

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

MS JEcol-2016-0422.R1

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Sevilla, October 10, 2016

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Key words: dispersal, frugivory, plant-animal interactions, pollination, seed dispersal

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

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 com-
11 ponent between source and target locations; and 3) a vector actually performing
12 the movement entailing the dispersal event. Here I 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.* I expect truncation of seed dispersal kernels to have multiple conse-
21 quences on demography and genetics, following to the loss of key dispersal services
22 in natural populations. Irrespective of neighborhood sizes, loss of LDD events may

23 result in more structured and less cohesive genetic pools, with increased isolation-
24 by-distance extending over broader areas. Proper characterization of the LDD
25 events helps to assess, for example, how the ongoing defaunation of large-bodied
26 frugivores pervasively entails the loss of crucial LDD functions.

27

²⁸ Introduction

²⁹ Dispersal is a key individual-based process influencing many life-history attributes
³⁰ and scaling up to population-level properties (e.g., metapopulation connectivity,
³¹ Cousens *et al.* 2008). In the specific case of plants, largely sessile organisms,
³² dispersal has three basic components: 1) a distinct (sessile) source, the maternal
³³ plant producing the fruits or the paternal tree acting as a source of pollen; 2) a
³⁴ distance component between source and target locations; and 3) a vector actually
³⁵ performing the movement entailing the dispersal event. While realized dispersal
³⁶ also depends upon stages subsequent to dissemination (e.g., successful germination
³⁷ and seedling establishment) Schupp (1995), the three previous components fully
³⁸ characterize the dispersal process per se. Therefore, plant movement differs in
³⁹ important natural history details from animal dispersal, yet both can be assessed
⁴⁰ within a common conceptual framework (e.g., Nathan, 2006). Characteristically,
⁴¹ animal-assisted plant dispersal has three distinct, highly integrated, components
⁴² missing in the process of animal dispersal: the properties of the source (parental)
⁴³ plant, that mediate in the foraging of the animal vector (pollinator or frugivore),
⁴⁴ the intrinsic properties of the propagule, and the functional characteristics of the
⁴⁵ animal vector who performs the movement (Nathan *et al.*, 2008a).

⁴⁶ The movement of pollen and seeds by animals and its consequences have intrigued
⁴⁷ population geneticists and field ecologists since the infancy of both research dis-
⁴⁸ ciplines. Each has generated an impressive body of theoretical and empirical re-
⁴⁹ search through the past decades, yet advances have long been co-existing in parallel

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

71 While my main focus is on population-level scenarios and the role of animal vec-
72 tors, recent research has shown how relevant is habitat and landscape context in

determining the occurrence and directionality of LDD (e.g. Schurr et al. 2008 *J Ecol*; Carlo et al. 2013). On the other hand, dealing with habitat effects seems obligated if aimed to discuss global change drivers (i.e. habitat loss and fragmentation). 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.

LDD events have two key characteristics that make them extremely important for population dynamics, yet being very difficult to characterize: LDD events are infrequent, but with a disproportionately high influence on contemporary gene flow and structure of the genetic pools (e.g., Schurr *et al.*, 2009; Clobert *et al.*, 2012;

96 Travis *et al.*, 2013). LDDs can connect disparate populations, allowing for genetic
97 connectivity, colonization of vacant habitat and range expansion across chang-
98 ing landscapes, and maintain global persistence in the face of local extinctions
99 (Trakhtenbrot *et al.*, 2005; Baguette & Schtickzelle, 2006; Ronce, 2007; Schloss
100 *et al.*, 2012). With their influence on the structure of genetic pools, LDD events
101 can also drive population differentiation and speciation (Ronce, 2007).

102 No explicit definition of what constitutes an LDD event exists. LDD is a charac-
103 teristically extreme event of propagule movement in any plant or animal popula-
104 tion, typically occurring with an extremely low probability but potentially reach-
105 ing an extremely long distance. Previous approaches (e.g., Nathan, 2006; Schurr
106 *et al.*, 2009) include both absolute and proportional definitions to characterize LDD
107 events. This means providing information about the absolute distances moved by
108 a given percentile of the events and/or providing data on the proportion of events
109 exceeding a given distance threshold, i.e., an operational definition (Nathan *et al.*,
110 2008b). The exact proportional or absolute thresholds selected remain somehow
111 arbitrary, as no reference spatial frame is provided within the definition of LDD.
112 This leaves the consideration of LDD as an extreme form of context-dependent
113 phenomenon, strongly dependent upon the scale of the biological process studied
114 (Kinlan *et al.*, 2005) and of the specific organism considered. For example, Kinlan
115 *et al.* (2005) used a spatial reference frame to characterize LDD events of ma-
116 rine organisms, where sedentary adults and larvae differ enormously in the spatial
117 scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent
118 and reach of LDD events requires reference to an explicit spatial frame or "local"

119 scale (Kinlan *et al.*, 2005; Byrne *et al.*, 2014).

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

129 Long-distance dispersal is currently one of the most debated topics in dispersal
130 ecology; it defines the connectedness within the network of local populations and
131 the possibilities for range expansion and successful colonization events. I propose
132 a first demogenetically-based, operational definition of what a LDD event actually
133 is, and review existing empirical literature on distance thresholds from population
134 and genetic perspectives. I also show how molecular tools have been used to
135 identify the respective contributions of different animal species to the LDD portion
136 of dispersal kernels of pollen and seeds by setting empirically-derived distance
137 thresholds. Finally, I highlight potential applications of molecular markers beyond
138 the quantification of just the dispersal distances that prevails in current studies,
139 e.g., experimental approaches to assess dispersal limitation and Janzen-Connell
140 effects.

¹⁴¹ **LDD within a demo-genetic perspective: a taxonomy of dis-**

¹⁴² **persal events**

¹⁴³ Here I propose an explicit definition of LDD and what constitutes a LDD event.

¹⁴⁴ Previous definitions of dispersal patterns emphasized only their distance compo-

¹⁴⁵ nents and characterized LDD events basically in terms of geographic distance be-

¹⁴⁶ tween a dispersed propagule (or an established early seedling) and its most likely

¹⁴⁷ maternal or paternal (in case of pollen) source. Absolute and proportional defini-

¹⁴⁸ tions for the LDD events have been proposed depending on arbitrary thresholds

¹⁴⁹ of either the distance beyond which a dispersal event is LDD or the proportion of

¹⁵⁰ events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).

¹⁵¹ Thus, two key biological aspects of LDD events involve the transport of propag-

¹⁵² ules outside a reference area: moving away from the source stand or population,

¹⁵³ and moving away from the area where relatives stand (Klinan *et al.*, 2005). These

¹⁵⁴ two movements do not necessarily concur: a propagule may move over a very

¹⁵⁵ long distance yet still be disseminated within the reach of the neighborhood where

¹⁵⁶ parental individuals mate. Within a demo-genetic framework it is easy to envision

¹⁵⁷ a combination of situations concerning the spatial scale of the dispersal processes

¹⁵⁸ (Table 1) and unambiguously define different types of LDD events. The idea that

¹⁵⁹ dispersal occurs in reference to these two spatial reference frames, i.e., the popu-

¹⁶⁰ lation or stand and the genetic neighborhood area, is motivated by the fact that

¹⁶¹ dispersal entails the movement of both an individual propagule (i.e., a pollen grain

¹⁶² or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or

¹⁶³ a seed genotype). Thus, dispersal entails simultaneous demographic and genetic

164 effects through recruitment of new individuals in the population and through con-
165 tributions to gene flow (Harper, 1977). When considered its combined influence
166 on demography and population genetics, the concept of LDD nicely bridges these
167 two paradigms embedded in the biological definition of population (Waples &
168 Gaggiotti, 2006).

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

187 A second consideration in terms of spatial boundaries, with effects on disper-
188 sal patterns, is the genetic neighborhood area N_e^b , i.e., the spatial extent includ-
189 ing a subset of panmictic individuals within a population (Wright, 1943, 1946).
190 Thus, the N_e^b area can be equal to the whole extent of the population whenever
191 the population is unstructured and there is evidence for random mating events
192 among all the individuals. However, most populations and stands of long-lived
193 trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006),
194 where relatively long distances may separate groups of individuals within the same
195 population. In these cases we might expect N_e^b area to be substantially smaller
196 than the total population area. Therefore, at least four possible scenarios exist
197 with distinct implications in terms of consequences for dispersal (Table 1). In the
198 case of dispersal events not extending beyond the geographic limits of the popu-
199 lation or reference area, actual LDD events may involve dissemination beyond a
200 reduced neighborhood area that is smaller than the geographic extent of the pop-
201 ulation, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig.
202 2A). Actual short-distance dispersal would then involve those situations where the
203 propagule is disseminated within *both* the population limits and the genetic neigh-
204 borhood boundary (SDD_{loc}). Along a similar reasoning, dispersal events outside
205 the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this
206 is expected in cases where the genetic neighborhoods are extensive, going beyond
207 the geographic limits of local populations, as in fig trees (Nason *et al.*, 1998) with
208 long-distance pollination, generating LDD events within the genetic neighborhood
209 (LDD_{neigh}). Note that pollen and seeds may have contrasting movement pat-

210 terns in reference to the distinct spatial scales of the population limits and of the
211 genetic neighbourhood. For example, wind-dispersed species with reduced seed
212 mobility (in terms of distance), such as oaks, can have large genetic neighbour-
213 hoods with extensive pollen dispersal (Streiff *et al.*, 1999) (but see, e.g., Smouse
214 *et al.*, 2001; Dutech *et al.*, 2005, for fragmented stands) so that LDD_{neigh} dis-
215 persal events might frequently move beyond the physical limits of the population,
216 patch, or stand but remain within the genetic neighbourhood. Finally, strict-sense
217 LDD events would involve dissemination outside *both* the population limits and
218 the genetic neighborhood boundary (LDD_{ss}) (Table 1, Fig. 2A).

219 While both SDD_{loc} and LDD_{loc} can be crucial for assuring the local persistence
220 of populations, LDD_{neigh} and LDD_{ss} would be extremely important contributors
221 to the structuring of genetic pools, realized gene flow, and maintaining connec-
222 tivity in metapopulation scenarios. I argue that both the demographic and the
223 genetic references are relevant for a proper definition of LDD. Accounting for these
224 references may have different implications in relation to the dispersal biology of
225 species. For example, frugivorous vertebrates, particularly the large-sized ones,
226 tend to disperse a high number of half-sibs propagules, from the same mother tree
227 to the same deposition site (Jordano *et al.*, 2007; Karubian *et al.*, 2010; Scofield
228 *et al.*, 2012), potentially increasing the frequency of LDD_{neigh} events if dispersal
229 distances are relatively short.

230 Individual and Population Neighborhoods as Reference

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

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

242 where δ is the density of adults per unit area and σ is the standard deviation of
 243 the distance between birth and breeding sites. This formulation is often called the
 244 neighborhood size and assumes a normal distribution of distances between parents
 245 and offspring (out in a perfect circular shape from the source). Thus, changes in
 246 the variance of dispersal distance can affect N_e^b (highly clumped populations will
 247 have reduced N_e^b). This is the basic model of "Isolation by Distance" proposed by
 248 Wright (1943, 1946). Under this type of model, migration (gene flow) is given by
 249 the variance in dispersal, and not by the proportion of the population that is com-

250 posed of migrants (denoted m), as is the case with island models (Slatkin, 1985).

251 With enough distance separating them, two plant individuals have a low probability
 252 of mating and can be considered members of distinct genetic populations even
 253 if they are not located in geographically distinct populations.

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

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

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

260 Neighborhood size in plants can be estimated by marking pollen and seeds with
 261 fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,
 262 these methods do not measure effective pollen or seed movement, but they may
 263 be combined with genetic analysis to assess genetic identity and relatedness with
 264 hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,
 265 2001) to achieve reliable estimates of both effective population size and neighbor-
 266 hood area.

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

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

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

Empirical analysis of contributions to LDD

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

tion can reliably assign the genotyped seeds to frugivore species groups based on specific characteristics of scats and regurgitations (Jordano *et al.*, 2007).

We inferred the frugivore groups contributing dispersal events by visually identifying scats and regurgitations in seed traps and line transects (see Jordano *et al.*, 2007, and Suppl. Mat. for additional details of methods). These frugivore functional groups include up to 38 bird and 4 mammal species feeding on *P. mahaleb* fruits (Jordano & Schupp, 2000). Here, we differentiate four major frugivore groups: large carnivorous mammals (such as foxes, badgers, and stone martens); two species of medium-sized frugivorous birds, mistle thrushes (*T. viscivorus*), and carrion crows (*Corvus corone*); and a pool of small-sized frugivorous birds, including warblers, redstarts, and robins (Jordano *et al.*, 2007).

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

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

316 **Long-Distance Dispersal: the ecology of extreme events**

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

323 On one hand, theoretical models fail to predict accurately the behavior of the tail
324 of the dispersal functions, and thus fail to predict very basic properties of LDD.

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

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

331 In addition, the framework outlined in Table 1 bridges the combined demographic
332 and genetic effects of LDD events. When methods available to assign frugivore

333 taxa to the analyzed dispersal events, as in the study case with *P. mahaleb*, a
334 classification in the four categories of events is possible.

335 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal
336 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect
337 that this extreme variation translates in an ample pattern of foraging modes, move-
338 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results
339 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the
340 functional roles of frugivore species in terms of contributions to LDD events are
341 structured in two distinct groups: small-bodied frugivores, with substantial con-
342 tributions to SDD events, and large-bodied species with a disproportionate contri-
343 bution to LDD events. Both components of this sort of diplochorous (vander Wall
344 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with
345 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied
346 frugivores largely contribute the short-distance dispersal key to support *in situ*
347 recruitment and population persistence. Yet the large-bodied frugivores distinctly
348 contribute LDD events that sustain the connectivity of metapopulation scenarios
349 (Urban & Keitt, 2001). As shown in Table 1, SDD and LDD events can be more
350 complex when we consider the contributions to gene flow via seed and the conse-
351 quences in terms of structure and spatial distributions of the genetic pools. For
352 example, local, within-population, dispersal events may vary enormously in terms
353 of genetic effects and local structuring of the genetic pools depending on whether
354 they specifically contribute SDD_{loc} or instead, LDD_{loc} . Note that only the latter
355 actually contribute erasing any form of local genetic structure by contributing to

356 increased genetic neighborhoods.

357 A number of classic studies have demonstrated that the activity of large frugivores
358 may also significantly contribute to SDD events and inefficient dispersal because
359 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,
360 frequent revisit of same trees and perches, etc., resulting in substantial SDD
361 events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright,
362 1991). Yet these large-bodied frugivores are crucial for both LDD_{loc} and LDD_{ss} ,
363 given that extensive movement patterns and extremely large foraging ranges may
364 frequently contribute dissemination beyond distance thresholds defined with ei-
365 ther spatial landscape or genetic references. Recent analyses of the movement
366 ecology of large frugivores, coupled with results of their seed dispersal services
367 emphasize that LDD are by no means exceptional, either in terms of frequency
368 and extent (e.g., Westcott *et al.*, 2005; Bueno *et al.*, 2013; Morales *et al.*, 2013;
369 Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.)
370 can contribute substantial LDD_{loc} events, i.e., local LDD events contributing to
371 erase local population genetic structuring, effectively increasing the size of genetic
372 neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events
373 are LDD_{loc} events. These birds are efficient seed dispersers of *P. mahaleb* and
374 other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo
375 *et al.*, 2013), also showing significant contributions of LDD_{ss} events.

376 Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed
377 shadows, accurately tracked with DNA-based genotyping methods, thus reflect
378 the complex effects of frugivore foraging, habitat preferences and heterogeneous

landscapes. This situation is probably generalizable to other plant-frugivore interactions where the combined spatial dynamics of habitat use and digestion processes determine complex seed shadows (?Jordano *et al.*, 2007; Nathan *et al.*, 2008b). Much of this complexity can be adequately handled by mechanistic models (Nathan *et al.*, 2002) incorporating very simple rules (Guttal *et al.*, 2011). For example, earlier results (Jordano, 2007) showed that the dispersal distances contributed by *P. mahaleb* frugivores closely map the spacing patterns of fruiting trees, but only up to a certain distance (≤ 100 m) (Fig. 10.3a in Jordano, 2007). Beyond this, frugivores were probably responding to other major landscape elements (e.g. rock outcrops, forest edges, large patches of open grassland, etc) that cause the fat tail of the seed dispersal distribution, adding more frequent LDD events than expected from a Brownian random walk pattern generated by a tracking of the crops of the fruiting trees. For instance, the long flights performed by *T. viscivorus* (Jordano & Schupp, 2000) frequently faced the pine forest edge, at distances ≥ 100 m of most *P. mahaleb* fruiting trees. If these medium-sized birds are selecting habitat with tall woody vegetation (e.g. pines ≥ 6 m height), then they should be perceiving a much more patchy landscape, and thus requiring longer flights, than for example, small warblers seeking vegetation cover < 0.5 m (Fig. 10.3b in Jordano, 2007).

As defined in our framework (Table 1), LDD, and in particular LDD_{ss} events are a specific case of extreme events (García & Borda-de Águia, 2017) consistently associated with large-sized frugivores, yet including also medium-sized and highly efficient frugivorous bird species. Robustly characterizing the expected frequencies

402 and extent of those extreme events would be crucial to properly assess the func-
403 tional role of frugivores and the full range of influences (demographic, genetic) in
404 plant populations.

405 Challenges and future avenues for research

406 Pollen and seed dispersal in plants are essentially spatially-structured processes
407 for which the outcomes of interactions with dispersal vectors is intimately linked
408 to landscape features. Given this mechanistic link between the features of the
409 vector and the environments where its displacement occurs (Nathan *et al.*, 2008a),
410 consideration of landscape is key to understand the consequences of LDD events.

411 Yet these consequences hit two central aspects of plant life-histories: the demo-
412 graphic recruitment process (Harper, 1977), and the genetic signatures of pollen-
413 and seed-mediated gene flow in complex landscapes (Sork *et al.*, 1999). Recent
414 evidences point out that the selective extinction of large-bodied frugivores may
415 significantly impact plant populations dependent on frugivores both in terms of
416 recruitment (Traveset *et al.*, 2012; Pérez-Méndez *et al.*, 2015) and genetic con-
417 nectivity (Pérez-Méndez *et al.*, 2016). Frugivore downsizing represents a lasting
418 challenge for the collapse of seed dispersal processes where LDD_{ss} events are cru-
419 cial for population persistence and the cohesion of fragmented populations within
420 metapopulation scenarios.

421 I advocate (also see Jordano & Godoy, 2002; Nathan *et al.*, 2003; Jones & Muller-
422 Landau, 2008; Hardesty *et al.*, 2011) a combination of approaches including large-

423 scale biotelemetry to characterize animal movement, coupled with large-scale ge-
424 netic sampling of dispersed propagules, and demogenetic approaches that combine
425 both demographic and genetic research. A crucial aspect would be to effectively
426 associate the role of individual frugivore species to specific dispersal outcomes, by
427 identifying the actual disperser contributing a dissemination event (González-Varo
428 *et al.*, 2014) and simultaneously characterizing the source maternal plant (Jordano
429 & Godoy, 2002).

430 LDD, and its variation across coexisting plant species, could also have far-reaching
431 consequences for community assembly and forest physiognomy. Yet very few pre-
432 vious analyses addressed this point. Comparative information on LDD across
433 species sharing a common environment have found strong differences in LDD po-
434 tential among plants with different (e.g. Clark *et al.* 1999 Ecology; Martnez *et al.*
435 2008 Oecologia) or even with the same dispersal syndrome (e.g. Garca *et al.* 2016
436 Basic Applied Ecology).

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

Acknowledgements. I am indebted to Cristina Garca, Jos A. Godoy, Manolo Car-
rin, Juan Luis Garca-Castao, Jess Rodrguez and, especially, Juan Miguel Arroyo
for generous help with field and laboratory work and making possible this study. I
appreciate the help and advice of Cristina Garca and Etienne Klein during the final
stages of the manuscript. The study was supported by a Junta de Andaluca Ex-
cellence Grant (RNM-5731), as well as a Severo Ochoa Excellence Award from the
Ministerio de Economia y Competitividad (SEV-2012-0262) and CGL2013-47429P
grant. The Consejera de Medio Ambiente, Junta de Andaluca, provided generous
facilities that made possible this study in the Andalusian natural parks (Sierra de
Cazorla, Alcornocales) and authorized my work there.

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

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

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

466

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

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

478

479 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function
480 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In
481 red, left (inset), frequencies of within-population dispersal events inferred from di-
482 rect assignment based on seed endocarp genotypes and maternal trees genotypes.
483 Larger frame, left, contributions of four functional frugivore groups (small birds,
484 medium- and large-sized birds, and mammals) to seed dissemination and propor-
485 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,
486 those not matching any maternal tree in the study population) (Jordano *et al.*,
487 2007).

488

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

497

498 **Online Support Material and data accessibility**

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







