

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

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## Abstract

- 1    1. Dispersal is a key individual-based process influencing many life-history at-  
2 tributes, scaling up to population-level properties (e.g., metapopulation connec-  
3 tivity). A persistent challenge in dispersal ecology has been the robust characteri-  
4 zation of dispersal functions (kernels), a fundamental tool to predict how dispersal  
5 processes respond under global change scenarios. Especially the rightmost tail  
6 of these functions, i.e. the long-distance dispersal (LDD) events, are difficult to  
7 characterize empirically and to model in realistic ways.
- 8    2. But, when is it a LDD event? In the specific case of plants, dispersal has three  
9 basic components: 1) a distinct (sessile) source, the maternal plant producing  
10 the fruits or the paternal tree acting as a source of pollen; 2) a distance 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

## <sup>28</sup> Introduction

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

<sup>46</sup> The movement of pollen and seeds by animals and its consequences have intrigued  
<sup>47</sup> population geneticists and field ecologists since the infancy of both research dis-  
<sup>48</sup> ciplines. Each has generated an impressive body of theoretical and empirical re-  
<sup>49</sup> 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 continental  
56 areas in response to climate modification (Clark *et al.*, 1998; Clark, 1998), among  
57 other persisting issues. This conceptual isolation has been exacerbated by techni-  
58 cal difficulties for the robust characterization of dispersal events, especially those  
59 involving movement over long-distances (long-distance dispersal, LDD). LDD is a  
60 characteristically extreme event of propagule movement in any plant population,  
61 typically occurring with an extremely low probability but potentially reaching  
62 an extremely long distance. Some progress has recently been made through the  
63 fast-paced implementation of molecular tools in ecological research labs and the  
64 availability of cutting-edge technology for biotelemetry applications. But much of  
65 the population geneticist and ecologist communities remains unaware of the state  
66 of the art in each other and likely under-appreciates their potential to validate  
67 and enrich dispersal studies (Jones & Muller-Landau, 2008). In particular, LDD  
68 events remain difficult to assess, both technically- with serious methodological  
69 problems for its reliable estimation- and conceptually. Our aim here is to review  
70 the LDD concept with a specific emphasis on dispersal of plant propagules (seeds  
71 and pollen), providing an extended definition that might be helpful in the robust  
72 quantification of LDD events.

While my main focus is on population-level scenarios and the role of animal vectors, recent research has shown how relevant is habitat and landscape context in determining the occurrence and directionality of LDD (e.g. Schurr et al. 2008 J Ecol; Carlo et al. 2013). On the other hand, dealing with habitat effects seems obligated if aimed to discuss global change drivers (i.e. habitat loss and fragmentation). Two main conceptual approaches have been used to assess dispersal (Fig. 1). The forward approach attempts to track the dispersal events away from the known sources, e.g., by tracking the movement patterns of frugivores as they leave fruiting plants after feeding (Fig. 1A). This is the main approach used in the movement ecology framework (Nathan *et al.*, 2008a), with extensive application to animal movement based on the use of advanced biotelemetry. The backward approach attempts to reconstruct the most likely source of a dispersed propagule by inferring the sources given the propagule delivery pattern, the fecundity of potential sources, and the dispersal function (Fig. 1B), i.e., by using an inverse modeling approach. The main technical challenge in Fig. 1A is to sample enough dispersal events away from the source to be able to fully characterize the tail (LDD events) of the dispersal function. In Fig. 1B, the main challenge is to have a robust sampling scheme with propagule collectors (e.g., seed traps) and a good characterization of the potential sources to derive robust estimates of the actual sources. Both approaches are limited logically by the difficulties to sample the vast areas required to assess LDD events from the focal source population.

LDD events have two key characteristics that make them extremely important for population dynamics, yet being very difficult to characterize: LDD events are in-

frequent, 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. Previous approaches (e.g., Nathan, 2006; Schurr *et al.*, 2009) include both absolute and proportional definitions to characterize LDD events. This means providing information about the absolute distances moved by a given percentile of the events and/or providing data on the proportion of events exceeding a given distance threshold (Nathan *et al.*, 2008b). The exact proportional or absolute thresholds selected remain arbitrary, as no reference spatial frame is provided within the definition of LDD. This leaves the consideration of LDD as an extreme form of context-dependent phenomenon, strongly dependent upon the scale of the biological process studied (Kinlan *et al.*, 2005) and of the specific organism considered. For example, Kinlan *et al.* (2005) used a spatial reference frame to characterize LDD events of marine organisms, where sedentary adults and larvae differ enormously in the spatial scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent and reach of LDD events requires reference to an explicit spatial frame or "local" scale (Kinlan *et al.*, 2005).

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

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

<sup>140</sup> **LDD within a demo-genetic perspective: a taxonomy of dis-**

<sup>141</sup> **persal events**

<sup>142</sup> Here I propose an explicit definition of LDD and what constitutes a LDD event.

<sup>143</sup> Previous definitions of dispersal patterns emphasized only their distance compo-

<sup>144</sup> nents and characterized LDD events basically in terms of geographic distance be-

<sup>145</sup> tween a dispersed propagule (or an established early seedling) and its most likely

<sup>146</sup> maternal or paternal (in case of pollen) source. Absolute and proportional defini-

<sup>147</sup> tions for the LDD events have been proposed depending on arbitrary thresholds

<sup>148</sup> of either the distance beyond which a dispersal event is LDD or the proportion of

<sup>149</sup> events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).

<sup>150</sup> Thus, two key biological aspects of LDD events involve the transport of propag-

<sup>151</sup> ules outside a reference area: moving away from the source stand or population,

<sup>152</sup> and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These

<sup>153</sup> two movements do not necessarily concur: a propagule may move over a very

<sup>154</sup> long distance yet still be disseminated within the reach of the neighborhood where

<sup>155</sup> parental individuals mate. Within a demo-genetic framework it is easy to envision

<sup>156</sup> a combination of situations concerning the spatial scale of the dispersal processes

<sup>157</sup> (Table 1) and unambiguously define different types of LDD events. The idea that

<sup>158</sup> dispersal occurs in reference to these two spatial reference frames, i.e., the popu-

<sup>159</sup> lation or stand and the genetic neighborhood area, is motivated by the fact that

<sup>160</sup> dispersal entails the movement of both an individual propagule (i.e., a pollen grain

<sup>161</sup> or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or

<sup>162</sup> a seed genotype). Thus, dispersal entails simultaneous demographic and genetic

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

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

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

209 the genetic neighborhood boundary ( $LDD_{ss}$ ) (Table 1, Fig. 2A).  
 210 While both  $SDD_{loc}$  and  $LDD_{loc}$  can be crucial for assuring the local persistence of  
 211 populations,  $LDD_{neigh}$  and  $LDD_{ss}$  would be extremely important contributors to  
 212 the structuring of genetic pools, realized gene flow, and maintaining connectivity  
 213 in metapopulation scenarios. I argue that both the demographic and the genetic  
 214 references are relevant for a proper definition of LDD.

## 215 Individual and Population Neighborhoods as Reference

216 Continuous populations can be modeled with the concepts of isolation by distance  
 217 and neighborhood size(Wright, 1943, 1946). The former refers to the case that  
 218 limited gene dispersal in continuous populations produces demes that are panmic-  
 219 tic internally, but are isolated to some extent from adjacent demes. Each group of  
 220 reproducing individuals is the neighborhood, defined as the population of a region  
 221 in a continuum, from which the parents of individuals born near the center may  
 222 be treated as if drawn at random (Wright, 1969). The importance and influence of  
 223 the dispersal process in determining the size of the neighborhood is given by this  
 224 equation, which shows how the spatial dispersion (pattern of spatial distribution)  
 225 of the population influences the effective population size. This influence on the  
 226 effective size is given by:

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

where  $\delta$  is the density of adults per unit area and  $\sigma$  is the standard deviation of the distance between birth and breeding sites. This formulation is often called the neighborhood size and assumes a normal distribution of distances between parents and offspring (out in a perfect circular shape from the source). Thus, changes in the variance of dispersal distance can affect  $N_e^b$  (highly clumped populations will have reduced  $N_e^b$ ). This is the basic model of "Isolation by Distance" proposed by Wright (1943, 1946). Under this type of model, migration (gene flow) is given by the variance in dispersal, and not by the proportion of the population that is composed of migrants (denoted  $m$ ), as is the case with island models (Slatkin, 1985). With enough distance separating them, two plant individuals have a low probability of mating and can be considered members of distinct genetic populations even if they are not located in geographically distinct populations.

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

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

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

Neighborhood size in plants can be estimated by marking pollen and seeds with fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However,

247 these methods do not measure effective pollen or seed movement, but they may  
248 be combined with genetic analysis to assess genetic identity and relatedness with  
249 hypervariable DNA markers (Levin, 1988; Nason *et al.*, 1998; Godoy & Jordano,  
250 2001) to achieve reliable estimates of both effective population size and neighbor-  
251 hood area.

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

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

## 267 Empirical analysis of contributions to LDD

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

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

286 To a large extent, short-distance dispersal events (strict-sense,  $SDD_{loc}$  events)  
287 are contributed by small- and medium-sized (*Turdus*) frugivorous birds (Table 2).  
288 Given the relatively reduced  $N_e^b$  area of *P. mahaleb* (Suppl. Mat. Table S1),

< 1km<sup>2</sup>, 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).

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

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

Long-distance dispersal (LDD) is a major component of the population dynamics, genetic structure, and biogeographic history of plant species. It determines the colonization ability of new habitats and the possibilities for fragmented populations to sustain a cohesive metapopulation by immigration-emigration dynamics that rely on LDD events (Nathan *et al.*, 2008b; Schurr *et al.*, 2009). Yet our current understanding of the extent, frequency, and consequences of LDD is very limited. On one hand, theoretical models fail to predict accurately the behavior of the tail of the dispersal functions, and thus fail to predict very basic properties of LDD.

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

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

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

320 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal  
321 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect  
322 that this extreme variation translates in an ample pattern of foraging modes, move-  
323 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results  
324 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the  
325 functional roles of frugivore species in terms of contributions to LDD events are  
326 structured in two distinct groups: small-bodied frugivores, with substantial con-  
327 tributions to SDD events, and large-bodied species with a disproportionate contri-  
328 bution to LDD events. Both components of this sort of diplochorous (vander Wall  
329 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with  
330 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied  
331 frugivores largely contribute the short-distance dispersal key to support *in situ*  
332 recruitment and population persistence. Yet the large-bodied frugivores distinctly

333 contribute LDD events that sustain the connectivity of metapopulation scenarios  
334 (Urban & Keitt, 2001). As shown in Table 1, SDD and LDD events can be more  
335 complex when we consider the contributions to gene flow via seed and the conse-  
336 quences in terms of structure and spatial distributions of the genetic pools. For  
337 example, local, within-population, dispersal events may vary enormously in terms  
338 of genetic effects and local structuring of the genetic pools depending on whether  
339 they specifically contribute  $SDD_{loc}$  or instead,  $LDD_{loc}$ . Note that only the latter  
340 actually contribute erasing any form of local genetic structure by contributing to  
341 increased genetic neighborhoods.

342 A number of classic studies have demonstrated that the activity of large frugivores  
343 may also significantly contribute to SDD events and inefficient dispersal because  
344 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,  
345 frequent revisit of same trees and perches, etc., resulting in substantial SDD  
346 events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright,  
347 1991). Yet these large-bodied frugivores are crucial for both  $LDD_{loc}$  and  $LDD_{ss}$ ,  
348 given that extensive movement patterns and extremely large foraging ranges may  
349 frequently contribute dissemination beyond distance thresholds defined with ei-  
350 ther spatial landscape or genetic references. Recent analyses of the movement  
351 ecology of large frugivores, coupled with results of their seed dispersal services  
352 emphasize that LDD are by no means exceptional, either in terms of frequency  
353 and extent (e.g., Westcott *et al.*, 2005; Bueno *et al.*, 2013; Morales *et al.*, 2013;  
354 Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.)  
355 can contribute substantial  $LDD_{loc}$  events, i.e., local LDD events contributing to

356 erase local population genetic structuring, effectively increasing the size of genetic  
357 neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events  
358 are  $LDD_{loc}$  events. These birds are efficient seed dispersers of *P. mahaleb* and  
359 other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo  
360 *et al.*, 2013), also showing significant contributions of  $LDD_{ss}$  events.

361 Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed  
362 shadows, accurately tracked with DNA-based genotyping methods, thus reflect  
363 the complex effects of frugivore foraging, habitat preferences and heterogeneous  
364 landscapes. This situation is probably generalizable to other plant–frugivore in-  
365 teractions where the combined spatial dynamics of habitat use and digestion pro-  
366 cesses determine complex seed shadows (?Jordano *et al.*, 2007; Nathan *et al.*,  
367 2008b). Much of this complexity can be adequately handled by mechanistic mod-  
368 els (Nathan *et al.*, 2002) incorporating very simple rules (Guttal *et al.*, 2011).  
369 For example, earlier results (Jordano, 2007) showed that the dispersal distances  
370 contributed by *P. mahaleb* frugivores closely map the spacing patterns of fruiting  
371 trees, but only up to a certain distance ( $\leq 100$  m) (Fig. 10.3a in Jordano, 2007).  
372 Beyond this, frugivores were probably responding to other major landscape ele-  
373 ments (e.g. rock outcrops, forest edges, large patches of open grassland, etc) that  
374 cause the fat tail of the seed dispersal distribution, adding more frequent LDD  
375 events than expected from a Brownian random walk pattern generated by a track-  
376 ing of the crops of the fruiting trees. For instance, the long flights performed by *T.*  
377 *viscivorus* (Jordano & Schupp, 2000) frequently faced the pine forest edge, at dis-  
378 tances  $\geq 100$  m of most *P. mahaleb* fruiting trees. If these medium-sized birds are

379 selecting habitat with tall woody vegetation (e.g. pines  $\geq 6$  m height), then they  
380 should be perceiving a much more patchy landscape, and thus requiring longer  
381 flights, than for example, small warblers seeking vegetation cover  $<0.5$  m (Fig.  
382 10.3b in Jordano, 2007).

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

## 390 Challenges and future avenues for research

391 Pollen and seed dispersal in plants are essentially spatially-structured processes  
392 for which the outcomes of interactions with dispersal vectors is intimately linked  
393 to landscape features. Given this mechanistic link between the features of the  
394 vector and the environments where its displacement occurs (Nathan *et al.*, 2008a),  
395 consideration of landscape is key to understand the consequences of LDD events.  
396 Yet these consequences hit two central aspects of plant life-histories: the demo-  
397 graphic recruitment process (Harper, 1977), and the genetic signatures of pollen-  
398 and seed-mediated gene flow in complex landscapes (Sork *et al.*, 1999). Recent  
399 evidences point out that the selective extinction of large-bodied frugivores may

400 significantly impact plant populations dependent on frugivores both in terms of  
401 recruitment (Traveset *et al.*, 2012; Pérez-Méndez *et al.*, 2015) and genetic con-  
402 nectivity (Pérez-Méndez *et al.*, 2016). Frugivore downsizing represents a lasting  
403 challenge for the collapse of seed dispersal processes where  $LDD_{ss}$  events are cru-  
404 cial for population persistence and the cohesion of fragmented populations within  
405 metapopulation scenarios.

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

415 LDD, and its variation across coexisting plant species, could also have far-reaching  
416 consequences for community assembly and forest physiognomy. Yet very few pre-  
417 vious analyses addressed this point. Comparative information on LDD across  
418 species sharing a common environment have found strong differences in LDD po-  
419 tential among plants with different (e.g. Clark *et al.* 1999 Ecology; Martnez *et al.*  
420 2008 Oecologia) or even with the same dispersal syndrome (e.g. Garca *et al.* 2016  
421 Basic Applied Ecology).

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

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

Genetic neighborhood limit	Population geographic limit
Within	Within
Outside	Outside
Within	Local, short-distance dispersal, $SDD_{loc}$
Outside	Local, long-distance dispersal, $LDD_{loc}$
Within	Within neighborhood, long-distance dispersal, $LDD_{neigh}$
Outside	Strict sense long-distance dispersal, $LDD_{ss}$

**Table 2:** Relative frequencies of *Prunus mahaleb* seed dispersal events for different frugivore groups according to population area limits and genetic neighborhood limits. See Fig. 2 for a graphical representation of the four scenarios.  $N = 655$  seeds (see Table 1 in Jordano *et al.*, 2007). Given that the estimated neighborhood size is smaller than population area,  $LDD_{neigh}$  would be zero.

Frugivore group	Within-population, within-neighborhood $SDD_{loc}$	Within-population, long-distance $LDD_{loc}$	Outside-population, within-neighborhood $LDD_{neigh}$	Strict-sense long-distance $LDD_{ss}$	$N$ seeds
Small-birds	0.7842	0.0171	0.00	0.1986	292
<i>Turdus</i>	0.2370	0.5549	0.00	0.2081	173
Large-birds	0.0435	0.3913	0.00	0.5652	23
Mammals	0.0120	0.2455	0.00	0.7425	167

## Figures

439 **Figure 1.** The two approaches used in analyses of dispersal processes in plants.  
440 A, the forward approach attempts to track the dispersal events away from the  
441 known sources, e.g., by tracking the movement patterns of frugivores as they leave  
442 fruiting plants after feeding. B, the backward approach attempts to reconstruct  
443 the most likely source of a dispersed propagule by inferring the sources given the  
444 propagule delivery pattern, the fecundity of potential sources, and the dispersal  
445 function. The main technical challenge in A is to sample enough dispersal events  
446 away from the source to be able to fully characterize the tail (long-distance dis-  
447 persal, LDD, events) of the dispersal function. In B, the main challenge is to have  
448 a robust sampling scheme with propagule collectors (e.g., seed traps) and a good  
449 characterization of the potential sources to derive robust estimates of the actual  
450 sources with inverse-modeling techniques.

451

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

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

463

464 **Figure 3.** Empirical frequency distributions of seed dispersal events as a function  
465 of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In  
466 red, left (inset), frequencies of within-population dispersal events inferred from di-  
467 rect assignment based on seed endocarp genotypes and maternal trees genotypes.  
468 Larger frame, left, contributions of four functional frugivore groups (small birds,  
469 medium- and large-sized birds, and mammals) to seed dissemination and propor-  
470 tional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e.,  
471 those not matching any maternal tree in the study population) (Jordano *et al.*,  
472 2007).

473

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

482

483 **Online Support Material and data accessibility**

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







