

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 disper-
65 sal studies (Jones & Muller-Landau, 2008). In particular, LDD events remain
66 difficult to assess, both technically- with serious methodological problems for its
67 reliable estimation- and conceptually. My aim 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). Despite such difficulties,
82 comparative approaches (e.g., Bohonak, 1999) demonstrate that dispersal makes
83 a measurable contribution to population genetic differentiation in most animal
84 species in nature, and that gene flow estimates are rarely so overwhelmed by pop-
85 ulation history, departures from equilibrium, or other microevolutionary forces as
86 to be uninformative. The relationship between dispersal and realized gene flow is
87 key to understand how migration interacts with drift in driving the dynamics of
88 genetic pools and population differentiation (Garant *et al.*, 2007).

89 While my main focus is on population-level scenarios and the role of animal vec-
90 tors, recent research has shown how relevant is habitat and landscape context in
91 determining the occurrence and directionality of LDD (Schurr *et al.*, 2008; Carlo
92 *et al.*, 2013). On the other hand, dealing with habitat effects seems obligated if
93 aimed to discuss global change drivers (i.e. habitat loss and fragmentation). Two
94 main conceptual approaches have been used to assess dispersal (Fig. 1). The
95 forward (Lagrangian) 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 (Eulerian) 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; 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

119 can also drive population differentiation and speciation (Garant *et al.*, 2007; Ronce,
120 2007).

121 No explicit definition of what constitutes an LDD event exists. LDD is a charac-
122 teristically extreme event of propagule movement in any plant or animal popula-
123 tion, typically occurring with an extremely low probability but potentially reach-
124 ing an extremely long distance. Previous approaches (e.g., Nathan, 2006; Schurr
125 *et al.*, 2009) include both absolute and proportional definitions to characterize LDD
126 events. This means providing information about the absolute distances moved by
127 a given percentile of the events and/or providing data on the proportion of events
128 exceeding a given distance threshold, i.e., an operational definition (Nathan *et al.*,
129 2008b). The exact proportional or absolute thresholds selected remain somehow
130 arbitrary, as no reference spatial frame is provided within the definition of LDD.
131 This leaves the consideration of LDD as an extreme form of context-dependent
132 phenomenon, strongly dependent upon the scale of the biological process studied
133 (Kinlan *et al.*, 2005) and of the specific organism considered. For example, Kinlan
134 *et al.* (2005) used a spatial reference frame to characterize LDD events of ma-
135 rine organisms, where sedentary adults and larvae differ enormously in the spatial
136 scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent
137 and reach of LDD events requires reference to an explicit spatial frame or "local"
138 scale (Kinlan *et al.*, 2005; Byrne *et al.*, 2014).

139 I aim at providing a general framework for the quantitative analysis of LDD events
140 so that estimates of their frequency and extent could be comparable across differ-
141 ent study systems. I argue that both demographic and genetic elements are needed

142 for this framework, most likely requiring a combination of field-based movement
143 data and genetic analyses. These elements can be overlaid on previous definitions
144 based on absolute and proportional characterizations of LDD. I start with a def-
145 inition of LDD events within a spatially-explicit mechanistic framework allowing
146 an unambiguous meaning for setting long-distance thresholds. I then use a case
147 study to assess differential contributions of animal frugivores performing LDD.

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

¹⁶⁰ **LDD within a demo-genetic perspective: a taxonomy of dis-**

¹⁶¹ **persal events**

¹⁶² Here I propose an explicit definition of LDD and what constitutes a LDD event.

¹⁶³ Previous definitions of dispersal patterns emphasized only their distance compo-

¹⁶⁴ nents and characterized LDD events basically in terms of geographic distance be-

¹⁶⁵ tween a dispersed propagule (or an established early seedling) and its most likely

¹⁶⁶ maternal or paternal (in case of pollen) source. Absolute and proportional defini-

¹⁶⁷ tions for the LDD events have been proposed depending on arbitrary thresholds

¹⁶⁸ of either the distance beyond which a dispersal event is LDD or the proportion of

¹⁶⁹ events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).

¹⁷⁰ Thus, two key biological aspects of LDD events involve the transport of propag-

¹⁷¹ ules outside a reference area: moving away from the source stand or population,

¹⁷² and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These

¹⁷³ two movements do not necessarily concur: a propagule may move over a very

¹⁷⁴ long distance yet still be disseminated within the reach of the neighborhood where

¹⁷⁵ parental individuals mate. Within a demo-genetic framework it is easy to envision

¹⁷⁶ a combination of situations concerning the spatial scale of the dispersal processes

¹⁷⁷ (Table 1) and unambiguously define different types of LDD events. The idea that

¹⁷⁸ dispersal occurs in reference to these two spatial reference frames, i.e., the popu-

¹⁷⁹ lation or stand and the genetic neighborhood area, is motivated by the fact that

¹⁸⁰ dispersal entails the movement of both an individual propagule (i.e., a pollen grain

¹⁸¹ or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or

¹⁸² a seed genotype). Thus, dispersal entails simultaneous demographic and genetic

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

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

206 A second consideration in terms of spatial boundaries, with effects on disper-
207 sal patterns, is the genetic neighborhood area N_e^b , i.e., the spatial extent includ-
208 ing a subset of panmictic individuals within a population (Wright, 1943, 1946).
209 Thus, the N_e^b area can be equal to the whole extent of the population whenever
210 the population is unstructured and there is evidence for random mating events
211 among all the individuals. However, most populations and stands of long-lived
212 trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006),
213 where relatively long distances may separate groups of individuals within the same
214 population. In these cases we might expect N_e^b area to be substantially smaller
215 than the total population area. Therefore, at least four possible scenarios exist
216 with distinct implications in terms of consequences for dispersal (Table 1). In the
217 case of dispersal events not extending beyond the geographic limits of the popu-
218 lation or reference area, actual LDD events may involve dissemination beyond a
219 reduced neighborhood area that is smaller than the geographic extent of the pop-
220 ulation, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig.
221 2A). Actual short-distance dispersal would then involve those situations where the
222 propagule is disseminated within *both* the population limits and the genetic neigh-
223 borhood boundary (SDD_{loc}). Along a similar reasoning, dispersal events outside
224 the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this
225 is expected in cases where the genetic neighborhoods are extensive, going beyond
226 the geographic limits of local populations, as in fig trees (Nason *et al.*, 1998) with
227 long-distance pollination, generating LDD events within the genetic neighborhood
228 (LDD_{neigh}). Note that pollen and seeds may have contrasting movement pat-

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

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

²⁴⁹ Individual and Population Neighborhoods as Reference

²⁵⁰ Continuous populations can be modeled with the concepts of isolation by distance
²⁵¹ and neighborhood size(Wright, 1943, 1946). The former refers to the case that
²⁵² limited gene dispersal in continuous populations produces demes that are panmic-
²⁵³ tic internally, but are isolated to some extent from adjacent demes. Each group of
²⁵⁴ reproducing individuals is the neighborhood, defined as the population of a region
²⁵⁵ in a continuum, from which the parents of individuals born near the center may
²⁵⁶ be treated as if drawn at random (Wright, 1969). The importance and influence of
²⁵⁷ the dispersal process in determining the size of the neighborhood is given by this
²⁵⁸ equation, which shows how the spatial dispersion (pattern of spatial distribution)
²⁵⁹ of the population influences the effective population size. This influence on the
²⁶⁰ effective size is given by:

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

²⁶¹ where δ is the density of adults per unit area and σ is the standard deviation of
²⁶² the distance between birth and breeding sites. This formulation is often called the
²⁶³ neighborhood size and assumes a normal distribution of distances between parents
²⁶⁴ and offspring (out in a perfect circular shape from the source). Thus, changes in
²⁶⁵ the variance of dispersal distance can affect N_e^b (highly clumped populations will
²⁶⁶ have reduced N_e^b). This is the basic model of "Isolation by Distance" proposed by
²⁶⁷ Wright (1943, 1946). Under this type of model, migration (gene flow) is given by
²⁶⁸ the variance in dispersal, and not by the proportion of the population that is com-

²⁶⁹ posed of migrants (denoted m), as is the case with island models (Slatkin, 1985).

²⁷⁰ With enough distance separating them, two plant individuals have a low probability
²⁷¹ of mating and can be considered members of distinct genetic populations even
²⁷² if they are not located in geographically distinct populations.

²⁷³ For plants, gene flow may be accomplished by both seeds and pollen, so the variance
²⁷⁴ may be decomposed to account for different patterns of seed and pollen
²⁷⁵ dispersal, and to take into account the mating system (outcrossing rate, t). Thus,
²⁷⁶ neighborhood size can be defined with the following equation (Crawford 1984) :

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

²⁷⁷ where σ_s is the standard deviation of seed dispersal distance, σ_p is the standard
²⁷⁸ deviation of pollen dispersal distance, and δ is the density of potential parents.

²⁷⁹ Neighborhood size in plants can be estimated by marking pollen and seeds with
²⁸⁰ fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,
²⁸¹ these methods do not measure effective pollen or seed movement, but they may
²⁸² be combined with genetic analysis to assess genetic identity and relatedness with
²⁸³ hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,
²⁸⁴ 2001) to achieve reliable estimates of both effective population size and neighborhood
²⁸⁵ area.

²⁸⁶ The extent of neighborhood area in plants can be extremely variable, depending
²⁸⁷ 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).

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

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

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

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

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

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

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

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

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

375 increased genetic neighborhoods.

376 A number of classic studies have demonstrated that the activity of large frugivores
377 may also significantly contribute to SDD events and inefficient dispersal because
378 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,
379 frequent revisit of same trees and perches, etc., resulting in substantial SDD
380 events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright,
381 1991). Yet these large-bodied frugivores are crucial for both LDD_{loc} and LDD_{ss} ,
382 given that extensive movement patterns and extremely large foraging ranges may
383 frequently contribute dissemination beyond distance thresholds defined with ei-
384 ther spatial landscape or genetic references. Recent analyses of the movement
385 ecology of large frugivores, coupled with results of their seed dispersal services
386 emphasize that LDD are by no means exceptional, either in terms of frequency
387 and extent (e.g., Westcott *et al.*, 2005; Bueno *et al.*, 2013; Morales *et al.*, 2013;
388 Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.)
389 can contribute substantial LDD_{loc} events, i.e., local LDD events contributing to
390 erase local population genetic structuring, effectively increasing the size of genetic
391 neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events
392 are LDD_{loc} events. These birds are efficient seed dispersers of *P. mahaleb* and
393 other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo
394 *et al.*, 2013), also showing significant contributions of LDD_{ss} events.

395 Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed
396 shadows, accurately tracked with DNA-based genotyping methods, thus reflect
397 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

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

424 Challenges and future avenues for research

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

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

440 I advocate (also see Jordano & Godoy, 2002; Nathan *et al.*, 2003; Jones & Muller-
441 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).

LDD, and its variation across coexisting plant species, could also have far-reaching consequences for community assembly and forest physiognomy. Yet very few previous analyses address this point. Comparative information on LDD across species sharing a common environment have found strong differences in LDD potential among plants with different (e.g., Clark *et al.*, 1999; Martínez & González-Taboada, 2008) or even with the same dispersal syndrome (García *et al.*, 2016).

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

References

- Baguette, M. & Schtickzelle, N. (2006) Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology*, **87**, 648–654.
- Bohonak, A. (1999) Dispersal, gene flow, and population structure. *Quarterly Review Of Biology*, **74**, 21–45.
- Bueno, R.S., Guevara, R., Ribeiro, M.C., Culot, L., Bufalo, F.S. & Galetti, M. (2013) Functional Redundancy and Complementarities of Seed Dispersal by the Last Neotropical Megafrugivores. *PLoS ONE*, **8**(2), e56252, doi:10.1371/journal.pone.0056252.s003.
- Byrne, A.W., Quinn, J.L., O'Keeffe, J.J., Green, S., Paddy Sleeman, D., Wayne Martin, S. & Davenport, J. (2014) Large-scale movements in European badgers: has the tail of the movement kernel been underestimated? *Journal of Animal Ecology*, **83**(4), 991–1001, doi:10.1111/1365-2656.12197.
- Carlo, T.A., García, D., Martínez, D., Gleditsch, J.M. & Morales, J.M. (2013) Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. *Ecology*, **94**(2), 301–307.
- Carlo, T., Tewksbury, J., Martínez, C. & Mart (2009) A new method to track seed dispersal and recruitment using ^{15}N isotope enrichment. *Ecology*, **90**, 3516–3525.
- Clark, J.S., Fastie, C., Hurt, G.C., Jackson, S.T., Johnson, C., King, G., Lewis, M., Lynch, J., Pacala, S., Prentice, C., Schupp, E., Webb III, T. & Wyckoff, P. (1998) Reid's paradox of rapid plant migration. *BioScience*, **48**, 13–24.

- Clark, J. (1998) Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, **152**, 204–224.
- Clark, J., Silman, M., Kern, R., Macklin, E. & Hilleris-Lambers, J. (1999) Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Clobert, J., Baguette, M., Benton, M.J., Bullock, J.M. & Duceatz, S. (2012) *Dispersal ecology and evolution*. Oxford University Press, Oxford, UK.
- Cousens, R.D., Dytham, C. & Law, R. (2008) *Dispersal in plants. A population perspective*. Oxford University Press, Oxford, UK.
- D'Aloia, C.C., Bogdanowicz, S.M., Majoris, J.E., Harrison, R.G. & Buston, P.M. (2013) Self-recruitment in a Caribbean reef fish: a method for approximating dispersal kernels accounting for seascape. *Molecular Ecology*, n/a–n/a, doi:10.1111/mec.12274.
- Dutech, C., Sork, V.L., Irwin, A.J., Smouse, P.E. & Davis, F.W. (2005) Gene flow and fine-scale genetic structure in a wind-pollinated tree species *Quercus lobata* (Fagaceae). *American Journal of Botany*, **92**, 252–261.
- Galetti, M., Guevara, R., Côrtes, M.C., Fadini, R., Von Matter, S., Leite, A.B., Labecca, F., Ribeiro, T., Carvalho, C.S., Collevatti, R.G., Pires, M.M., Guimaraes, P.R., Brancalion, P.H., Ribeiro, M.C. & Jordano, P. (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, **340**(6136), 1086–1090, doi:10.1126/science.1233774.

Garant, D., Forde, S.E. & Hendry, A.P. (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, **21**(3), 434–443, doi:10.1111/j.1365-2435.2006.01228.x.

Garcia, C., Arroyo, J., Godoy, J. & Jordano, P. (2005) Mating patterns, pollen dispersal, and the ecological maternal neighbourhood in a *Prunus mahaleb* L. population. *Molecular Ecology*, **14**, 1821–1830, doi:10.1111/j.1365-294X.2005.02542.x.

Garcia, C., Jordano, P. & Godoy, J.A. (2007) Contemporary pollen and seed dispersal in a *Prunus mahaleb* population: patterns in distance and direction. *Molecular Ecology*, **16**, 1947–1955, doi:10.1111/j.1365-294X.2006.03126.x.

García, C. & Borda-de Água, L. (2017) Extended dispersal kernels: insights from statistics of extremes. *Journal of Ecology*, **00**, 000–000.

García, D., Carlo, T.A. & Martínez, D. (2016) Differential effect of landscape structure on the large-scale dispersal of co-occurring bird-dispersed trees. *Basic And Applied Ecology*, **17**(5), 428–437, doi:10.1016/j.baae.2016.01.003.

Godoy, J.A. & Jordano, P. (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology*, **10**(9), 2275–2283.

González-Varo, J.P., Arroyo, J.M. & Jordano, P. (2014) Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. *Methods in Ecology and Evolution*, **5**(8), 806–814, doi:10.1111/2041-210X.12212.

- Guttal, V., Bartumeus, F., Hartvigsen, G. & Nevai, A.L. (2011) Retention Time Variability as a Mechanism for Animal Mediated Long-Distance Dispersal. *PLoS ONE*, **6**(12), e28447, doi:10.1371/journal.pone.0028447.t003.
- Hampe, A. & Jump, A.S. (2011) Climate Relicts: Past, Present, Future. *Annual Review of Ecology Evolution and Systematics*, **42**(1), 313–333, doi:10.1146/annurev-ecolsys-102710-145015.
- Hardesty, B.D., Hubbell, S.P. & Bermingham, E. (2006) Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecology Letters*, **9**, 516–525.
- Hardesty, B.D., Metcalfe, S.S. & Westcott, D.A. (2011) Persistence and spread in a new landscape: Dispersal ecology and genetics of Miconia invasions in Australia. *Acta Oecologica*, **37**(6), 657–665, doi:10.1016/j.actao.2011.06.006.
- Harper, J. (1977) *Population Biology of Plants*, 1st edn. Academic Press, London.
- Howe, H.F. & Miriti, M.N. (2004) When seed dispersal matters. *BioScience*, **54**(7), 651–660.
- Jones, F.A. & Muller-Landau, H.C. (2008) Measuring long-distance seed dispersal in complex natural environments: an evaluation and integration of classical and genetic methods. *Journal of Ecology*, **96**(4), 642–652, doi:10.1111/j.1365-2745.2008.01400.x.
- Jordano, P. (2007) Frugivores, seeds, and genes: analysing the key components of seed shadows. *Seed Dispersal: Theory and its Application in a Changing World*

(eds. A.J. Dennis, R. Green, E.W. Schupp & A.J. Wescott). CAB International, Wallingford, UK, pp. 229–251.

Jordano, P., García, C., Godoy, J.A. & García-Castaño, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings Of The National Academy Of Sciences Of The United States Of America*, **104**(9), 3278–3282, doi:10.1073/pnas.0606793104.

Jordano, P. & Godoy, J. (2002) Frugivore-generated seed shadows: a landscape view of demographic and genetic effects. *Seed dispersal and frugivory: ecology, evolution, and conservation* (eds. D. Levey, W. Silva & M. Galetti). Book chapter, Wallingford, UK, pp. 305–321.

Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**(4), 591–615, doi:10.2307/2657187?ref=no-x-route:1d70d282eb4ed20cce6eac7274a631bb.

Karubian, J., Sork, V.L., Roorda, T., Durães, R. & Smith, T.B. (2010) Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology*, **19**(8), 1745–1753, doi:10.1111/j.1365-294X.2010.04600.x.

Kinlan, B., Gaines, S. & Lester, S. (2005) Propagule dispersal and the scales of marine community process. *Diversity and Distributions*, **11**, 139–148, doi:10.1111/j.1366-9516.2005.00158.x.

- Kramer, A., Ison, J., Ashley, M. & Howe, H. (2008) The paradox of forest fragmentation genetics. *Conservation Biology*, 8, doi:10.1111/j.1523-1739.2008.00944.x.
- Levin, D.A. (1988) The paternity pools of plants. *The American Naturalist*, **132**, 309–317, doi:10.2307/2461984.
- Mallet, J. (2001) Gene flow. *Insect movement mechanisms and consequences* (eds. I.P. Wolwood, D.R. Reynolds & C. Thomas). Wallingford, UK, pp. 337–360.
- Martinez, I. & González-Taboada, F. (2008) Seed dispersal patterns in a temperate forest during a mast event: performance of alternative dispersal kernels. *Oecologia*, **159**(2), 389–400, doi:10.1007/s00442-008-1218-4.
- Morales, J.M., García, D., Martínez, D., Rodríguez-Pérez, J. & Herrera, J.M. (2013) Frugivore Behavioural Details Matter for Seed Dispersal: A Multi-Species Model for Cantabrian Thrushes and Trees. *PLoS ONE*, **8**(6), e65216, doi:10.1371/journal.pone.0065216.s005.
- Nason, J.D., Herre, E. & Hamrick, J.L. (1998) The breeding structure of a tropical keystone plant resource. *Nature*, **391**, 685–687.
- Nathan, R., Horn, H.S., Chave, J. & Levin, S.A. (2002) Mechanistic models for tree seed dispersal by wind in dense forests and open landscapes. *Seed dispersal and frugivory: ecology, evolution and conservation* (eds. D.J. Levey, W.R. Silva & M. Galetti). Commonwealth Agricultural Bureau International, Wallingford, UK, pp. 69–82.

Nathan, R., Perry, G., Cronin, J.T., Strand, A.E. & Cain, M.L. (2003) Methods for estimating long-distance dispersal. *Oikos*, **103**, 261–273.

Nathan, R. (2005) Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distributions*, **11**(2), 125–130, doi:10.1111/j.1366-9516.2005.00159.x.

Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008a) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA*, **105**(49), 19052–19059, doi:10.1073/pnas.0800375105.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008b) Mechanisms of long-distance seed dispersal. *Trends In Ecology & Evolution*, **23**(11), 638–647, doi:10.1016/j.tree.2008.08.003.

Pérez-Méndez, N., Jordano, P. & Valido, A. (2015) Downsized mutualisms: Consequences of seed dispersers' body-size reduction for early plant recruitment. *Perspectives In Plant Ecology Evolution And Systematics*, **17**(2), 151–159, doi: 10.1016/j.ppees.2014.12.001.

Pérez-Méndez, N., Jordano, P. & Valido, A. (2016) Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. *In 2nd. review.*

- Pratt, T. (1984) Examples of tropical frugivores defending fruit-bearing plants. *Condor*, **86**, 123–129.
- Pratt, T. & Stiles, E. (1983) How long fruit-eating birds stay in the plants where they feed - implications for seed dispersal. *The American Naturalist*, **122**(6), 797–805.
- Ronce, O. (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics*, **38**(1), 231–253, doi:10.1146/annurev.ecolsys.38.091206.095611.
- Rousset, F. (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, **145**(4), 1219–1228, doi:10.2307/40419201?ref=no-x-route:35b111e059d3f1727b77c9c51a9f7d0e.
- Schloss, C.A., Nunez, T.A. & Lawler, J.J. (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences USA*, **109**(22), 8606–8611, doi:10.1073/pnas.1116791109.
- Schupp, E. (1995) Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409, doi:10.2307%2F2445586.
- Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, R. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38**, 204–237.
- Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal

- in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**(4), 628–641, doi:10.1111/j.1365-2745.2008.01371.x.
- Scofield, D.G., Smouse, P.E., Karubian, J. & Sork, V.L. (2012) Use of Alpha, Beta, and Gamma Diversity Measures to Characterize Seed Dispersal by Animals. *The American Naturalist*, **180**(6), 719–732, doi:10.1086/668202.
- Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, 2132–2137, doi:10.1371/journal.pbio.0040344.
- Slatkin, M. (1985) Gene flow in natural populations. *Annual Review of Ecology and Systematics*, doi:10.2307/2097054.
- Smouse, P.E., Dyer, R.J., Westfall, R.D. & Sork, V.L. (2001) Two-generation analysis of pollen flow across a landscape. I. Male gamete heterogeneity among females. *Evolution*, **55**(2), 260–271.
- Snow, B. & Snow, D. (1984) Long-term defence of fruit by mistle thrushes *Turdus viscivorus*. *Ibis*, **126**, 39–49.
- Snow, B. & Snow, D. (1988) *Birds and berries*. Poyser, Calton, UK.
- Sork, V., Nason, J., Campbell, D. & Fernández, J. (1999) Landscape approaches to historical and contemporary gene flow in plants. *Trends In Ecology & Evolution*, **14**, 224–224.
- Streiff, R., Ducoussو, A., Lexer, C., Steinkellner, H., Gloessl, J. & Kremer, A. (1999) Pollen dispersal inferred from paternity analysis in a mixed oak stand of *Quercus robur* L. and *Q. petraea* (Matt.) Liebl. *Molecular Ecology*, **8**, 831–841.

- Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D. (2005) The importance of long-distance dispersal in biodiversity conservation. *Diversity And Distributions*, **11**, 173–181, doi:10.1111/j.1366-9516.2005.00156.x.
- Traveset, A., González-Varo, J.P. & Valido, A. (2012) Long-term demographic consequences of a seed dispersal disruption. *Proceedings Of The Royal Society B-Biological Sciences*, doi:10.1098/rspb.2012.0535.
- Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoní, K., Bonte, D., Boulangéat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M. & Bullock, J.M. (2013) Dispersal and species' responses to climate change. *Oikos*, **122**(11), 1532–1540, doi:10.1111/j.1600-0706.2013.00399.x.
- Urban, D. & Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology*, **82**, 1205–1218.
- vander Wall, S. & Longland, W. (2004) Diplochory: are two seed dispersers better than one? *Trends In Ecology & Evolution*, **19**, 155–161, doi:10.1016/j.tree.2003.12.004.
- Waples, R. & Gaggiotti, O. (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Molecular Ecology*, **15**, 1419–1439, doi:10.1111/j.1365-294X.2006.02890.x.
- Westcott, D.A., Bentupperbaumer, J., Bradford, M.G. & McKeown, A. (2005)

Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia*, **146**, 57–67.

Wheelwright, N. (1991) How long do fruit-eating birds stay in the plants where they feed? *Biotropica*, **23**(1), 29–40.

Wright, S. (1943) Isolation by distance. *Genetics*, **28**, 114–138.

Wright, S. (1946) Isolation by distance under diverse systems of mating. *Genetics*, **31**, 39–59.

Wright, S. (1969) *Evolution and the genetics of populations. Vol. 2: The theory of gene frequencies*. University of Chicago Press, Chicago, USA.

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

⁴⁷² **Figure 1.** The two approaches used in analyses of dispersal processes in plants. A,
⁴⁷³ the forward approach attempts to track the dispersal events away from the known
⁴⁷⁴ sources, e.g., by tracking the movement patterns of frugivores as they leave fruiting
⁴⁷⁵ plants after feeding (i.e., the Lagrangian approach; Nathan *et al.*, 2003). B, the
⁴⁷⁶ backward approach attempts to reconstruct the most likely source of a dispersed
⁴⁷⁷ propagule by inferring the sources given the propagule delivery pattern, the fecun-
⁴⁷⁸ dity of potential sources, and the dispersal function (i.e., the Eulerian approach).
⁴⁷⁹ The main technical challenge in A is to sample enough dispersal events away from
⁴⁸⁰ the source to be able to fully characterize the tail (long-distance dispersal, LDD,
⁴⁸¹ events) of the dispersal function. In B, the main challenge is to have a robust
⁴⁸² sampling scheme with propagule collectors (e.g., seed traps) and a good charac-
⁴⁸³ terization of the potential sources to derive robust estimates of the actual sources
⁴⁸⁴ with inverse-modeling techniques.

⁴⁸⁵

⁴⁸⁶ **Figure 2.** Schematic representation of different types of long-distance dispersal
⁴⁸⁷ events in relation to the geographical limits of local populations (dashed lines)
⁴⁸⁸ and the genetic neighborhood area N_e^b (grey area) of specific individual plants
⁴⁸⁹ (squares). Dispersal events (arrows) can be classified depending on their actual
⁴⁹⁰ incidence on propagule movement outside these spatially-explicit reference areas
⁴⁹¹ (Table 1). Strict-sense long-distance dispersal events (LDD_{ss}) just include the
⁴⁹² LDD events that disseminate propagules out of *both* the population and genetic

493 neighborhood boundaries. A, the neighborhood area is included within the geo-
494 graphic limits of the population, with some dispersal events potentially contribut-
495 ing local LDD; B, the neighborhood area is much larger than the geographic limits
496 of the population. Both LDD_{ss} and LDD_{loc} may contribute genetic novelty by
497 moving propagules outside the N_e^b area or the population limit, area or both.

498

499 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function
500 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In
501 red, left (inset), frequencies of within-population dispersal events inferred from di-
502 rect assignment based on seed endocarp genotypes and maternal trees genotypes.
503 Larger frame, left, contributions of four functional frugivore groups (small birds,
504 medium- and large-sized birds, and mammals) to seed dissemination and propor-
505 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,
506 those not matching any maternal tree in the study population) (Jordano *et al.*,
507 2007).

508

509 **Figure 4.** Differential contributions of functional groups of frugivores to the
510 four combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1.
511 These result from dissemination within (yellow) or outside (blue) the population
512 geographic limits; within-population dispersal events can either be short-distance
513 (SDD_{loc}) or local LDD (LDD_{loc}) depending on the size of the genetic neighborhood.
514 Dispersal outside the local population can entail short-distance dispersal, if within
515 the genetic neighborhood area limits (SDD_{neigh}) (yellow) or represent strict-sense

₅₁₆ LDD (LDD_{ss}) (blue).

₅₁₇

518 **Online Support Material and data accessibility**

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







