

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

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Abstract

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

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

25 Introduction

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

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

47 worlds' and the great synergistic potential of population genetics and demography
48 for the study of plant dispersal by animals remains little explored. Knowledge
49 gaps still having the imprint of this conceptual disconnection include the idea of
50 long distance dispersal, and the paradoxes of forest fragmentation effects on ge-
51 netic diversity (Kramer *et al.*, 2008), survival and persistence of relict tree species
52 (Hampe & Jump, 2011), rapid post-Pleistocene recolonization of vast continental
53 areas in response to climate modification (Clark *et al.*, 1998; Clark, 1998), among
54 other persisting issues. This conceptual isolation has been exacerbated by techni-
55 cal difficulties for the robust characterization of dispersal events, especially those
56 involving movement over long-distances (long-distance dispersal, LDD). LDD is a
57 characteristically extreme event of propagule movement in any plant population,
58 typically occurring with an extremely low probability but potentially reaching
59 an extremely long distance. Some progress has recently been made through the
60 fast-paced implementation of molecular tools in ecological research labs and the
61 availability of cutting-edge technology for biotelemetry applications. But much of
62 the population geneticist and ecologist communities remains unaware of the state
63 of the art in each other and likely under-appreciates their potential to validate
64 and enrich dispersal studies (Jones & Muller-Landau, 2008). In particular, LDD
65 events remain difficult to assess, both technically- with serious methodological
66 problems for its reliable estimation- and conceptually. Our aim here is to review
67 the LDD concept with a specific emphasis on dispersal of plant propagules (seeds
68 and pollen), providing an extended definition that might be helpful in the robust
69 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) and of the specific organism considered.
96 For example, Kinlan *et al.* (2005) used a spatial reference frame to characterize
97 LDD events of marine organisms, where sedentary adults and larvae differ enormously
98 in the spatial scales of their dispersal (D'Aloia *et al.*, 2013). Therefore,
99 any measure of extent and reach of LDD events requires reference to an explicit
100 spatial frame or "local" scale (Kinlan *et al.*, 2005).

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

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

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

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

125 Here we propose an explicit definition of LDD and what constitutes a LDD event.
126 Previous definitions of dispersal patterns emphasized only their distance compo-
127 nents and characterized LDD events basically in terms of geographic distance be-
128 tween a dispersed propagule (or an established early seedling) and its most likely
129 maternal or paternal (in case of pollen) source. Absolute and proportional defini-
130 tions for the LDD events have been proposed depending on arbitrary thresholds
131 of either the distance beyond which a dispersal event is LDD or the proportion of
132 events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).
133 Thus, two key biological aspects of LDD events involve the transport of propag-
134 ules outside a reference area: moving away from the source stand or population,
135 and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These
136 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

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

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

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

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

226 where σ_s is the standard deviation of seed dispersal distance, σ_p is the standard
 227 deviation of pollen dispersal distance, and δ is the density of potential parents.

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

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

244 turing of genetic pools and contributing to gene dispersal.

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

250 Empirical analysis of contributions to LDD

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

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

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

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

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

284 Long-Distance Dispersal: the ecology of extreme events

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

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

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

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

325 A number of classic studies have demonstrated that the activity of large frugivores
326 may also significantly contribute to SDD events and inefficient dispersal because
327 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,
328 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.

351 Challenges and future avenues for research

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

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

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

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

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

405

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

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

417

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

427

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

436

⁴³⁷ **Online Support Material and data accessibility**

⁴³⁸ This review does not use new raw data, but includes some re-analyses of pre-
⁴³⁹ viously published material. All the original data supporting the paper, R code,
⁴⁴⁰ supplementary figures, and summaries of analytical protocols is available at the
⁴⁴¹ author's GitHub repository (https://github.com/pedroj/MS_LDD), with DOI:
⁴⁴² #/zenodo.#.







