

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

MS JEcol-2016-0422.R1

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Sevilla, October 11, 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 An added difficulty to bridge ecological processes of dispersal with their genetic
72 consequences is the fact that dispersal per se does not necessarily imply realized

73 gene flow (Mallet, 2001). Yet in the genetics literature, the inescapable difficulty
74 to robustly estimate σ_x , the standard deviation of parent-offspring distances,
75 as an estimate of realized gene flow distance, is analogous to the ecological sce-
76 nario. Strongly leptokurtic distributions of dispersal distances would lead to severe
77 underestimation of σ_x , e.g., in mark-recapture studies limited to local sites where
78 the long tail of LDD events escapes detection beyond the edges of the study area
79 (Mallet, 2001). Thus, fat-tailed distributions of dispersal distances tend to ho-
80 mogenize distant populations, leading to stronger reductions in F_{st} than expected
81 from local records of dispersal events (Rousset, 1997).

82 While my main focus is on population-level scenarios and the role of animal vec-
83 tors, recent research has shown how relevant is habitat and landscape context in
84 determining the occurrence and directionality of LDD (e.g. Schurr et al. 2008 J
85 Ecol; Carlo et al. 2013). On the other hand, dealing with habitat effects seems
86 obligated if aimed to discuss global change drivers (i.e. habitat loss and fragmen-
87 tation). Two main conceptual approaches have been used to assess dispersal (Fig.
88 1). The forward approach attempts to track the dispersal events away from the
89 known sources, e.g., by tracking the movement patterns of frugivores as they leave
90 fruiting plants after feeding (Fig. 1A). This is the main approach used in the
91 movement ecology framework (Nathan et al., 2008a), with extensive application
92 to animal movement based on the use of advanced biotelemetry. The backward
93 approach attempts to reconstruct the most likely source of a dispersed propag-
94 ule by inferring the sources given the propagule delivery pattern, the fecundity of
95 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; Travis *et al.*, 2013). LDDs can connect disparate populations, allowing for genetic connectivity, colonization of vacant habitat and range expansion across changing landscapes, and maintain global persistence in the face of local extinctions (Trakhtenbrot *et al.*, 2005; Baguette & Schtickzelle, 2006; Ronce, 2007; Schloss *et al.*, 2012). With their influence on the structure of genetic pools, LDD events can also drive population differentiation and speciation (Ronce, 2007).

No explicit definition of what constitutes an LDD event exists. LDD is a characteristically extreme event of propagule movement in any plant or animal population, typically occurring with an extremely low probability but potentially reaching an extremely long distance. 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

119 a given percentile of the events and/or providing data on the proportion of events
120 exceeding a given distance threshold, i.e., an operational definition (Nathan *et al.*,
121 2008b). The exact proportional or absolute thresholds selected remain somehow
122 arbitrary, as no reference spatial frame is provided within the definition of LDD.
123 This leaves the consideration of LDD as an extreme form of context-dependent
124 phenomenon, strongly dependent upon the scale of the biological process studied
125 (Kinlan *et al.*, 2005) and of the specific organism considered. For example, Kinlan
126 *et al.* (2005) used a spatial reference frame to characterize LDD events of ma-
127 rine organisms, where sedentary adults and larvae differ enormously in the spatial
128 scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent
129 and reach of LDD events requires reference to an explicit spatial frame or "local"
130 scale (Kinlan *et al.*, 2005; Byrne *et al.*, 2014).

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

140 Long-distance dispersal is currently one of the most debated topics in dispersal
141 ecology; it defines the connectedness within the network of local populations and

the possibilities for range expansion and successful colonization events. I propose a first demogenetically-based, operational definition of what a LDD event actually is, and review existing empirical literature on distance thresholds from population and genetic perspectives. I also show how molecular tools have been used to identify the respective contributions of different animal species to the LDD portion of dispersal kernels of pollen and seeds by setting empirically-derived distance thresholds. Finally, I highlight potential applications of molecular markers beyond the quantification of just the dispersal distances that prevails in current studies, e.g., experimental approaches to assess dispersal limitation and Janzen-Connell effects.

LDD within a demo-genetic perspective: a taxonomy of dispersal events

Here I propose an explicit definition of LDD and what constitutes a LDD event. Previous definitions of dispersal patterns emphasized only their distance components and characterized LDD events basically in terms of geographic distance between a dispersed propagule (or an established early seedling) and its most likely maternal or paternal (in case of pollen) source. Absolute and proportional definitions for the LDD events have been proposed depending on arbitrary thresholds of either the distance beyond which a dispersal event is LDD or the proportion of events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b). Thus, two key biological aspects of LDD events involve the transport of propag-

163 rules outside a reference area: moving away from the source stand or population,
164 and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These
165 two movements do not necessarily concur: a propagule may move over a very
166 long distance yet still be disseminated within the reach of the neighborhood where
167 parental individuals mate. Within a demo-genetic framework it is easy to envision
168 a combination of situations concerning the spatial scale of the dispersal processes
169 (Table 1) and unambiguously define different types of LDD events. The idea that
170 dispersal occurs in reference to these two spatial reference frames, i.e., the popu-
171 lation or stand and the genetic neighborhood area, is motivated by the fact that
172 dispersal entails the movement of both an individual propagule (i.e., a pollen grain
173 or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or
174 a seed genotype). Thus, dispersal entails simultaneous demographic and genetic
175 effects through recruitment of new individuals in the population and through con-
176 tributions to gene flow (Harper, 1977). When considered its combined influence
177 on demography and population genetics, the concept of LDD nicely bridges these
178 two paradigms embedded in the biological definition of population (Waples &
179 Gaggiotti, 2006).

180 Two important components of plant dispersal ecology concern the movement of
181 propagules away from the source population, a type of dispersal relevant to col-
182 onization ability and range expansion (Howe & Miriti, 2004), and the movement
183 away from the location of close relatives, i.e., a movement away from the genetic
184 neighborhood (Hardesty *et al.*, 2006; Jones & Muller-Landau, 2008). If we classify
185 dispersal events according to these two spatial frameworks (Table 1) we end up

with four distinct types of events depending on whether or not dispersed propagules are disseminated within these reference areas. Setting the limits of a population can be problematic (Waples & Gaggiotti, 2006) yet we can identify with relative ease the geographical limits of plant stands, patches, habitat spots or other types of habitat or microhabitat discontinuities that determine landmark boundaries of biological significance (see Kinlan *et al.*, 2005, for further discussion of boundaries for dispersal). These "frontiers" set biological limits to what a LDD event is in relation to the geographic limits of the source population. Most plants are distributed as clumped patches, discrete stands, or relatively isolated populations, so we may distinguish between short-distance and long-distance dispersal events that end up with dissemination within or beyond, respectively, the stand or population geographic boundaries (Table 1, SDD_{loc} or LDD_{loc}) (Figure 2).

A second consideration in terms of spatial boundaries, with effects on dispersal patterns, is the genetic neighborhood area N_e^b , i.e., the spatial extent including a subset of panmictic individuals within a population (Wright, 1943, 1946). Thus, the N_e^b area can be equal to the whole extent of the population whenever the population is unstructured and there is evidence for random mating events among all the individuals. However, most populations and stands of long-lived trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006), where relatively long distances may separate groups of individuals within the same population. In these cases we might expect N_e^b area to be substantially smaller than the total population area. Therefore, at least four possible scenarios exist with distinct implications in terms of consequences for dispersal (Table 1). In the

case of dispersal events not extending beyond the geographic limits of the population or reference area, actual LDD events may involve dissemination beyond a reduced neighborhood area that is smaller than the geographic extent of the population, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig. 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) with long-distance pollination, generating LDD events within the genetic neighborhood (LDD_{neigh}). Note that pollen and seeds may have contrasting movement patterns in reference to the distinct spatial scales of the population limits and of the genetic neighbourhood. For example, wind-dispersed species with reduced seed mobility (in terms of distance), such as oaks, can have large genetic neighbourhoods with extensive pollen dispersal (Streiff *et al.*, 1999) (but see, e.g., Smouse *et al.*, 2001; Dutech *et al.*, 2005, for fragmented stands) so that LDD_{neigh} dispersal events might frequently move beyond the physical limits of the population, patch, or stand but remain within the genetic neighbourhood. 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

232 to the structuring of genetic pools, realized gene flow, and maintaining connec-
233 tivity in metapopulation scenarios. I argue that both the demographic and the
234 genetic references are relevant for a proper definition of LDD. Accounting for these
235 references may have different implications in relation to the dispersal biology of
236 species. For example, frugivorous vertebrates, particularly the large-sized ones,
237 tend to disperse a high number of half-sibs propagules, from the same mother tree
238 to the same deposition site (Jordano *et al.*, 2007; Karubian *et al.*, 2010; Scofield
239 *et al.*, 2012), potentially increasing the frequency of LDD_{neigh} events if dispersal
240 distances are relatively short.

241 Individual and Population Neighborhoods as Reference

242 Continuous populations can be modeled with the concepts of isolation by distance
243 and neighborhood size(Wright, 1943, 1946). The former refers to the case that
244 limited gene dispersal in continuous populations produces demes that are panmic-
245 tic internally, but are isolated to some extent from adjacent demes. Each group of
246 reproducing individuals is the neighborhood, defined as the population of a region
247 in a continuum, from which the parents of individuals born near the center may
248 be treated as if drawn at random (Wright, 1969). The importance and influence of
249 the dispersal process in determining the size of the neighborhood is given by this
250 equation, which shows how the spatial dispersion (pattern of spatial distribution)
251 of the population influences the effective population size. This influence on the

252 effective size is given by:

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

253 where δ is the density of adults per unit area and σ is the standard deviation of
 254 the distance between birth and breeding sites. This formulation is often called the
 255 neighborhood size and assumes a normal distribution of distances between parents
 256 and offspring (out in a perfect circular shape from the source). Thus, changes in
 257 the variance of dispersal distance can affect N_e^b (highly clumped populations will
 258 have reduced N_e^b). This is the basic model of "Isolation by Distance" proposed by
 259 Wright (1943, 1946). Under this type of model, migration (gene flow) is given by
 260 the variance in dispersal, and not by the proportion of the population that is com-
 261 posed of migrants (denoted m), as is the case with island models (Slatkin, 1985).
 262 With enough distance separating them, two plant individuals have a low probabil-
 263 ity of mating and can be considered members of distinct genetic populations even
 264 if they are not located in geographically distinct populations.
 265 For plants, gene flow may be accomplished by both seeds and pollen, so the vari-
 266 ance may be decomposed to account for different patterns of seed and pollen
 267 dispersal, and to take into account the mating system (outcrossing rate, t). Thus,
 268 neighborhood size can be defined with the following equation (Crawford 1984) :

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

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

271 Neighborhood size in plants can be estimated by marking pollen and seeds with
272 fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,
273 these methods do not measure effective pollen or seed movement, but they may
274 be combined with genetic analysis to assess genetic identity and relatedness with
275 hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,
276 2001) to achieve reliable estimates of both effective population size and neighbor-
277 hood area.

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

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

288 Whenever there is a large discrepancy between population area extent and N_e^b
289 we might expect the frequency of LDD_{loc} and LDD_{neigh} differ enormously. For
290 example, relatively small N_e^b may rise the importance of LDD_{loc} in preserving

291 scenarios of panmixia within a local population, as most distant dispersal events
292 will disseminate seeds outside the neighborhood of maternal plants.

293 **Empirical analysis of contributions to LDD**

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

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

312 To a large extent, short-distance dispersal events (strict-sense, SDD_{loc} events)
313 are contributed by small- and medium-sized (*Turdus*) frugivorous birds (Table 2).
314 Given the relatively reduced N_e^b area of *P. mahaleb* (Suppl. Mat. Table S1),
315 $< 1km^2$, well below the extent of the local study population (Garcia *et al.*, 2007,
316 2005), we cannot estimate LDD_{neigh} events (Table 2), as all LDD events outside
317 the reference population occur, by definition, outside the N_e^b area. Larger fru-
318 givores such as corvids and the pigeon *Columba palumbus* contribute most LDD
319 events, and most immigrant seeds potentially dispersed from other populations
320 (Fig. S2). Notably, strict-sense long-distance dispersal (LDD_{ss}) appears consis-
321 tently associated with large-bodied frugivores (Table 2), most likely associated
322 with a greater frequency of movements outside the local population (Fig. 4).

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

327 Long-Distance Dispersal: the ecology of extreme events

328 Long-distance dispersal (LDD) is a major component of the population dynamics,
329 genetic structure, and biogeographic history of plant species. It determines the
330 colonization ability of new habitats and the possibilities for fragmented populations
331 to sustain a cohesive metapopulation by immigration-emigration dynamics that
332 rely on LDD events (Nathan *et al.*, 2008b; Schurr *et al.*, 2009). Yet our current

333 understanding of the extent, frequency, and consequences of LDD is very limited.

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

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

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

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

346 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal
347 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect
348 that this extreme variation translates in an ample pattern of foraging modes, move-
349 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results
350 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the
351 functional roles of frugivore species in terms of contributions to LDD events are
352 structured in two distinct groups: small-bodied frugivores, with substantial con-
353 tributions to SDD events, and large-bodied species with a disproportionate contri-
354 bution to LDD events. Both components of this sort of diplochorous (vander Wall
355 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with

356 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied
357 frugivores largely contribute the short-distance dispersal key to support *in situ*
358 recruitment and population persistence. Yet the large-bodied frugivores distinctly
359 contribute LDD events that sustain the connectivity of metapopulation scenarios
360 (Urban & Keitt, 2001). As shown in Table 1, SDD and LDD events can be more
361 complex when we consider the contributions to gene flow via seed and the conse-
362 quences in terms of structure and spatial distributions of the genetic pools. For
363 example, local, within-population, dispersal events may vary enormously in terms
364 of genetic effects and local structuring of the genetic pools depending on whether
365 they specifically contribute SDD_{loc} or instead, LDD_{loc} . Note that only the latter
366 actually contribute erasing any form of local genetic structure by contributing to
367 increased genetic neighborhoods.

368 A number of classic studies have demonstrated that the activity of large furgivores
369 may also significantly contribute to SDD events and inefficient dispersal because
370 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,
371 frequent revisit of same trees and perches, etc., resulting in substantial SDD
372 events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright,
373 1991). Yet these large-bodied frugivores are crucial for both LDD_{loc} and LDD_{ss} ,
374 given that extensive movement patterns and extremely large foraging ranges may
375 frequently contribute dissemination beyond distance thresholds defined with ei-
376 ther spatial landscape or genetic references. Recent analyses of the movement
377 ecology of large frugivores, coupled with results of their seed dispersal services
378 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.

Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed shadows, accurately tracked with DNA-based genotyping methods, thus reflect 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 track-

ing 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 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.

Challenges and future avenues for research

Pollen and seed dispersal in plants are essentially spatially-structured processes for which the outcomes of interactions with dispersal vectors is intimately linked to landscape features. Given this mechanistic link between the features of the vector and the environments where its displacement occurs (Nathan *et al.*, 2008a), consideration of landscape is key to understand the consequences of LDD events. Yet these consequences hit two central aspects of plant life-histories: the demo-

graphic recruitment process (Harper, 1977), and the genetic signatures of pollen- and seed-mediated gene flow in complex landscapes (Sork *et al.*, 1999). Recent evidences point out that the selective extinction of large-bodied frugivores may significantly impact plant populations dependent on frugivores both in terms of recruitment (Traveset *et al.*, 2012; Pérez-Méndez *et al.*, 2015) and genetic connectivity (Pérez-Méndez *et al.*, 2016). Frugivore downsizing represents a lasting challenge for the collapse of seed dispersal processes where LDD_{ss} events are crucial for population persistence and the cohesion of fragmented populations within metapopulation scenarios.

I advocate (also see Jordano & Godoy, 2002; Nathan *et al.*, 2003; Jones & Muller-Landau, 2008; Hardesty *et al.*, 2011) a combination of approaches including large-scale biotelemetry to characterize animal movement, coupled with large-scale genetic sampling of dispersed propagules, and demogenetic approaches that combine both demographic and genetic research. A crucial aspect would be to effectively associate the role of individual frugivore species to specific dispersal outcomes, by identifying the actual disperser contributing a dissemination event (González-Varo *et al.*, 2014) and simultaneously characterizing the source maternal plant (Jordano & Godoy, 2002).

LDL, and its variation across coexisting plant species, could also have far-reaching consequences for community assembly and forest physiognomy. Yet very few previous analyses addressed this point. Comparative information on LDL across species sharing a common environment have found strong differences in LDL potential among plants with different (e.g. Clark *et al.* 1999 Ecology; Martnez *et al.*

⁴⁴⁶ 2008 *Oecologia*) or even with the same dispersal syndrome (e.g. Garca et al. 2016
⁴⁴⁷ Basic Applied Ecology).

⁴⁴⁸ The actual challenges to properly characterize the typologies of LDD events out-
⁴⁴⁹ lined in Table 1 will probably persist. We need more efficient quantitative ap-
⁴⁵⁰ proaches to assess these infrequent events, that occur over enormous spatial scales
⁴⁵¹ and that need to be documented with sample sizes sufficient to facilitate modeling
⁴⁵² efforts and robust statistical inferences. These are not trivial difficulties given the
⁴⁵³ urgency to assess how forest loss, defaunation, genetic purging due to logging, etc.,
⁴⁵⁴ alter plant populations.

455 *Acknowledgements.* I am indebted to Cristina Garca, Jos A. Godoy, Manolo Car-
456 rin, Juan Luis Garca-Castao, Jess Rodrguez and, especially, Juan Miguel Arroyo
457 for generous help with field and laboratory work and making possible this study. I
458 appreciate the help and advice of Cristina Garca and Etienne Klein during the final
459 stages of the manuscript. The study was supported by a Junta de Andaluca Ex-
460 cellence Grant (RNM-5731), as well as a Severo Ochoa Excellence Award from the
461 Ministerio de Economia y Competitividad (SEV-2012-0262) and CGL2013-47429P
462 grant. The Consejera de Medio Ambiente, Junta de Andaluca, provided generous
463 facilities that made possible this study in the Andalusian natural parks (Sierra de
464 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

⁴⁶⁵ **Figure 1.** The two approaches used in analyses of dispersal processes in plants.
⁴⁶⁶ A, the forward approach attempts to track the dispersal events away from the
⁴⁶⁷ known sources, e.g., by tracking the movement patterns of frugivores as they leave
⁴⁶⁸ fruiting plants after feeding. B, the backward approach attempts to reconstruct
⁴⁶⁹ the most likely source of a dispersed propagule by inferring the sources given the
⁴⁷⁰ propagule delivery pattern, the fecundity of potential sources, and the dispersal
⁴⁷¹ function. The main technical challenge in A is to sample enough dispersal events
⁴⁷² away from the source to be able to fully characterize the tail (long-distance dis-
⁴⁷³ persal, LDD, events) of the dispersal function. In B, the main challenge is to have
⁴⁷⁴ a robust sampling scheme with propagule collectors (e.g., seed traps) and a good
⁴⁷⁵ characterization of the potential sources to derive robust estimates of the actual
⁴⁷⁶ sources with inverse-modeling techniques.

⁴⁷⁷
⁴⁷⁸ **Figure 2.** Schematic representation of different types of long-distance dispersal
⁴⁷⁹ events in relation to the geographical limits of local populations (dashed lines)
⁴⁸⁰ and the genetic neighborhood area N_e^b (grey area) of specific individual plants
⁴⁸¹ (squares). Dispersal events (arrows) can be classified depending on their actual
⁴⁸² incidence on propagule movement outside these spatially-explicit reference areas
⁴⁸³ (Table 1). Strict-sense long-distance dispersal events (LDD_{ss}) just include the
⁴⁸⁴ LDD events that disseminate propagules out of *both* the population and genetic
⁴⁸⁵ neighborhood boundaries. A, the neighborhood area is included within the geo-

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

489

490 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function
491 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In
492 red, left (inset), frequencies of within-population dispersal events inferred from di-
493 rect assignment based on seed endocarp genotypes and maternal trees genotypes.
494 Larger frame, left, contributions of four functional frugivore groups (small birds,
495 medium- and large-sized birds, and mammals) to seed dissemination and propor-
496 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,
497 those not matching any maternal tree in the study population) (Jordano *et al.*,
498 2007).

499

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

508

509 **Online Support Material and data accessibility**

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







