neighborhood area, is motivated by the fact that dispersal entails the movement of both an individual propagule (i.e., a pollen grain or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or a seed genotype). Thus, dispersal entails simultaneous demographic and genetic effects through recruitment of new individuals in the population and through contributions to gene flow (Harper, 1977). When considered its combined influence on demography and population genetics, the concept of LDD nicely bridges these two paradigms embedded in the biological definition of population (Waples & 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

161 ease the geographical limits of plant stands, patches, habitat spots or other types  
162 of habitat or microhabitat discontinuities that determine landmark boundaries of  
163 biological significance (see Kinlan *et al.*, 2005, for further discussion of boundaries  
164 for dispersal). These "frontiers" set biological limits to what a LDD event is in  
165 relation to the geographic limits of the source population. Most plants are dis-  
166 tributed as clumped patches, discrete stands, or relatively isolated populations, so  
167 we may distinguish between short-distance and long-distance dispersal events that  
168 end up with dissemination within or beyond, respectively, the stand or population  
169 geographic boundaries (Table 1,  $SDD_{loc}$  or  $LDD_{loc}$ ) (Figure 2).

170 A second consideration in terms of spatial boundaries, with effects on disper-  
171 sal patterns, is the genetic neighborhood area  $N_e^b$ , i.e., the spatial extent includ-  
172 ing a subset of panmictic individuals within a population (Wright, 1943, 1946).  
173 Thus, the  $N_e^b$  area can be equal to the whole extent of the population whenever  
174 the population is unstructured and there is evidence for random mating events  
175 among all the individuals. However, most populations and stands of long-lived  
176 trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006),  
177 where relatively long distances may separate groups of individuals within the same  
178 population. In these cases we might expect  $N_e^b$  area to be substantially smaller  
179 than the total population area. Therefore, at least four possible scenarios exist  
180 with distinct implications in terms of consequences for dispersal (Table 1). In the  
181 case of dispersal events not extending beyond the geographic limits of the popu-  
182 lation or reference area, actual LDD events may involve dissemination beyond a  
183 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  $SDD_{loc}$  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:

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

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

225 dispersal, and to take into account the mating system (outcrossing rate,  $t$ ). Thus,  
 226 neighborhood size can be defined with the following equation (Crawford 1984) :

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

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

229 Neighborhood size in plants can be estimated by marking pollen and seeds with  
 230 fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,  
 231 these methods do not measure effective pollen or seed movement, but they may  
 232 be combined with genetic analysis to assess genetic identity and relatedness with  
 233 hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,  
 234 2001) to achieve reliable estimates of both effective population size and neighbor-  
 235 hood area.

236 The extent of neighborhood area in plants can be extremely variable, depending  
 237 on life-history attributes such as life-span, spacing patterns, mating system, etc.  
 238 Even a limited sample of available information (Table S1) highlights the fact that  
 239 the size of neighborhood areas can in some cases exceed the geographic limits of  
 240 local populations (Nason *et al.*, 1998). The size of neighborhood areas may en-  
 241 compass at least four orders of magnitude,  $10^{-2} - 10^2$  km in radius, and include  
 242 many individuals. Therefore, reference to this "genetic/evolutionary" paradigm  
 243 and reference to the geographic boundaries (*sensu* Waples & Gaggiotti, 2006) may  
 244 be instrumental to understand the actual role of LDD events in shaping the struc-

245 turing of genetic pools and contributing to gene dispersal.

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

## 251 **Empirical analysis of contributions to LDD**

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

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

266 groups: large carnivorous mammals (such as foxes, badgers, and stone martens);  
267 two species of medium-sized frugivorous birds, mistle thrushes (*T. viscivorus*),  
268 and carrion crows (*Corvus corone*); and a pool of small-sized frugivorous birds,  
269 including warblers, redstarts, and robins (Jordano *et al.*, 2007).

270 To a large extent, short-distance dispersal events (strict-sense,  $SDD_{loc}$  events)  
271 are contributed by small- and medium-sized (*Turdus*) frugivorous birds (Table 2).  
272 Given the relatively reduced  $N_e^b$  area of *P. mahaleb* (Suppl. Mat. Table S1),  
273  $< 1km^2$ , well below the extent of the local study population (Garcia *et al.*, 2007,  
274 2005), we cannot estimate  $LDD_{neigh}$  events (Table 2), as all LDD events outside  
275 the reference population occur, by definition, outside the  $N_e^b$  area. Larger fru-  
276 givores such as corvids and the pigeon *Columba palumbus* contribute most LDD  
277 events, and most immigrant seeds potentially dispersed from other populations  
278 (Fig. S2). Notably, strict-sense long-distance dispersal ( $LDD_{ss}$ ) appears consis-  
279 tently associated with large-bodied frugivores (Table 2), most likely associated  
280 with a greater frequency of movements outside the local population (Fig. 4).

281 Empirically mapping of dispersal events for either pollen or seed disseminated by  
282 animals may result in a complex pattern of different combinations of dispersal  
283 events (Fig. S1), as animal movements are overlaid onto plant populations occu-  
284 pying complex landscapes, resulting in different types of SDD and LDD events.

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

286 Long-distance dispersal (LDD) is a major component of the population dynamics,  
287 genetic structure, and biogeographic history of plant species. It determines the  
288 colonization ability of new habitats and the possibilities for fragmented populations  
289 to sustain a cohesive metapopulation by immigration-emigration dynamics that  
290 rely on LDD events (Nathan *et al.*, 2008b; Schurr *et al.*, 2009). Yet our current  
291 understanding of the extent, frequency, and consequences of LDD is very limited.  
292 On one hand, theoretical models fail to predict accurately the behavior of the tail  
293 of the dispersal functions, and thus fail to predict very basic properties of LDD. On  
294 the other hand, we still have very limited documentation of actual LDD events in  
295 natural populations and we still see LDD as a sporadic, rarely far-reaching process  
296 still marked with the stamp of natural history curiosity.

297 Combining spatially-explicit references to the geographic population limits and the  
298 genetic neighborhood area extent ( $N_e^b$ ) helps avoiding some imprecision in setting  
299 distance thresholds to characterize LDD events (Jones & Muller-Landau, 2008).  
300 In addition, the framework outlined in Table 1 bridges the combined demographic  
301 and genetic effects of LDD events. When methods available to assign frugivore  
302 taxa to the analyzed dispersal events, as in the study case with *P. mahaleb*, a  
303 classification in the four categories of events is possible.

304 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal  
305 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect  
306 that this extreme variation translates in an ample pattern of foraging modes, move-

307 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results  
308 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the  
309 functional roles of frugivore species in terms of contributions to LDD events are  
310 structured in two distinct groups: small-bodied frugivores, with substantial con-  
311 tributions to SDD events, and large-bodied species with a disproportionate contri-  
312 bution to LDD events. Both components of this sort of diplochorous (vander Wall  
313 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with  
314 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied  
315 frugivores largely contribute the short-distance dispersal key to support *in situ*  
316 recruitment and population persistence. Yet the large-bodied frugivores distinctly  
317 contribute LDD events that sustain the connectivity of metapopulation scenarios  
318 (Urban & Keitt, 2001). As shown in Table 1, SDD and LDD events can be more  
319 complex when we consider the contributions to gene flow via seed and the conse-  
320 quences in terms of structure and spatial distributions of the genetic pools. For  
321 example, local, within-population, dispersal events may vary enormously in terms  
322 of genetic effects and local structuring of the genetic pools depending on whether  
323 they specifically contribute  $SDD_{loc}$  or instead,  $LDD_{loc}$ . Note that only the latter  
324 actually contribute erasing any form of local genetic structure by contributing to  
325 increased genetic neighborhoods.

326 A number of classic studies have demonstrated that the activity of large frugivores  
327 may also significantly contribute to SDD events and inefficient dispersal because  
328 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,  
329 frequent revisit of same trees and perches, etc., resulting in substantial SDD

events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright, 1991). Yet these large-bodied frugivores are crucial for both  $LDD_{loc}$  and  $LDD_{ss}$ , given that extensive movement patterns and extremely large foraging ranges may frequently contribute dissemination beyond distance thresholds defined with either spatial landscape or genetic references. Recent analyses of the movement ecology of large frugivores, coupled with results of their seed dispersal services emphasize that LDD are by no means exceptional, either in terms of frequency and extent (e.g., Westcott *et al.*, 2005; Bueno *et al.*, 2013; Morales *et al.*, 2013; Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.) can contribute substantial  $LDD_{loc}$  events, i.e., local LDD events contributing to erase local population genetic structuring, effectively increasing the size of genetic neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events are  $LDD_{loc}$  events. These birds are efficient seed dispersers of *P. mahaleb* and other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo *et al.*, 2013), also showing significant contributions of  $LDD_{ss}$  events.

As defined in our framework (Table 1), LDD, and in particular  $LDD_{ss}$  events are a specific case of extreme events (García & Borda-de Água, 2017) consistently associated with large-sized frugivores, yet including also medium-sized and highly efficient frugivorous bird species. Robustly characterizing the expected frequencies and extent of those extreme events would be crucial to properly assess the functional role of frugivores and the full range of influences (demographic, genetic) in plant populations.

### 352 Challenges and future avenues for research

353 Pollen and seed dispersal in plants are essentially spatially-structured processes  
354 for which the outcomes of interactions with dispersal vectors is intimately linked  
355 to landscape features. Given this mechanistic link between the features of the  
356 vector and the environments where its displacement occurs (Nathan *et al.*, 2008a),  
357 consideration of landscape is key to understand the consequences of LDD events.  
358 Yet these consequences hit two central aspects of plant life-histories: the demo-  
359 graphic recruitment process (Harper, 1977), and the genetic signatures of pollen-  
360 and seed-mediated gene flow in complex landscapes (Sork *et al.*, 1999). Recent  
361 evidences point out that the selective extinction of large-bodied frugivores may  
362 significantly impact plant populations dependent on frugivores both in terms of  
363 recruitment (Traveset *et al.*, 2012; Pérez-Méndez *et al.*, 2015) and genetic con-  
364nectivity (Pérez-Méndez *et al.*, 2016). Frugivore downsizing represents a lasting  
365 challenge for the collapse of seed dispersal processes where  $LDD_{ss}$  events are cru-  
366 cial for population persistence and the cohesion of fragmented populations within  
367 metapopulation scenarios.

368 We advocate (also see Jordano & Godoy, 2002; Nathan *et al.*, 2003; Jones &  
369 Muller-Landau, 2008; Hardesty *et al.*, 2011) a combination of approaches includ-  
370 ing large-scale biotelemetry to characterize animal movement, coupled with large-  
371 scale genetic sampling of dispersed propagules, and demogenetic approaches that  
372 combine both demographic and genetic research. A crucial aspect would be to  
373 effectively associate the role of individual frugivore species to specific dispersal

374 outcomes, by identifying the actual disperser contributing a dissemination event  
375 (González-Varo *et al.*, 2014) and simultaneously characterizing the source maternal  
376 plant (Jordano & Godoy, 2002).

377 The actual challenges to properly characterize the typologies of LDD events out-  
378 lined in Table 1 will probably persist. We need more efficient quantitative ap-  
379 proaches to assess these infrequent events, that occur over enormous spatial scales  
380 and that need to be documented with sample sizes sufficient to facilitate modeling  
381 efforts and robust statistical inferences. These are not trivial difficulties given the  
382 urgency to assess how forest loss, defaunation, genetic purging due to logging, etc.,  
383 alter plant populations.

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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

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

406

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

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

418

419 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function  
420 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In  
421 red, left (inset), frequencies of within-population dispersal events inferred from di-  
422 rect assignment based on seed endocarp genotypes and maternal trees genotypes.  
423 Larger frame, left, contributions of four functional frugivore groups (small birds,  
424 medium- and large-sized birds, and mammals) to seed dissemination and propor-  
425 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,  
426 those not matching any maternal tree in the study population) (Jordano *et al.*,  
427 2007).

428

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

437

438 **Online Support Material and data accessibility**

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







