

## DISPERSAL PROCESSES DRIVING PLANT MOVEMENT: RANGE SHIFTS IN A CHANGING WORLD

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

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## Summary

1. Dispersal is a key individual-based process influencing many life-history attributes and scaling up to population-level properties (e.g. metapopulation connectivity). A persistent challenge in dispersal ecology has been the robust characterization of dispersal functions (kernels), a fundamental tool to predict how dispersal processes respond under global change scenarios. Particularly, the rightmost tail of these functions, that is the long-distance dispersal (LDD) events, are difficult to characterize empirically and to model in realistic ways.

2. But, when is it a LDD event? In the specific case of plants, dispersal has three basic components: (i) a distinct (sessile) source, the maternal plant producing the fruits or the paternal tree acting as a source of pollen; (ii) a distance component between source and target locations; and (iii) a vector actually performing the movement entailing the dispersal event. Here, I discuss operative definitions of LDD based on their intrinsic properties: (i) events crossing geographic boundaries among stands; and (ii) events contributing to effective gene flow and propagule migration.

3. Strict-sense long-distance dispersal involves movement both outside the stand geographic limits and outside the genetic neighbourhood area of individuals. Combinations of propagule movements within/outside these two spatial reference frames result in four distinct modes of LDD.

4. *Synthesis.* I expect truncation of seed dispersal kernels to have multiple consequences on demography and genetics, following to the loss of key dispersal services in natural populations. Irrespective of neighbourhood sizes, loss of LDD events may result in more structured and less cohesive genetic pools, with increased isolation by distance extending over broader areas. Proper characterization of the LDD events helps to assess, for example, how the ongoing defaunation of large-bodied frugivores pervasively entails the loss of crucial LDD functions.

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

## Introduction

Dispersal is a key individual-based process influencing many life-history attributes and scaling up to population-level properties (e.g. metapopulation connectivity; Cousens, Dytham & Law 2008). In the specific case of plants, largely sessile organisms, dispersal has three basic components: (i) a distinct (sessile) source, the maternal plant producing the fruits or the paternal tree acting as a source of pollen; (ii) a distance component between source and target locations; and (iii) a vector actually performing the movement entailing the dispersal event. While realized dispersal also depends upon stages subsequent to dissemination (e.g. successful germination and

seedling establishment; Schupp 1995), the three previous components fully characterize the dispersal process per se. Therefore, plant movement differs in important natural history details from animal dispersal, yet both can be assessed within a common conceptual framework (e.g. Nathan 2006). Characteristically, animal-assisted plant dispersal has three distinct, highly integrated components missing in the process of animal dispersal: the properties of the source (parental) plant, that mediate in the foraging of the animal vector (pollinator or frugivore), the intrinsic properties of the propagule and the functional characteristics of the animal vector who performs the movement (Nathan *et al.* 2008a).

The movement of pollen and seeds by animals and its consequences have intrigued population geneticists and field ecologists since the infancy of both research disciplines. Each has

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generated an impressive body of theoretical and empirical research through the past decades, yet advances have long been coexisting 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), and rapid post-Pleistocene recolonization of vast continental areas in response to climate modification (Clark 1998; Clark *et al.* 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). Some progress has recently been made through the fast-paced implementation of molecular tools in ecological research laboratories and the availability of cutting-edge technology for biotelemetry applications. But much of the population geneticist and ecologist communities remains unaware of the state of the art in each other and likely underappreciates 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. My aim 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 LD events.

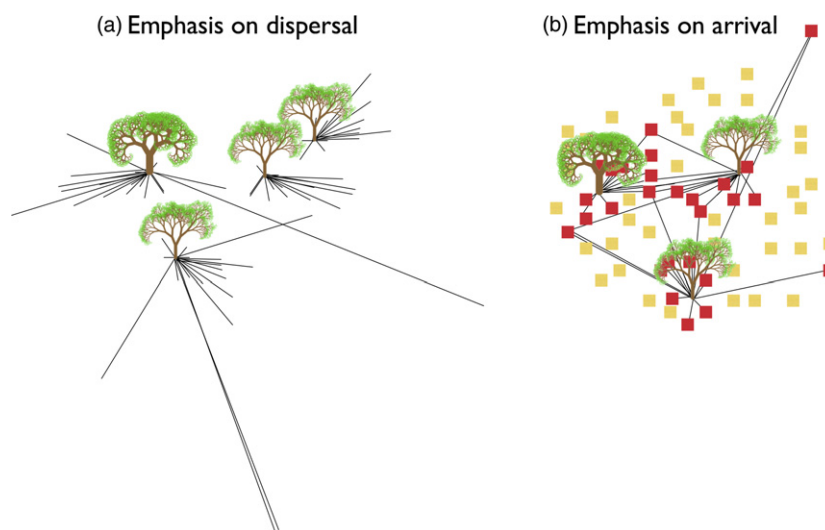
An added difficulty to bridge ecological processes of dispersal with their genetic consequences is the fact that dispersal per se does not necessarily imply realized gene flow (Mallet 2001). Yet in the genetics literature, the inescapable difficulty to robustly estimate the standard deviation of parent–offspring distances,  $\sigma_x$ , as a proxy for realized gene flow distance, is analogous to the ecological scenario. Strongly leptokurtic distributions of dispersal distances would lead to severe underestimation of  $\sigma_x$ , for example in mark–recapture studies limited to local sites where the long tail of LDD events escapes detection beyond the edges of the study area (Mallet 2001). Thus, fat-tailed distributions of dispersal distances tend to homogenize distant populations, leading to stronger reductions in  $F_{st}$  than expected from local records of dispersal events (Rousset 1997). Despite such difficulties, comparative approaches (e.g. Bohonak 1999) demonstrate that dispersal makes a measurable contribution to population genetic differentiation in most animal species in nature and that gene flow estimates are rarely so overwhelmed by population history, departures from equilibrium or other microevolutionary forces as to be uninformative. The relationship between dispersal and realized gene flow is key to understand how migration interacts with drift in driving the dynamics of genetic pools and population differentiation (Garant, Forde & Hendry 2007).

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 (Schurr, Steinitz &

Nathan 2008; 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 (Lagrangian) approach attempts to track the dispersal events away from the known sources, for example 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), that is using an inverse-modelling 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 logistically by the difficulties to sample the vast areas required to assess LDD events from the focal source population.

Long-distance dispersal 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). Long-distance dispersals 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, Nunez & Lawler 2012). With their influence on the structure of genetic pools, LDD events can also drive population differentiation and speciation (Garant, Forde & Hendry 2007; Ronce 2007).

No explicit definition of what constitutes an LDD event exists. Long-distance dispersal is a characteristically extreme event of propagule movement in any plant or animal population, typically occurring with an extremely low probability but potentially reaching an extremely long distance. Previous approaches (e.g. Nathan 2006; Schurr *et al.* 2009) include both absolute and proportional definitions to characterize LDD events. This means providing information about the absolute distances moved by a given percentile of the events and/or providing data on the proportion of events exceeding a given distance threshold, that is an operational definition (Nathan *et al.* 2008b). The exact proportional or absolute thresholds selected remain somehow 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, Gaines &



**Fig. 1.** The two approaches used in analyses of dispersal processes in plants. (a) The forward approach attempts to track the dispersal events away from the known sources, for example by tracking the movement patterns of frugivores as they leave fruiting plants after feeding (i.e. the Lagrangian approach; Nathan *et al.* 2003). (b) 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 (i.e. the Eulerian approach). The main technical challenge in 'a' is to sample enough dispersal events away from the source to be able to fully characterize the tail (long-distance dispersal (LDD) events) of the dispersal function. In 'b', 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 with inverse-modelling techniques. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Lester 2005) and of the specific organism considered. For example, Kinlan, Gaines & Lester (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, Gaines & Lester 2005; Byrne *et al.* 2014).

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

Long-distance dispersal is currently one of the most debated topics in dispersal ecology; it defines the connectedness within the network of local populations and the possibilities for range expansion and successful colonization events. I propose a first demogenetically based, operational definition of what a LDD event actually is, and review existing empirical literature on distance thresholds from population and genetic perspectives. I also show how molecular tools have been used to identify the respective contributions of different animal species to the LDD portion of dispersal kernels of pollen and seeds by setting empirically derived distance

thresholds. Finally, I highlight potential applications of molecular markers beyond the quantification of just the dispersal distances that prevails in current studies, for example experimental approaches to assess dispersal limitation and Janzen–Connell effects.

### LDD within a demogenetic perspective: a taxonomy of dispersal events

Here, I propose an explicit definition of LDD and what constitutes a LDD event. Previous definitions of dispersal patterns emphasized only their distance components and characterized LDD events basically in terms of geographic distance between a dispersed propagule (or an established early seedling) and its most likely maternal or paternal (in case of pollen) source. Absolute and proportional definitions for the LDD events have been proposed depending on arbitrary thresholds of either the distance beyond which a dispersal event is LDD or the proportion of events occurring beyond a specific distance (Nathan 2005; Nathan *et al.* 2008b). Thus, two key biological aspects of LDD events involve the transport of propagules outside a reference area: moving away from the source stand or population, and moving away from the area where relatives stand (Kinlan, Gaines & Lester 2005). These two movements do not necessarily concur: a propagule may move over a very long distance yet still be disseminated within the reach of the neighbourhood where parental individuals mate. Within a demogenetic 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

**Table 1.** Types of dispersal as a function of population area limits and genetic neighbourhood limits

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

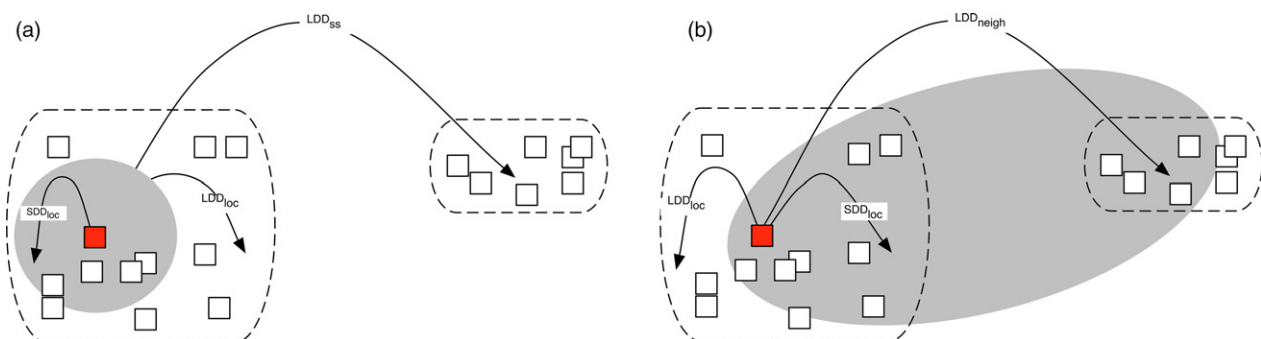
See Fig. 2 for a graphical representation of the four scenarios.

idea that dispersal occurs in reference to these two spatial reference frames, that is the population or stand and the genetic neighbourhood 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, that is a movement away from the genetic neighbourhood (Hardesty, Hubbell & Bermingham 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 geographic limits of plant stands, patches, habitat spots or other types of habitat or microhabitat discontinuities that determine landmark boundaries of biological significance (see Kinlan, Gaines & Lester 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 LDD events that end up with dissemination within or beyond, respectively, the stand or population geographic boundaries (Table 1;  $SDD_{loc}$  or  $LDD_{loc}$ ) (Fig. 2).

A second consideration in terms of spatial boundaries, with effects on dispersal patterns, is the genetic neighbourhood area  $N_e^b$ , that is the spatial extent including a subset of panmictic individuals within a population (Wright 1943, 1946). Thus, the  $N_e^b$  area can be equal to the whole extent of the population whenever the population is unstructured and there is evidence for random mating events among all the individuals. However, most populations and stands of long-lived trees show highly aggregated and clumped distributions (Seidler & Plotkin 2006), where relatively long distances may separate groups of individuals within the same population. In these cases, we might expect  $N_e^b$  area to be substantially smaller than the total population area. Therefore, at least four possible scenarios exist with distinct implications in terms of consequences for dispersal (Table 1). In the case of dispersal events not extending beyond the geographic limits of the population or reference area, actual LDD events may involve dissemination beyond a reduced neighbourhood area that is smaller than the geographic extent of the population, originating local LDD ( $LDD_{loc}$ ) events (Table 1; Fig. 2a). Actual short-distance dispersal would then involve those situations where the propagule is disseminated within both the population limits and the genetic neighbourhood boundary ( $SDD_{loc}$ ). Along a



**Fig. 2.** Schematic representation of different types of long-distance dispersal events in relation to the geographic limits of local populations (dashed lines) and the genetic neighbourhood area  $N_e^b$  (grey area) of specific individual plants (squares). Dispersal events (arrows) can be classified depending on their actual incidence on propagule movement outside these spatially explicit reference areas (Table 1). Strict-sense long-distance dispersal events ( $LDD_{ss}$ ) just include the LDD events that disseminate propagules out of both the population and genetic neighbourhood boundaries. (a) The neighbourhood area is included within the geographic limits of the population, with some dispersal events potentially contributing local LDD; (b) the neighbourhood area is much larger than the geographic limits of the population. Both  $LDD_{ss}$  and  $LDD_{loc}$  may contribute genetic novelty by moving propagules outside the  $N_e^b$  area or the population limit, area or both. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



similar reasoning, dispersal events outside the population limits will not necessarily convey LDD (Table 1; Fig. 2b): this is expected in cases where the genetic neighbourhoods are extensive, going beyond the geographic limits of local populations, as in fig trees (Nason, Herre & Hamrick 1998) with long-distance pollination, generating LDD events within the genetic neighbourhood ( $LDD_{neigh}$ ). Note that pollen and seeds may have contrasting movement patterns in reference to the distinct spatial scales of the population limits and of the genetic neighbourhood. For example, wind-dispersed species with reduced seed mobility (in terms of distance), such as oaks, can have large genetic neighbourhoods with extensive pollen dispersal (Streiff *et al.* 1999) (but see, e.g., Smouse *et al.* 2001; Dutech *et al.* 2005; for fragmented stands) so that  $LDD_{neigh}$  dispersal events might frequently move beyond the physical limits of the population, patch, or stand but remain within the genetic neighbourhood. Finally, strict-sense LDD events would involve dissemination outside *both* the population limits and the genetic neighbourhood boundary ( $LDD_{ss}$ ) (Table 1; Fig. 2a).

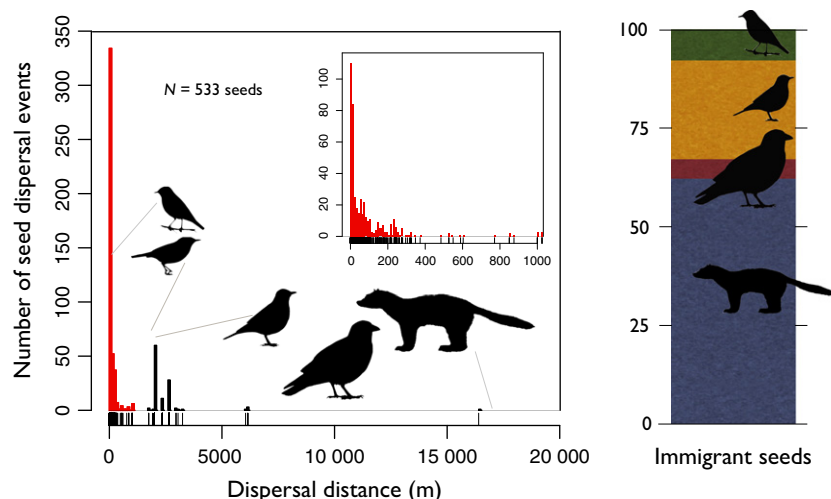
While both  $SDD_{loc}$  and  $LDD_{loc}$  can be crucial for assuring the local persistence of populations,  $LDD_{neigh}$  and  $LDD_{ss}$  would be extremely important contributors to the structuring of genetic pools, realized gene flow and maintaining connectivity in metapopulation scenarios. I argue that both the demographic and the genetic references are relevant for a proper definition of LDD. Accounting for these references may have different implications in relation to the dispersal biology of species. For example, frugivorous vertebrates, particularly the large-sized ones, tend to disperse a high number of half-sibs propagules, from the same mother tree to the same deposition site (Jordano *et al.* 2007; Karubian *et al.* 2010; Scofield *et al.* 2012), potentially increasing the frequency of  $LDD_{neigh}$  events if dispersal distances are relatively short (Fig. 3).

## Individual and population neighbourhoods as reference

Continuous populations can be modelled with the concepts of isolation by distance and neighbourhood size (Wright 1943, 1946). The former refers to the case that limited gene dispersal in continuous populations produces demes that are panmictic internally, but are isolated to some extent from adjacent demes. Each group of reproducing individuals is the neighbourhood, defined as the population of a region in a continuum, from which the parents of individuals born near the centre may be treated as if drawn at random (Wright 1969). The importance and influence of the dispersal process in determining the size of the neighbourhood is given by this equation, which shows how the spatial dispersion (pattern of spatial distribution) of the population influences the effective population size. This influence on the effective size is given by:

$$N_e^b = 4\pi\sigma\delta \quad \text{eqn 1}$$

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 neighbourhood 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



**Fig. 3.** Empirical frequency distributions of seed dispersal events as a function of dispersal distance by animal frugivores consuming *Prunus mahaleb* fruits. In red, left (inset), frequencies of within-population dispersal events inferred from direct assignment based on seed endocarp genotypes and maternal trees genotypes. Larger frame, left, contributions of four functional frugivore groups (small birds, medium- and large-sized birds, and mammals) to seed dissemination and proportional contributions (right bar) to dispersal of the inferred immigrant seeds (i.e. those not matching any maternal tree in the study population) (Jordano *et al.* 2007). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**Table 2.** Relative frequencies of *Prunus mahaleb* seed dispersal events for different frugivore groups according to population area limits and genetic neighbourhood limits

Frugivore group	Within-population, within-neighbourhood $SDD_{loc}$	Within-population, long-distance $LDD_{loc}$	Outside-population, within-neighbourhood $LDD_{neigh}$	Strict-sense long-distance $LDD_{ss}$	<i>N</i> 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

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 neighbourhood size is smaller than population area,  $LDD_{neigh}$  would be zero.

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, neighbourhood size can be defined with the following equation (Crawford 1984):

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

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.

Neighbourhood size in plants can be estimated by marking pollen and seeds with fluorescent dyes, tags or stable isotope enrichment (Carlo, Tewksbury & Martínez 2009). However, these methods do not measure effective pollen or seed movement, but they may be combined with genetic analysis to assess genetic identity and relatedness with hypervariable DNA markers (Levin 1988; Nason, Herre & Hamrick 1998; Godoy & Jordano 2001) to achieve reliable estimates of both effective population size and neighbourhood area.

The extent of neighbourhood area in plants can be extremely variable, depending on life-history attributes such as life span, spacing patterns and mating system. Even a limited sample of available information (Table S1, Supporting Information) highlights the fact that the size of neighbourhood areas can in some cases exceed the geographic limits of local populations (Nason, Herre & Hamrick 1998). The size of neighbourhood 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  $LDD_{neigh}$  to differ enormously. For example, relatively small  $N_e^b$  may raise the importance of  $LDD_{loc}$  in preserving scenarios of panmixia within a local population, as most distant dispersal events will disseminate seeds outside the neighbourhood of maternal plants.

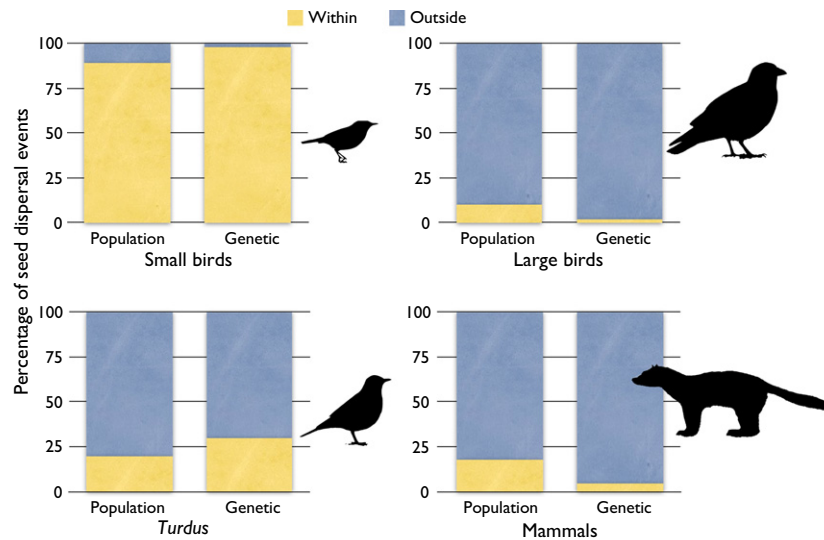
## Empirical analysis of contributions to LDD

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, Arroyo & Jordano 2014). Otherwise, visual identification 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 Appendix S1). These frugivore functional groups include up to 38 bird and four mammal species feeding on *Prunus 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 (*Turdus viscivorus*) and carrion crows (*Corvus corone*); and a pool of small-sized frugivorous birds, including warblers, redstarts and robins (Jordano *et al.* 2007; Fig. 3).

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* (Table S1),  $<1$  km<sup>2</sup>, well below the extent of the local study population (García *et al.* 2005; García, Jordano & Godoy 2007), 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. 3; Fig. S2). Notably, strict-sense LDD ( $LDD_{ss}$ ) 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



**Fig. 4.** Differential contributions of functional groups of frugivores to the four combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1. These result from dissemination within (yellow) or outside (blue) the population geographic limits; within-population dispersal events can either be short-distance ( $SDD_{loc}$ ) or local LDD ( $LDD_{loc}$ ) depending on the size of the genetic neighbourhood. Dispersal outside the local population can entail short-distance dispersal, if within the genetic neighbourhood area limits ( $SDD_{neigh}$ ) (yellow) or represent strict-sense LDD ( $LDD_{ss}$ ) (blue). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

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

Combining spatially explicit references to the geographic population limits and the genetic neighbourhood area extent ( $N_e^b$ ) helps avoiding some imprecision in setting distance thresholds to characterize LDD events (Jones & Muller-Landau 2008). In addition, the framework outlined in Table 1 bridges the combined demographic and genetic effects of LDD events. When methods available to assign frugivore taxa to the analysed dispersal events, as in the study case with *P. mahaleb*, a classification in the four categories of events is possible.

The frugivore assemblage of *P. mahaleb* is composed by a diversified set of animal species spanning a wide size range,

c. 12–14 000 g in body mass. We might expect that this extreme variation translates in an ample pattern of foraging modes, movement distances and fruit/seed processing (Jordano & Schupp 2000). If the results for *P. mahaleb* are generalizable to other disperser assemblages, it seems that the functional roles of frugivore species in terms of contributions to LDD events are structured in two distinct groups: small-bodied frugivores, with substantial contributions to SDD events, and large-bodied species, with a disproportionate contribution to LDD events. Both components of this sort of diplochorous (vander Wall & Longland 2004) dispersal system are very frequent in fleshy-fruited plants with diversified frugivore assemblages (Galetti *et al.* 2013). In such cases, small-bodied frugivores largely contribute the short-distance dispersal key to support in situ recruitment and population persistence. Yet the large-bodied frugivores distinctly contribute LDD events that sustain the connectivity of metapopulation scenarios (Urban & Keitt 2001). As shown in Table 1, SDD and LDD events can be more complex when we consider the contributions to gene flow via seed and the consequences in terms of structure and spatial distributions of the genetic pools. For example, local, within-population dispersal events may vary enormously in terms of genetic effects and local structuring of the genetic pools depending on whether they specifically contribute  $SDD_{loc}$  or, instead,  $LDD_{loc}$ . Note that only the latter actually contribute erasing any form of local genetic structure by contributing to increased genetic neighbourhoods.

A number of classic studies have demonstrated that the activity of large frugivores may also significantly contribute to SDD events and inefficient dispersal because of, that is, territorial defence, short gut retention times relative to on-tree foraging, frequent revisitation of same trees and perches, etc., resulting in substantial SDD events (Pratt & Stiles 1983; Pratt

1984; Snow & Snow 1984, 1988; Wheelwright 1991). Yet these large-bodied frugivores are crucial for both  $LDD_{loc}$  and  $LDD_{ss}$ , given that extensive movement patterns and extremely large foraging ranges may frequently contribute dissemination beyond distance thresholds defined with either spatial landscape or genetic references. Recent analyses of the movement ecology of large frugivores, coupled with results of their seed dispersal services emphasize that LDD are by no means exceptional, either in terms of frequency and extent (e.g. Westcott *et al.* 2005; Bueno *et al.* 2013; Carlo *et al.* 2013; Morales *et al.* 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.) can contribute substantial  $LDD_{loc}$  events, that is local LDD events contributing to erase local population genetic structuring, effectively increasing the size of genetic neighbourhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events are  $LDD_{loc}$  events. These birds are efficient seed dispersers of *P. mahaleb* and other fleshy-fruited species (Snow & Snow 1988; Jordano & Schupp 2000; Carlo *et al.* 2013), also showing significant contributions of  $LDD_{ss}$  events.

Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed shadows, accurately tracked with DNA-based genotyping methods, thus reflect the complex effects of frugivore foraging, habitat preferences and heterogeneous landscapes. This situation is probably generalizable to other plant–frugivore interactions where the combined spatial dynamics of habitat use and digestion processes determine complex seed shadows (Jordano *et al.* 2007; Nathan *et al.* 2008b). Much of this complexity can be adequately handled by mechanistic models (Nathan *et al.* 2002) incorporating very simple rules (Guttal *et al.* 2011). For example, earlier results (Jordano 2007) showed that the dispersal distances contributed by *P. mahaleb* frugivores closely map the spacing patterns of fruiting trees, but only up to a certain distance ( $\leq 100$  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) 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  $\geq 100$  m of most *P. mahaleb* fruiting trees. If these medium-sized birds are selecting habitat with tall woody vegetation (e.g. pines  $\geq 6$  m height), then they should be perceiving a much more patchy landscape, and thus requiring longer flights than, for example, small warblers seeking vegetation cover  $< 0.5$  m (Fig. 10.3b in Jordano 2007).

As defined in our framework (Table 1), LDD and, in particular,  $LDD_{ss}$  events are a specific case of extreme events (García & Borda-de-Água 2017), consistently associated with large-sized frugivores, yet including also medium-sized and highly efficient frugivorous bird species. Robustly characterizing the expected frequencies and extent of those extreme events would be crucial to properly assess the functional role

of frugivores and the full range of influences (demographic, genetic) in plant populations.

## Challenges and future avenues for research

Pollen and seed dispersal in plants are essentially spatially structured processes for which the outcomes of interactions with dispersal vectors is intimately linked to landscape features. Given this mechanistic link between the features of the vector and the environments where its displacement occurs (Nathan *et al.* 2008a), consideration of landscape is key to understand the consequences of LDD events. Yet these consequences hit two central aspects of plant life histories: the demographic 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, González-Varo & Valido 2012; Pérez-Méndez, Jordano & Valido 2015) and genetic connectivity (Pérez-Méndez, Jordano & Valido 2016). Frugivore downsizing represents a lasting challenge for the collapse of seed dispersal processes where  $LDD_{ss}$  events are crucial for population persistence and the cohesion of fragmented populations within metapopulation scenarios.

I advocate (also see Jordano & Godoy 2002; Nathan *et al.* 2003; Jones & Muller-Landau 2008; Hardesty, Metcalfe & Westcott 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, Arroyo & Jordano 2014) and simultaneously characterizing the source maternal plant (Jordano & Godoy 2002).

Long-distance dispersal, 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, Carlo & Martínez 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 modelling 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.



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## Data accessibility

This review does not use new raw data, but includes some re-analyses of previously published material. All the original data supporting the paper, R code, supplementary figures and summaries of analytical protocols are available at the author's GitHub repository (<https://github.com/pedroj>) and also deposited in the Dryad Digital Repository (Jordano 2017): <http://datadryad.org/resource/doi:10.5061/dryad.k0v67>.

## 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**, e6252.
- 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**, 991–1001.
- Carlo, T., Tewksbury, J. & Martínez, C. (2009) A new method to track seed dispersal and recruitment using  $^{15}\text{N}$  isotope enrichment. *Ecology*, **90**, 3516–3525.
- 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**, 301–307.
- Clark, J. (1998) Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *The American Naturalist*, **152**, 204–224.
- Clark, J.S., Fastie, C., Hurr, G.C. *et al.* (1998) Reid's paradox of rapid plant migration. *BioScience*, **48**, 13–24.
- 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. & Ducatez, 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.
- Crawford, T.J. (1984) The estimation of neighbourhood parameters for plant populations. *Heredity*, **52**, 273–283.
- 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*, **22**, 2563–2572.
- 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. *et al.* (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, **340**, 1086–1090.
- Garant, D., Forde, S.E. & Hendry, A.P. (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, **21**, 434–443.
- García, C. & Borda-de-Água, L. (2017) Extended dispersal kernels: insights from statistics of extremes. *Journal of Ecology*.
- 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**, 428–437.
- García, 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.
- García, 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.
- Godoy, J.A. & Jordano, P. (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology*, **10**, 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**, 806–814.
- 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**, e28447.
- Hampe, A. & Jump, A.S. (2011) Climate relicts: past, present, future. *Annual Review of Ecology and Systematics*, **42**, 313–333.
- 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**, 657–665.
- Harper, J. (1977) *Population Biology of Plants*, 1st edn. Academic Press, London, UK.
- Howe, H.F. & Miriti, M.N. (2004) When seed dispersal matters. *BioScience*, **54**, 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**, 642–652.
- 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), pp. 229–251. CAB International, Wallingford, UK.
- Jordano, P. (2017) Data from: What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, <http://datadryad.org/resource/doi:10.5061/dryad.k0v67>.
- 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), pp. 305–321. CAB International, Wallingford, UK.
- Jordano, P. & Schupp, E.W. (2000) Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**, 591–615.
- 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**, 3278–3282.
- Karubian, J., Sork, V.L., Roorda, T., Durães, T. & Smith, T.B. (2010) Destination-based seed dispersal homogenizes genetic structure of a tropical palm. *Molecular Ecology*, **19**, 1745–1753.
- Kinlan, B., Gaines, S. & Lester, S. (2005) Propagule dispersal and the scales of marine community process. *Diversity and Distributions*, **11**, 139–148.
- Kramer, A., Ison, J., Ashley, M. & Howe, H. (2008) The paradox of forest fragmentation genetics. *Conservation Biology*, **22**, 878–885.
- Levin, D.A. (1988) The paternity pools of plants. *The American Naturalist*, **132**, 309–317.
- Mallet, J. (2001) Gene flow. *Insect Movement Mechanisms and Consequences* (eds I.P. Wolwood, D.R. Reynolds & C. Thomas), pp. 337–360. CAB International, Wallingford, UK.
- Martínez, I. & González-Taboada, F. (2008) Seed dispersal patterns in a temperate forest during a mast event: performance of alternative dispersal kernels. *Oecologia*, **159**, 389–400.
- 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**, e65216.
- Nason, J.D., Herre, E. & Hamrick, J.L. (1998) The breeding structure of a tropical keystone plant resource. *Nature*, **391**, 685–687.
- Nathan, R. (2005) Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distributions*, **11**, 125–130.
- Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.
- 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), pp. 69–82. Commonwealth Agricultural Bureau International, Wallingford, UK.
- 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., 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 of the United States of America*, **105**, 19052–19059.
- 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**, 638–647.
- 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**, 151–159.
- Pérez-Méndez, N., Jordano, P. & Valido, A. (2016) Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. *Ecology*. (in press).
- 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**, 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**, 231–253.
- Rousset, F. (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, **145**, 1219–1228.
- 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 of the United States of America*, **109**, 8606–8611.
- Schupp, E. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.
- 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**, 628–641.
- Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A. & Nathan, R. (2009) Long-distance seed dispersal. *Annual Plant Reviews*, **38**, 204–237.
- 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**, 719–732.
- Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, 2132–2137.
- Slatkin, M. (1985) Gene flow in natural populations. *Annual Review of Ecology Evolution and Systematics*, **139**, 457–462.
- 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**, 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., Ducousso, 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.
- 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*, **279**, 3298–3303.
- Travis, J.M.J., Delgado, M., Bocedi, G. et al. (2013) Dispersal and species' responses to climate change. *Oikos*, **122**, 1532–1540.
- 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.
- 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.
- Westcott, D.A., Bentrupperbaumer, 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**, 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, IL, USA.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

### Appendix S1. Methods.

**Fig. S1.** Dispersal events for pollen (left) and seeds (right) traced for *Prunus mahaleb* trees (white dots).

**Fig. S2.** Differential contributions of functional groups of frugivores to the short ( $SDD_{loc}$ ) and long-distance ( $LDD_{loc}$ ) local seed dispersal events for *Prunus mahaleb*.

**Table S1.** Summary of neighbourhood area sizes and estimated neighbourhood radius for tree species with different combination of dispersal modes.