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

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Abstract

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

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

²⁵ Introduction

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

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

‘parallel worlds’ and the great synergistic potential of population genetics and demography for the study of plant dispersal by animals remains little explored. Knowledge gaps still having the imprint of this conceptual disconnection include the idea of long distance dispersal, and the paradoxes of forest fragmentation effects on genetic diversity (Kramer *et al.*, 2008), survival and persistence of relict tree species (Hampe & Jump, 2011), rapid post-Pleistocene recolonization of vast continental areas in response to climate modification (Clark *et al.*, 1998; Clark, 1998), among other persisting issues. This conceptual isolation has been exacerbated by technical difficulties for the robust characterization of dispersal events, especially those involving movement over long-distances (long-distance dispersal, LDD). LDD is a characteristically extreme event of propagule movement in any plant population, typically occurring with an extremely low probability but potentially reaching an extremely long distance. Some progress has recently been made through the fast-paced implementation of molecular tools in ecological research labs and the availability of cutting-edge technology for biotelemetry applications [REF]. But much of the population geneticist and ecologist communities remains unaware of the state of the art in each other and likely under-appreciates their potential to validate and enrich dispersal studies (Jones & Muller-Landau, 2008). In particular, LDD events remain difficult to assess, both technically- with serious methodological problems for its reliable estimation- and conceptually. Our aim here is to review the LDD concept with a specific emphasis on dispersal of plant propagules (seeds and pollen), providing an extended definition that might be helpful in the robust quantification of LDD events.

Two main conceptual approaches have been used to assess dispersal (Fig. 1). The “forward” approach attempts to track the dispersal events away from the known sources, e.g., by tracking the movement patterns of frugivores as they leave fruiting plants after feeding (Fig. 1A). This is the main approach used in the movement ecology framework (Nathan *et al.*, 2008a), with extensive application to animal movement based on the use of advanced biotelemetry. The “backward” approach attempts to reconstruct the most likely source of a dispersed propagule by inferring the sources given the propagule delivery pattern, the fecundity of potential sources, and the dispersal function (Fig. 1B), i.e., by using an inverse modeling approach. The main technical challenge in Fig. 1A is to sample enough dispersal events away from the source to be able to fully characterize the tail (LDD events) of the dispersal function. In Fig. 1B, the main challenge is to have a robust sampling scheme with propagule collectors (e.g., seed traps) and a good characterization of the potential sources to derive robust estimates of the actual sources. Both approaches are limited logically by the difficulties to sample the vast areas required to assess LDD events from the focal source population.

No explicit definition of what constitutes an LDD event exists. Previous approaches (e.g., Nathan, 2006; Schurr *et al.*, 2009) include both absolute and proportional definitions to characterize LDD events. This means providing information about the absolute distances moved by a given percentile of the events and/or providing data on the proportion of events exceeding a given distance threshold (Nathan *et al.*, 2008b). The exact proportional or absolute thresholds selected remain arbitrary, as no reference spatial frame is provided within the

93 definition of LDD. This leaves the consideration of LDD as an extreme form of
94 context-dependent phenomenon, strongly dependent upon the scale of the biological
95 process studied (Kinlan *et al.*, 2005). For example, Kinlan *et al.* (2005) used
96 a spatial reference frame to characterize LDD events of marine organisms, where
97 sedentary adults and larvae differ enormously in the spatial scales of their dispersal
98 (D'Aloia *et al.*, 2013). Therefore, any measure of extent and reach of LDD events
99 requires reference to an explicit spatial frame or "local" scale (Kinlan *et al.*, 2005).

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

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

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

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

124 Here we propose an explicit definition of LDD and what constitutes a LDD event.
125 Previous definitions of dispersal patterns emphasized only their distance compo-
126 nents and characterized LDD events basically in terms of geographic distance be-
127 tween a dispersed propagule (or an established early seedling) and its most likely
128 maternal or paternal (in case of pollen) source. Absolute and proportional defini-
129 tions for the LDD events have been proposed depending on arbitrary thresholds
130 of either the distance beyond which a dispersal event is LDD or the proportion of
131 events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b).
132 Thus, two key biological aspects of LDD events involve the transport of propag-
133 ules outside a reference area: moving away from the source stand or population,
134 and moving away from the area where relatives stand (Kinlan *et al.*, 2005). These
135 two movements do not necessarily concur: a propagule may move over a very
136 long distance yet still be disseminated within the reach of the neighborhood where

parental individuals mate. Within a demo-genetic framework it is easy to envision a combination of situations concerning the spatial scale of the dispersal processes (Table 1) and unambiguously define different types of LDD events. The idea that dispersal occurs in reference to these two spatial reference frames, i.e., the population or stand and the genetic neighborhood area, is motivated by the fact that dispersal entails the movement of both an individual propagule (i.e., a pollen grain or a seed) and a distinct set of genes (i.e., the male genotype in case of pollen, or a seed genotype). Thus, dispersal entails simultaneous demographic and genetic effects through recruitment of new individuals in the population and through contributions to gene flow (Harper, 1977). When considered its combined influence on demography and population genetics, the concept of LDD nicely bridges these two paradigms embedded in the biological definition of population (Waples & Gaggiotti, 2006).

Two important components of plant dispersal ecology concern the movement of propagules away from the source population, a type of dispersal relevant to colonization ability and range expansion (Howe & Miriti, 2004), and the movement away from the location of close relatives, i.e., a movement away from the genetic neighborhood (Hardesty *et al.*, 2006; Jones & Muller-Landau, 2008). If we classify dispersal events according to these two spatial frameworks (Table 1) we end up with four distinct types of events depending on whether or not dispersed propagules are disseminated within these reference areas. Setting the limits of a population can be problematic (Waples & Gaggiotti, 2006) yet we can identify with relative ease the geographical limits of plant stands, patches, habitat spots or other types

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

A second consideration in terms of spatial boundaries, with effects on dispersal patterns, is the genetic neighborhood area N_b , i.e., the spatial extent including a subset of panmictic individuals within a population (Wright, 1943, 1946). Thus, the N_b area can be equal to the whole extent of the population whenever the population is unstructured and there is evidence for random mating events among all the individuals. However, most populations and stands of long-lived trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006), where relatively long distances may separate groups of individuals within the same population. In these cases we might expect N_b area to be substantially smaller than the total population area. Therefore, at least four possible scenarios exist with distinct implications in terms of consequences for dispersal (Table 1). In the case of dispersal events not extending beyond the geographic limits of the population or reference area, actual LDD events may involve dissemination beyond a reduced neighborhood area that is smaller than the geographic extent of the population, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig.

183 2A). Actual short-distance dispersal would then involve those situations where the
184 propagule is disseminated within *both* the population limits and the genetic neigh-
185 borhood boundary (SDD_{loc}). Along a similar reasoning, dispersal events outside
186 the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this is
187 expected in cases where the genetic neighborhoods are extensive, going beyond the
188 geographic limits of local populations, as in fig trees (Nason *et al.*, 1998), generat-
189 ing LDD events within the genetic neighborhood (LDD_{neigh}). Finally, strict-sense
190 LDD events would involve dissemination outside *both* the population limits and
191 the genetic neighborhood boundary (LDD_{ss}) (Table 1, Fig. 2A).

192 While both SDD_{loc} and LDD_{loc} can be crucial for assuring the local persistence of
193 populations, LDD_{neigh} and LDD_{ss} would be extremely important contributors to
194 the structuring of genetic pools, realized gene flow, and maintaining connectivity
195 in metapopulation scenarios. We argue that both the demographic and the genetic
196 references are relevant for a proper definition of LDD.

197 Individual and Population Neighborhoods as Reference

198 Continuous populations can be modeled with the concepts of isolation by distance
199 and neighborhood size(Wright, 1943, 1946). The former refers to the case that
200 limited gene dispersal in continuous populations produces demes that are panmic-
201 tic internally, but are isolated to some extent from adjacent demes. Each group of
202 reproducing individuals is the neighborhood, defined as the population of a region
203 in a continuum, from which the parents of individuals born near the center may

204 be treated as if drawn at random (Wright, 1969). The importance and influence of
 205 the dispersal process in determining the size of the neighborhood is given by this
 206 equation, which shows how the spatial dispersion (pattern of spatial distribution)
 207 of the population influences the effective population size. This influence on the
 208 effective size is given by:

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

209 where δ is the density of adults per unit area and σ is the standard deviation of
 210 the distance between birth and breeding sites. This formulation is often called the
 211 neighborhood size and assumes a normal distribution of distances between parents
 212 and offspring (out in a perfect circular shape from the source). Thus, changes in
 213 the variance of dispersal distance can affect N_e^b (highly clumped populations will
 214 have reduced N_e^b). This is the basic model of "Isolation by Distance" proposed by
 215 Wright (1943, 1946). Under this type of model, migration (gene flow) is given by
 216 the variance in dispersal, and not by the proportion of the population that is com-
 217 posed of migrants (denoted m), as is the case with island models (Slatkin, 1985).
 218 With enough distance separating them, two plant individuals have a low probabil-
 219 ity of mating and can be considered members of distinct genetic populations even
 220 if they are not located in geographically distinct populations.
 221 For plants, gene flow may be accomplished by both seeds and pollen, so the vari-
 222 ance may be decomposed to account for different patterns of seed and pollen
 223 dispersal, and to take into account the mating system (outcrossing rate, t). Thus,

224 neighborhood size can be defined with the following equation (Crawford 1984) :

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

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

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

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

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

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

249 **Empirical analysis of contributions to LDD**

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

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

265 two species of medium-sized frugivorous birds, mistle thrushes (*T. viscivorus*),
 266 and carrion crows (*Corvus corone*); and a pool of small-sized frugivorous birds,
 267 including warblers, redstarts, and robins (Jordano *et al.*, 2007).

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

279 Long-Distance Dispersal: the ecology of extreme events

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

286 On one hand, theoretical models fail to predict accurately the behavior of the tail
287 of the dispersal functions, and thus fail to predict very basic properties of LDD. On
288 the other hand, we still have very limited documentation of actual LDD events in
289 natural populations and we still see LDD as a sporadic, rarely far-reaching process
290 still marked with the stamp of natural history curiosity.

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

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

298 The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal
299 species spanning a wide size range, ca. 12-14000 g in body mass. We might expect
300 that this extreme variation translates in an ample pattern of foraging modes, move-
301 ment distances, and fruit/seed processing (Jordano & Schupp, 2000). If the results
302 for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the
303 functional roles of frugivore species in terms of contributions to LDD events are
304 structured in two distinct groups: small-bodied frugivores, with substantial con-
305 tributions to SDD events, and large-bodied species with a disproportionate contri-
306 bution to LDD events. Both components of this sort of diplochorous (vander Wall
307 & Longland, 2004) dispersal system are very frequent in fleshy-fruited plants with
308 diversified frugivore assemblages (Galetti *et al.*, 2013). In such cases, small-bodied

309 frugivores largely contribute the short-distance dispersal key to support *in situ*
310 recruitment and population persistence. Yet the large-bodied frugivores distinctly
311 contribute LDD events that sustain the connectivity of metapopulation scenarios
312 (Urban & Keitt, 2001). As shown in Table 1, SDD and LDD events can be more
313 complex when we consider the contributions to gene flow via seed and the conse-
314 quences in terms of structure and spatial distributions of the genetic pools. For
315 example, local, within-population, dispersal events may vary enormously in terms
316 of genetic effects and local structuring of the genetic pools depending on whether
317 they specifically contribute SDD_{loc} or instead, LDD_{loc} . Note that only the latter
318 actually contribute erasing any form of local genetic structure by contributing to
319 increased genetic neighborhoods.

320 A number of classic studies have demonstrated that the activity of large furgivores
321 may also significantly contribute to SDD events and inefficient dispersal because
322 of, i.e., territorial defence, short gut retention times relative to on-tree foraging,
323 frequent revisit of same trees and perches, etc., resulting in substantial SDD
324 events (Pratt & Stiles, 1983; Pratt, 1984; Snow & Snow, 1984, 1988; Wheelwright,
325 1991). Yet these large-bodied frugivores are crucial for both LDD_{loc} and LDD_{ss} ,
326 given that extensive movement patterns and extremely large foraging ranges may
327 frequently contribute dissemination beyond distance thresholds defined with ei-
328 ther spatial landscape or genetic references. Recent analyses of the movement
329 ecology of large frugivores, coupled with results of their seed dispersal services
330 emphasize that LDD are by no means exceptional, either in terms of frequency
331 and extent (e.g., Westcott *et al.*, 2005; Bueno *et al.*, 2013; Morales *et al.*, 2013;

332 Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.)
333 can contribute substantial LDD_{loc} events, i.e., local LDD events contributing to
334 erase local population genetic structuring, effectively increasing the size of genetic
335 neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events
336 are LDD_{loc} events. These birds are efficient seed dispersers of *P. mahaleb* and
337 other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo
338 *et al.*, 2013), also showing significant contributions of LDD_{ss} events.

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

346 Challenges and future avenues for research

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

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

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

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

- 376 urgency to assess how forest loss, defaunation, genetic purging due to logging, etc.,
377 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

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

400

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

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

412

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

422

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

431

432 **Online Support Material and data accessibility**

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







