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

MS JEcol-2016-0422.R1

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Sevilla, October 10, 2016

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

Manuscript information: ** Words; ** Chars; ** Pages, * Figures; * Tables.

Abstract

1. Dispersal is a key individual-based process influencing many life-history attributes, 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. Especially the rightmost tail of these functions, i.e. 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: 1) a distinct (sessile) source, the maternal plant producing the fruits or the paternal tree acting as a source of pollen; 2) a distance component between source and target locations; and 3) a vector actually performing the movement entailing the dispersal event. Here I discuss operative definitions of LDD based on their intrinsic properties: 1) events crossing geographic boundaries among stands; and 2) 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 neighborhood area of individuals. Combinations of propagule movements within/outside these two spatial reference frames results 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 neighborhood 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.

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 *et al.* 2008). In the specific case of plants, largely sessile organisms, dispersal has three basic components: 1) a distinct (sessile) source, the maternal plant producing the fruits or the paternal tree acting as a source of pollen; 2) a distance component between source and target locations; and 3) 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 generated an impressive body of theoretical and empirical 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). 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. 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.

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

LDD events have two key characteristics that make them extremely important for population dynamics, yet being very difficult to characterize: LDD events are infrequent, but with a disproportionately high influence on contemporary gene flow and structure of the genetic pools (e.g., Schurr *et al.*, 2009; Clobert *et al.*, 2012;

Travis *et al.*, 2013). LDDs can connect disparate populations, allowing for genetic connectivity, colonization of vacant habitat and range expansion across changing landscapes, and maintain global persistence in the face of local extinctions (Trakhtenbrot *et al.*, 2005; Baguette & Schtickzelle, 2006; Ronce, 2007; Schloss *et al.*, 2012). With their influence on the structure of genetic pools, LDD events can also drive population differentiation and speciation (Ronce, 2007).

No explicit definition of what constitutes an LDD event exists. LDD is a characteristically extreme event of propagule movement in any plant or animal population, typically occurring with an extremely low probability but potentially reaching an extremely long distance. Previous approaches (e.g., Nathan, 2006; Schurr *et al.*, 2009) include both absolute and proportional definitions to characterize LDD events. This means providing information about the absolute distances moved by a given percentile of the events and/or providing data on the proportion of events exceeding a given distance threshold, i.e., 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 *et al.*, 2005) and of the specific organism considered. For example, Kinlan *et al.* (2005) used a spatial reference frame to characterize LDD events of marine organisms, where sedentary adults and larvae differ enormously in the spatial scales of their dispersal (D'Aloia *et al.*, 2013). Therefore, any measure of extent and reach of LDD events requires reference to an explicit spatial frame or "local" scale (Kinlan *et al.*, 2005; 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, e.g., experimental approaches to assess dispersal limitation and Janzen-Connell effects.

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

Here I propose an explicit definition of LDD and what constitutes a LDD event. Previous definitions of dispersal patterns emphasized only their distance components and characterized LDD events basically in terms of geographic distance between a dispersed propagule (or an established early seedling) and its most likely maternal or paternal (in case of pollen) source. Absolute and proportional definitions for the LDD events have been proposed depending on arbitrary thresholds of either the distance beyond which a dispersal event is LDD or the proportion of events occurring beyond a specific distance (Nathan, 2005; Nathan *et al.*, 2008b). Thus, two key biological aspects of LDD events involve the transport of propagules outside a reference area: moving away from the source stand or population, and moving away from the area where relatives stand (Kinlan *et al.*, 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 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, SDD_{loc} or LDD_{loc}) (Figure 2).

A second consideration in terms of spatial boundaries, with effects on dispersal patterns, is the genetic neighborhood area N_e^b, i.e., the spatial extent including a subset of panmictic individuals within a population (Wright, 1943, 1946). Thus, the N_e^b area can be equal to the whole extent of the population whenever the population is unstructured and there is evidence for random mating events among all the individuals. However, most populations and stands of long-lived trees show highly aggregated and clumped distributions (Seidler & Plotkin, 2006), where relatively long distances may separate groups of individuals within the same population. In these cases we might expect N_e^b area to be substantially smaller than the total population area. Therefore, at least four possible scenarios exist with distinct implications in terms of consequences for dispersal (Table 1). In the case of dispersal events not extending beyond the geographic limits of the population or reference area, actual LDD events may involve dissemination beyond a reduced neighborhood area that is smaller than the geographic extent of the population, originating local long-distance (LDD_{loc}) dispersal events (Table 1, Fig. 2A). Actual short-distance dispersal would then involve those situations where the propagule is disseminated within *both* the population limits and the genetic neighborhood boundary (SDD_{loc}). Along a similar reasoning, dispersal events outside the population limits will not necessarily convey LDD (Table 1, Fig. 2B): this is expected in cases where the genetic neighborhoods are extensive, going beyond the geographic limits of local populations, as in fig trees (Nason *et al.*, 1998) with long-distance pollination, generating LDD events within the genetic neighborhood (LDD_{neigh}). Note that pollen and seeds may have contrasting movement patterns in rference to the distinct spatial scales of the population limits and of the genetic neighbourhood. For example, wind-dispersed species with reduced seed mobility (in terms of distance), such as oaks, can have large genetic neighbourhoods with extensive pollen dispersal (Streiff *et al.*, 1999) (but see, e.g., Smouse *et al.*, 2001; Dutech *et al.*, 2005, for fragmented stands) so that LDD_{neigh} dispersal events might frequently move beyond the physical limits of the population, patch, or stand but remain within the genetic neighbourhood. Finally, strict-sense LDD events would involve dissemination outside *both* the population limits and the genetic neighborhood boundary (LDD_{ss}) (Table 1, Fig. 2A).

While both SDD_{loc} and LDD_{loc} can be crucial for assuring the local persistence of populations, LDD_{neigh} and LDD_{ss} would be extremely important contributors 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.

Individual and Population Neighborhoods as Reference

Continuous populations can be modeled with the concepts of isolation by distance and neighborhood 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 neighborhood, defined as the population of a region in a continuum, from which the parents of individuals born near the center may be treated as if drawn at random (Wright, 1969). The importance and influence of the dispersal process in determining the size of the neighborhood 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:

$$N_e^b = 4\pi\sigma\delta \tag{1}$$

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

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

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

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

Neighborhood size in plants can be estimated by marking pollen and seeds with fluorescent dyes, tags, or stable isotope enrichment (Carlo *et al.*, 2009). However, 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 *et al.*, 1998; Godoy & Jordano, 2001) to achieve reliable estimates of both effective population size and neighborhood area.

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

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

Empirical analysis of contributions to LDD

Empirical evaluation of differential contributions to the different forms of LDD events outlined in Table 1 requires identification of source trees as well as assignment of the dispersed propagules to specific vectors or functional groups of vectors (Jordano *et al.*, 2007). Recently, DNA-barcoding techniques have been developed and successfully applied to the identification of frugivore species contributing to specific seed dispersal events whose source can be identified with genetic, direct assignment techniques (González-Varo *et al.*, 2014). Otherwise, visual 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 Suppl. Mat. for additional details of methods). These frugivore functional groups include up to 38 bird and 4 mammal species feeding on *P. mahaleb* fruits (Jordano & Schupp, 2000). Here, we differentiate four major frugivore groups: large carnivorous mammals (such as foxes, badgers, and stone martens);

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

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

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

Long-Distance Dispersal: the ecology of extreme events

Long-distance dispersal (LDD) is a major component of the population dynamics, genetic structure, and biogeographic history of plant species. It determines the colonization ability of new habitats and the possibilities for fragmented populations to sustain a cohesive metapopulation by immigration-emigration dynamics that rely on LDD events (Nathan *et al.*, 2008b; Schurr *et al.*, 2009). Yet our current understanding of the extent, frequency, and consequences of LDD is very limited. On one hand, theoretical models fail to predict accurately the behavior of the tail of the dispersal functions, and thus fail to predict very basic properties of LDD. 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 neighborhood 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 analyzed 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, ca. 12-14000 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 neigborhoods.

A number of classic studies have demonstrated that the activity of large furgivores may also significantly contribute to SDD events and inefficient dispersal because of, i.e., 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; Morales *et al.*, 2013; Carlo *et al.*, 2013). In addition, medium-sized birds such as thrushes (*Turdus* spp.) can contribute substantial LDD_{loc} events, i.e., local LDD events contributing to erase local population genetic structuring, effectively increasing the size of genetic neighborhoods. In the case of *P. mahaleb* up to 55.49% of their dispersal events are LDD_{loc} events. These birds are efficient seed dispersers of *P. mahaleb* and other fleshy-fruited species (Snow & Snow, 1988; Jordano & Schupp, 2000; Carlo *et al.*, 2013), also showing significant contributions of LDD_{ss} events.

Two-dimensional patterns in the *P. mahaleb* seed rain and the individual seed shadows, accurately tracked with DNA-based genotyping methods, thus reflect the complex effects of frugivore foraging, habitat preferences and heterogeneous landscapes. This situation is probably generalizable to other plant–frugivore interactions where the combined spatial dynamics of habitat use and digestion processes determine complex seed shadows (**?**Jordano *et al.*, 2007; Nathan *et al.*, 2008b). Much of this complexity can be adequately handled by mechanistic models (Nathan *et al.*, 2002) incorporating very simple rules (Guttal *et al.*, 2011). For example, earlier results (Jordano, 2007) showed that the dispersal distances contributed by *P. mahaleb* frugivores closely map the spacing patterns of fruiting trees, but only up to a certain distance (≤100 m) (Fig. 10.3a in Jordano, 2007). Beyond this, frugivores were probably responding to other major landscape elements (e.g. rock outcrops, forest edges, large patches of open grassland, etc) that cause the fat tail of the seed dispersal distribution, adding more frequent LDD events than expected from a Brownian random walk pattern generated by a tracking of the crops of the fruiting trees. For instance, the long flights performed by *T. viscivorus* (Jordano & Schupp, 2000) frequently faced the pine forest edge, at distances ≥100 m of most *P. mahaleb* fruiting trees. If these medium-sized birds are selecting habitat with tall woody vegetation (e.g. pines ≥6 m height), then they should be perceiving a much more patchy landscape, and thus requiring longer flights, than for example, small warblers seeking vegetation cover <0.5 m (Fig. 10.3b in Jordano, 2007).

As defined in our framework (Table 1), LDD, and in particular LDD_{ss} events are a specific case of extreme events (García & Borda-de 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 *et al.*, 2012; Pérez-Méndez *et al.*, 2015) and genetic connectivity (Pérez-Méndez *et al.*, 2016). Frugivore downsizing represents a lasting challenge for the collapse of seed dispersal processes where LDD_{ss} events are crucial for population persistence and the cohesion of fragmented populations within metapopulation scenarios.

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

LDD, and its variation across coexisting plant species, could also have far-reaching consequences for community assembly and forest physiognomy. Yet very few previous analyses addressed 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 Ecology; Martnez et al. 2008 Oecologia) or even with the same dispersal syndrome (e.g. Garca et al. 2016 Basic Applied Ecology).

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

Acknowledgements. I am indebted to Cristina Garca, Jos A. Godoy, Manolo Carrin, Juan Luis Garca-Castao, Jess Rodrguez and, especially, Juan Miguel Arroyo for generous help with field and laboratory work and making possible this study. I appreciate the help and advice of Cristina Garca and Etienne Klein during the final stages of the manuscript. The study was supported by a Junta de Andaluca Excellence Grant (RNM-5731), as well as a Severo Ochoa Excellence Award from the Ministerio de Economa y Competitividad (SEV-2012-0262) and CGL2013-47429P grant. The Consejera de Medio Ambiente, Junta de Andaluca, provided generous facilities that made possible this study in the Andalusian natural parks (Sierra de Cazorla, Alcornocales) and authorized my work there.

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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.

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

Figure 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, e.g., by tracking the movement patterns of frugivores as they leave fruiting plants after feeding. 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. 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-modeling techniques.

Figure 2. Schematic representation of different types of long-distance dispersal events in relation to the geographical limits of local populations (dashed lines) and the genetic neighborhood 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 neighborhood boundaries. A, the neighborhood area is included within the geo-

graphic limits of the population, with some dispersal events potentially contributing local LDD; B, the neighborhood area is much larger than the geographic limits of the population.

Figure 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).

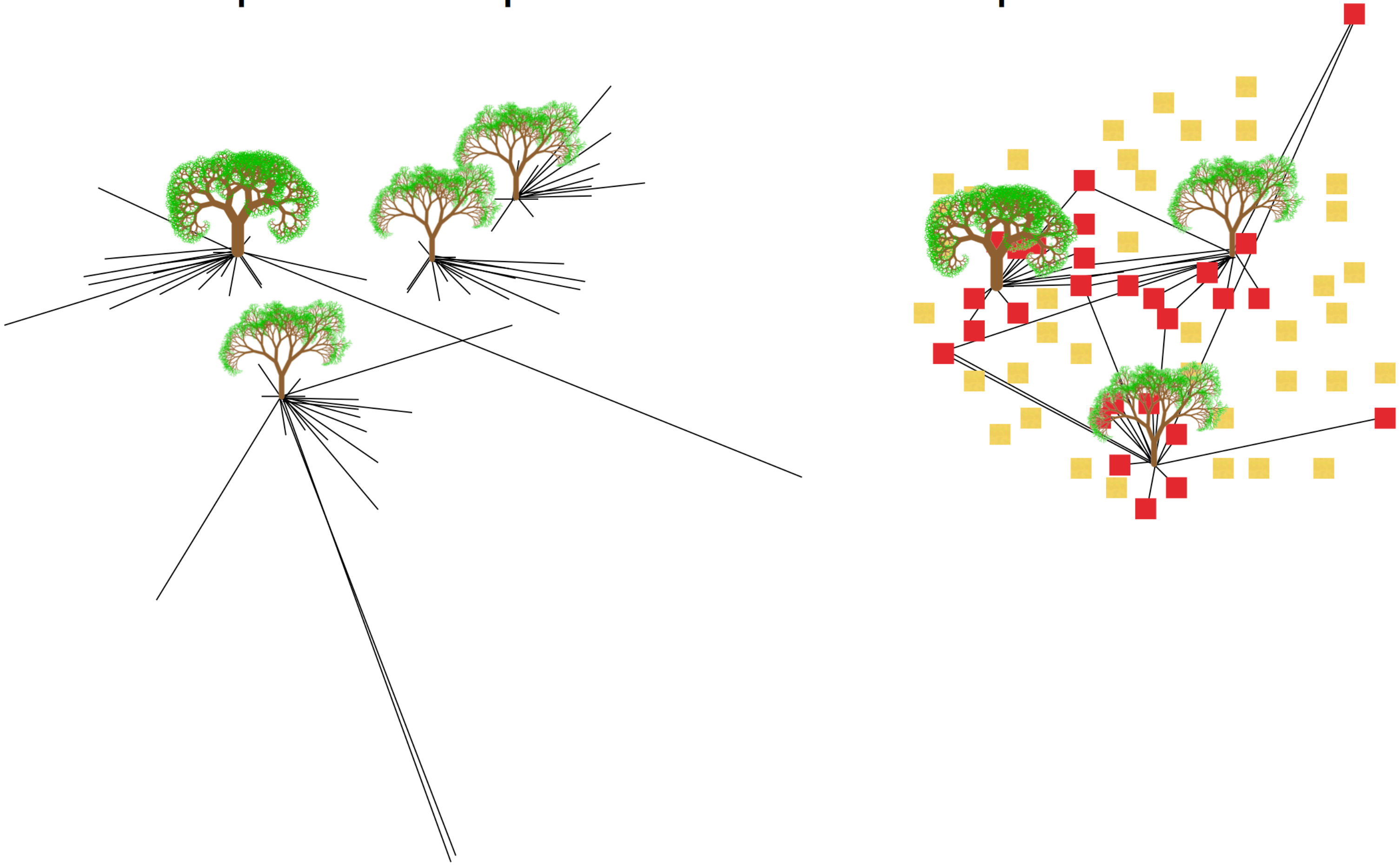
Figure 4. Differential contributions of functional groups of frugivores to the four combinations of *Prunus mahaleb* seed dispersal events outlined in Table 1. These result from dissemination within (yellow) or outside (blue) the population geographic limits; within-population dispersal events can either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

Online Support Material and data accessiblity

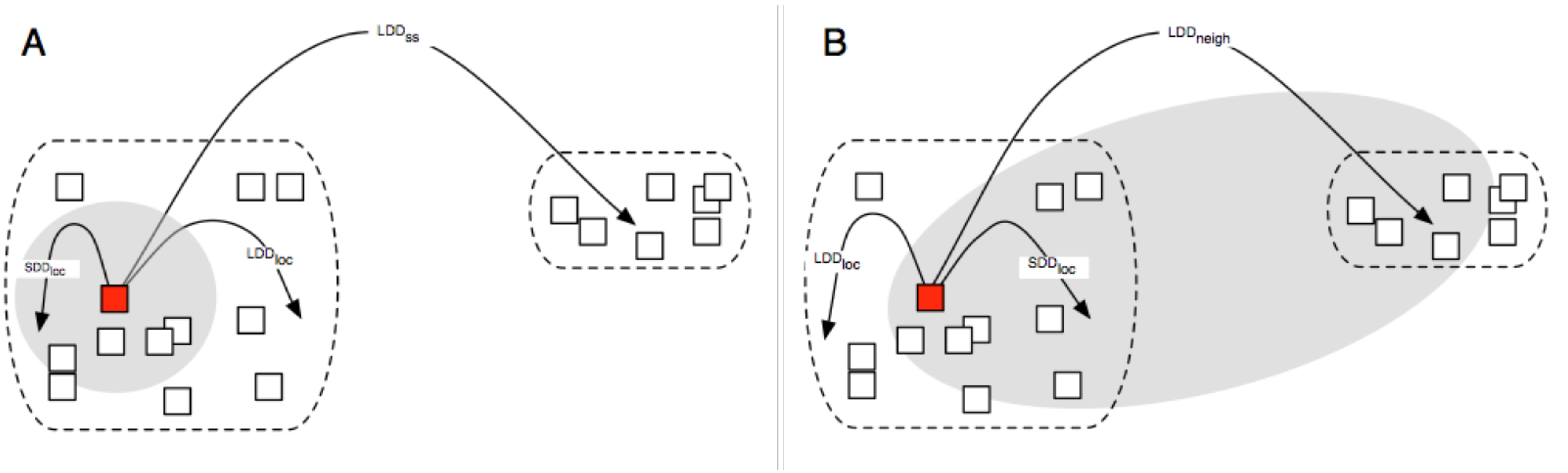
This review does not use new raw data, but includes some re-analyses of previously published material. All the original data supporting the paper, R code, supplementary figures, and summaries of analytical protocols is available at the author's GitHub repository (`https://github.com/pedroj/MS_LDD`),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

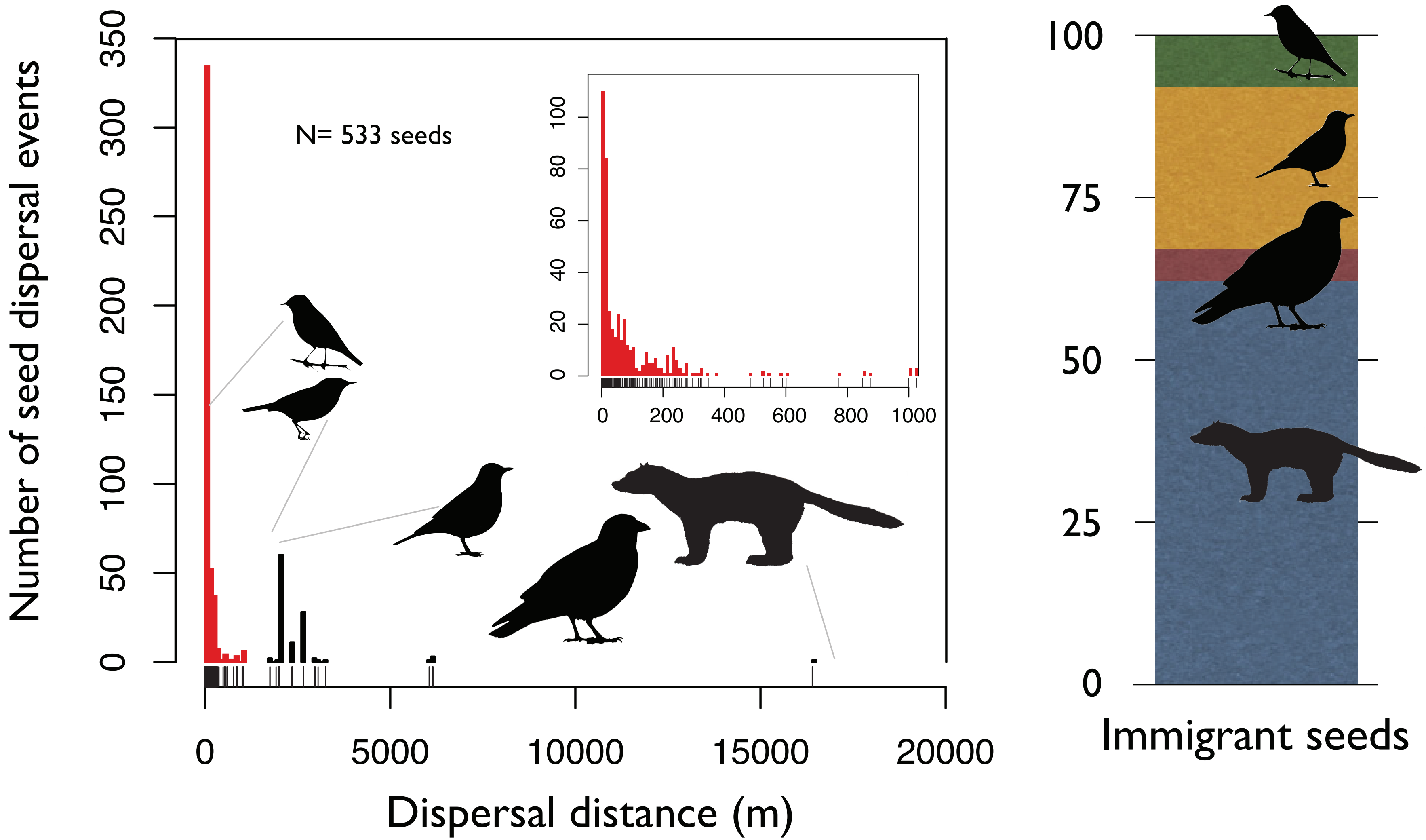
A. Emphasis on dispersal

B. Emphasis on arrival

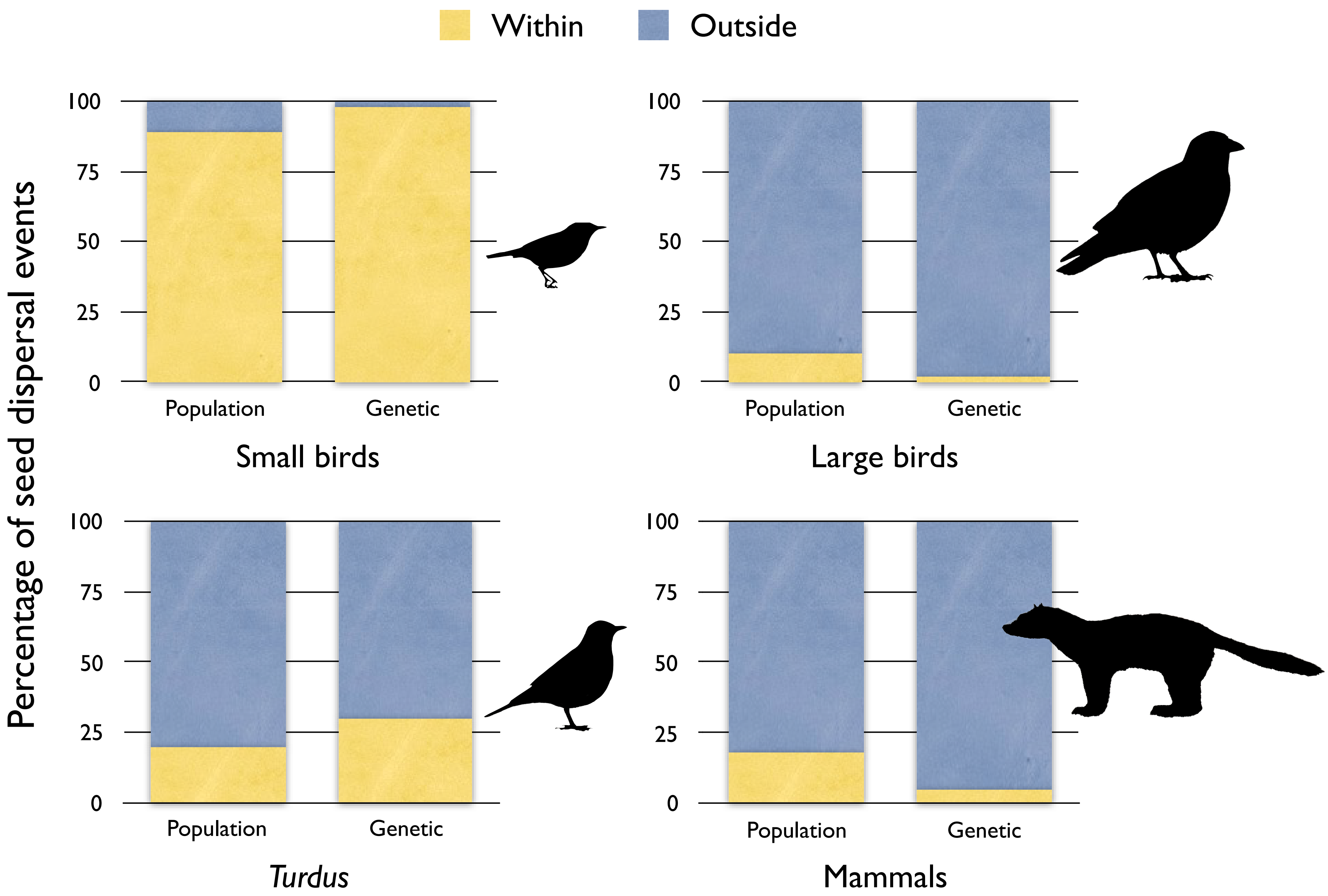


Jordano - Figure 1


A
LDDss
SDDloc
LDDloc
B
LDDneigh
LDDloc
SDDloc



Number of seed dispersal events
0
50
100
150
200
250
300
350
N= 533 seeds
0
20
40
60
80
100
0
200
400
600
800
1000
0
5000
10000
15000
20000
Dispersal distance (m)
100
75
50
25
0
Immigrant seeds


Within
Outside
Percentage of seed dispersal events
100
75
50
25
0
Population
Genetic
Small birds
Large birds
Turdus
Mammals