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Molecular insights into seed dispersal mutualisms driving plant population recruitment

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ABSTRACT

Most plant species require mutualistic interactions with animals to fulfil their demographic cycle. In this regard frugivory (i.e., the intake of fruits by animals) enhances natural regeneration by mobilizing a large amount of seeds from source trees to deposition sites across the landscape. By doing so, frugivores move propagules, and the genotypes they harbour creating the spatial, ecological, and genetic environment under which subsequent recruitment proceeds. Recruitment patterns can be envisioned as the result of two density- and distance-dependent processes: seed dispersal and seed/seedling survival (the Janzen–Connell model). Population genetic studies add another layer of complexity for understanding the fate of dispersed propagules: the genetic relatedness among neighbouring seeds within a seed clump, a major outcome of frugivore activity, modifies their chances of germinating and surviving. Yet, we virtually ignore how the spatial distribution of maternal progenies and recruitment patterns relate with each other in frugivore-generated seed rains.

Here we focus on the critical role of frugivore-mediated seed dispersal in shaping the spatial distribution of maternal progenies in the seed rain. We first examine which genetic mechanisms underlying recruitment are influenced by the spatial distribution of maternal progenies. Next, we examine those studies depicting the spatial distribution of maternal progenies in a frugivore-generated seed rain. In doing so, we briefly review the most suitable analytical approaches applied to track the contribution of fruiting trees to the seed rain based on molecular data. Then we look more specifically at the role of distinct frugivore guilds in determining maternal genetic correlations and their expected consequences for recruitment patterns. Finally we posit some general conclusions and suggest future research directions that would provide a more comprehensive understanding of the ecological and evolutionary consequences of dispersal mutualisms in plant populations.

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1. Overview

Frugivore activity, among other biological interactions, sets the spatial, numerical, and ecological templates where plant recruitment dynamics proceed in natural populations (Gómez et al., 2004; Nathan and Muller-Landau, 2000; Schupp and Fuentes, 1995). Great efforts have been devoted in recent decades to evaluate the quantitative aspects of seed dispersal and to understand their influence on regeneration dynamics (Clobert et al., 2001; Dennis et al., 2007; Forget et al., 2005; Howe and Smallwood, 1982; Jordano, 2007; Levey et al., 2002; Schupp et al., 2010). Recruitment patterns can be predicted based on the combined action of seed dispersal and seed survival curves according to the Janzen and Connell model

(Connell, 1971; Janzen, 1970). Under this framework plant recruitment can be envisioned as the interaction between a seed density curve that declines with distance from the mother tree and a seed/seedling survival curve that reflects decreasing mortality due to the declining pathogens/predator activity with distance. As a result, the recruitment curve is expected to peak at some intermediate distance from the source tree. Field data satisfactorily fit the JC model in a wide variety of populations (Augspurger and Kelly, 1984; Bagchi et al., 2010; Clark and Clark, 1984; Hansen et al., 2008; Hyatt et al., 2003; Schupp, 1992; Terborgh et al., 2008). However, other recruitment functions emerge as dispersal curves show a predictable decay from the source tree, but survival functions widely differ among populations yielding a diverse array of recruitment patterns (McCanny, 1985; Nathan and Casagrandi, 2004). Differential survival curves might arise not only as a consequence of density dependent processes, such as predation, but also as a result of specific genetic mechanisms modulating seed survival as a function

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of the genetic neighbourhood. Experimental studies document influence of the genetic relatedness among neighbour seeds on germination and survival rates (Donohue, 2003; Kalisz et al., 1999; Linhart, 1999; Tonsor, 1989; Vander Kloet, 1984; Willson et al., 1987). However, in spite of being a major outcome of dispersal mutualisms, the spatial distribution of the maternal progenies in frugivore-generated seed rains has been largely neglected in the ecological literature (García et al., 2009; Grivet et al., 2009). Only by understanding the connection between dispersal activity; the numerical, spatial, and genetic settings of frugivore-generated seeds rains; and the genetic mechanisms underlying recruitment patterns will we fully understand the ecological and evolutionary role of dispersal mutualisms in plant populations (Fig. 1) (Jordano, 2007; Schupp et al., 2010).

How do different types of frugivores distribute maternal progenies across the landscape? Do they consistently aggregate seeds from a nearby mother tree in discrete clumps? Or do they deliver highly diverse arrays of maternal progenies away from mother trees? Answering these questions requires tracking maternal progenies in the seed rain and identifying their sources trees. Nowadays this is a feasible task thanks to the incorporation of molecular markers to dispersal ecology studies (Ashley, 2010; García et al., 2007; Grivet et al., 2005; Jones et al., 2010; Jordano et al., 2007; Karubian et al., 2010; Scofield et al., 2010; Wang et al., 2007). It is timely to integrate the study of maternal genetic correlations into the research agenda of dispersal mutualisms and to bring population genetic theory into a dispersal ecology framework (Fig. 1).

Here we focus on the critical role of frugivore-mediated seed dispersal in shaping the spatial distribution of maternal progenies in the seed rain. We first examine the most relevant population genetic literature documenting how genetic relatedness among nearby seeds influences their performance. Then, we summarize a few ecological studies depicting maternally structured seed rains as a result of vertebrate activity and synthesize major observed trends among different study systems. Next, we briefly present major methodological techniques based on molecular markers available to track seed movement across the landscape. We additionally extend this conceptual umbrella to make quantitative predictions on the role of frugivores in shaping recruitment patterns as a result of maternally-structured seed rains. Finally, we summarize our major conclusions and highlight future directions to move forward our understanding of the ecological and evolutionary consequences of dispersal mutualisms for plant populations.

2. Genetic mechanisms underlying recruitment patterns

Identifying the key ecological and evolutionary factors that determine recruitment success is a long-lasting issue in plant ecology (Harper, 1977). The spatial variation of local regeneration success can be partially explained based on fecundity patterns, the heterogeneous spatial distribution of dispersed seeds (Clark et al., 2007; Dalling et al., 2002; Harms et al., 2002) and the microhabitat quality (Russell and Schupp, 1998). However, these factors insufficiently explain why natural regeneration success varies

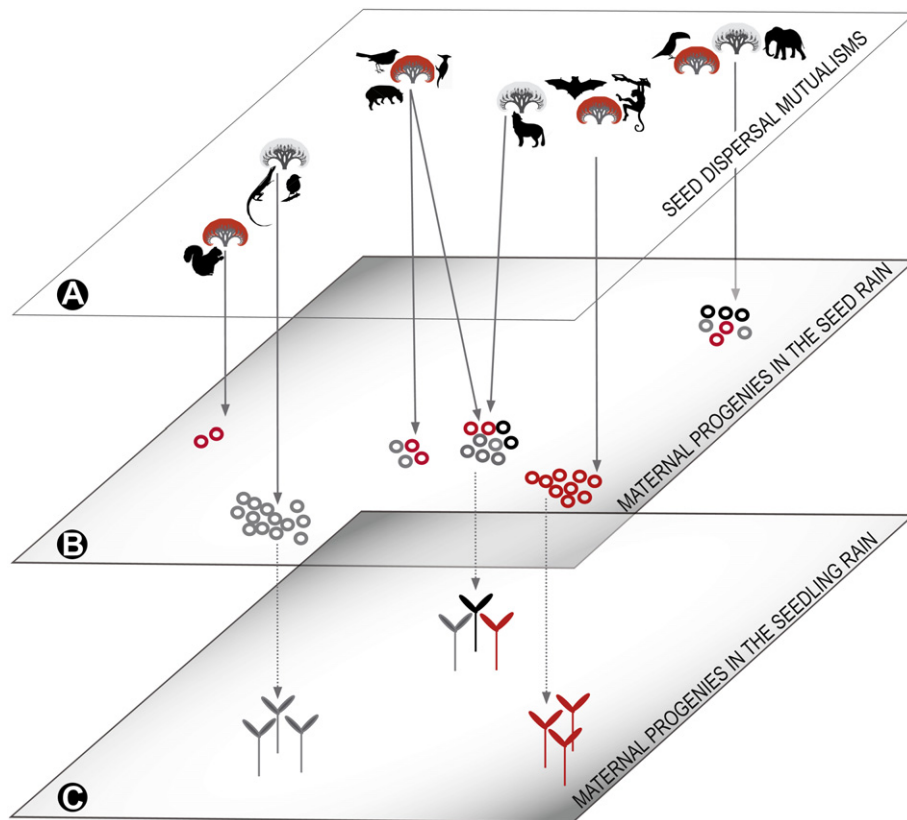


Fig. 1. Frugivorous vertebrates mobilize a large amount of seeds across the landscape by ingesting fruits (A). Their size, foraging and mating behaviour determine the spatial distribution of maternal progenies in the seed rain (B). Thus, small-sized vertebrates might tend to disperse groups of kin propagules near the source tree (such as small passeriform birds, rodents, or lizards). Medium- to large-sized vertebrates might create complex seed rains where seed clumps of kin propagules are combined with large seed clumps contributed by several maternal trees. Mother trees contributing to these seed clumps can be located within the focal population (maternal progenies in red and grey colours) or at certain distance of our focal population (maternal progenies in black colour) as a result of long distance dispersal events. Variable maternal genetic correlations in the seed rain are a major output of dispersal mutualisms with potential influence on regeneration dynamics that would explain different recruitment success across the landscape (C). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

across the landscape when a similar number of propagules reach equally suitable patches. Population genetics posits local relatedness (i.e., genetic relatedness among nearby or interacting individuals) as a major ecological genetic factor underlying competitive dynamics (Koelewijn, 2004; Tonsor, 1989), plant fitness (Donohue, 2003), population growth (Antonovics and Levin, 1980), and colonization success (Crawford and Whitney, 2010). The probability of seeds to germinate and survive are influenced by the number and relatedness of nearby genotypes, even though the magnitude and the sign of this effect changes among studies (Leimu et al., 2006). These experimental studies where researchers set the level of genetic relatedness among neighbouring seeds rarely examine the role of dispersal agents in shaping genetic relationships among dispersed propagules (but see Kalisz et al., 1999).

When does genetic relatedness among neighbours influence their chances of germinating and surviving? When plant fitness is mediated by kin selection, dispersed seeds should perform better when they germinate surrounded by sibling than non-sibling neighbours (Donohue, 2003; Kelly, 1996; Tonsor, 1989). Many plant species show dispersal limitation that results in highly aggregated clumps of maternal progenies around the source tree or in clump deposition typical of dispersal in tropical systems (Kalisz et al., 1999; Schupp et al., 2002; Schuster and Mitton, 1991). However, molecular markers show that the spatial aggregation of maternal progenies in the seed rain can be mediated by long distance dispersal events. This is the case for multi-seeded fruits and for species dispersed by vertebrates performing frequent flights from the same fruiting tree to the same deposition site (García et al., 2009; Grivet et al., 2005; Karubian et al., 2010; Scofield et al., 2010; Torimaru et al., 2007).

Some experimental studies provide evidence for alternative genetic mechanisms where decreased genetic relatedness correlates with increased yield or reproductive output. On the one hand, the elbow-room model states that genetic variation (involving less genetic relatedness among neighbours) allows for niche partitioning that optimizes the use of local resources, increasing local productivity (Young, 1981). On the other hand, the lottery model suggests that increased genetic diversity among less correlated neighbours raises the probability that a survivor genotype is present under high spatially or temporally heterogeneous environments (Hanski and Saccheri, 2006). Finally, it is also documented that positive or negative frequency-dependent selection, observed in the presence of pathogen attack or herbivory, shapes individual fitness' genotypes (Koelewijn, 2004). Under a negative frequency-dependent context rare and genetically less related genotypes within a seed clump are less likely to be attacked, and thus they are more likely to survive than common genotypes in high density situations (Antonovics and Ellstrand, 1984).

These scenarios with decreased genetic relatedness among dispersed seeds would correspond to dispersal activity promoting seed shadow overlapping (mixing of maternal progenies at deposition sites). These dispersal patterns are found when frugivores feed on numerous fruiting trees and then return recurrently to the same sites in the population, such as forest gaps (Wenny and Levey, 1998) or leks (Karubian et al., 2010), perch trees (Jordano and Schupp, 2000), sleeping and roots sites (Julliot, 1997; Schupp et al., 2002). For a fixed dispersal range, plant density positively correlates with seed shadow overlapping. Thus, seed clumps in high density populations are expected to contain a wider range of maternal progenies than seed clumps in low density populations for a given dispersal system. Additionally, certain foraging behaviours are expected to create extensive seed shadow overlapping when the rate of changing among different fruiting individuals is faster than the rate of meal processing. Some vertebrates can ingest fruits from different trees and gather the seeds in their mouth (such

as monkeys) or stomach (such as large mammals) before being regurgitated or defecated all together (Clark et al., 2005; Fragoso et al., 2003). Therefore, dispersal mutualisms not only determine recruitment success by disseminating a sufficient amount of seeds at certain distance from the mother tree, but they also might modify the chances of a propagule to germinate and survive by aggregating a variable number of maternal progenies among different microhabitats.

3. Maternal genetic correlations in a frugivore-generated seed rain

Frugivores display a wide range of foraging behaviours by which they feed over a non-random set of fruiting trees where they spend a variable amount of time, ingest their fruits, and move to selected sites where they defecate or regurgitate a load of seeds that combine diverse arrays of maternal progenies (Dennis et al., 2007; Howe and Smallwood, 1982). For example, frugivorous vertebrates strongly respond to the spatial distribution of adult trees and the density and identity of surrounding trees around the fruiting trees (Kwit et al., 2007; Morales and Carlo, 2006). By doing so, frugivores also influence the genetic environment under which dispersed seeds might eventually emerge, namely: i) the identity and number of fruiting trees contributing to a given seed clump; and ii) the relative contribution of each fruiting tree. These aspects, linked to frugivore activity in endozoochorous species, determine the maternal genetic correlations in the seed rain, i.e., the spatial distribution of the maternal progenies across the landscape relative to their source tree and other conspecifics (García et al., 2009).

We refer to correlated maternity as the proportion of maternal half-sibs in a deposition site or seed clump. Correlated maternity can be expressed as the probability of maternal identity (PMI), which is the probability that two dispersed seeds randomly drawn from the same deposition site come from the same mother tree (Grivet et al., 2005). Correlated maternity is analogous to correlated paternity, i.e., the fraction of maternal progeny sired by the same pollen donor (paternal half-sibs) a widely used concept in mating system studies (Ritland, 1989). High values of PMI (close to 1) indicate that all or nearly all seeds in a given deposition site are contributed by the same mother tree, whereas low values (close to 0) suggest that most dispersed seeds within a seed clump are contributed by different mother trees. The study unit when estimating correlated maternity is the local seed clump or deposition site where propagules are dispersed. Given that a few deposition sites are likely to receive a disproportionate number of dispersed seeds whereas most sites receive few (if any) propagules (Howe and Smallwood, 1982; Schupp et al., 2002), PMI estimation requires accurate statistics not biased by small sample sizes (see details in Grivet et al. (2005)). The number of maternal trees contributing to a given deposition site or seed clump is referred as maternal richness. Also of interest is the genetic relatedness among those mothers contributing seeds to the same site, which is known as maternal relatedness. Correlated maternity, maternal richness, and maternal relatedness are the three elements that depict the maternal genetic correlations (García et al., 2009) that result from dispersal mutualisms in zoochorous species.

4. Molecular methods for tracking maternal progenies in the seed rain

Methods used to measure maternal genetic correlations require the identification of the maternal progenies in the seed rain (Fig. 2). This identification can be achieved by genotyping maternally-derived tissues present in the seed that, by definition, has identical genotype of the maternal source tree. Both angiosperms and

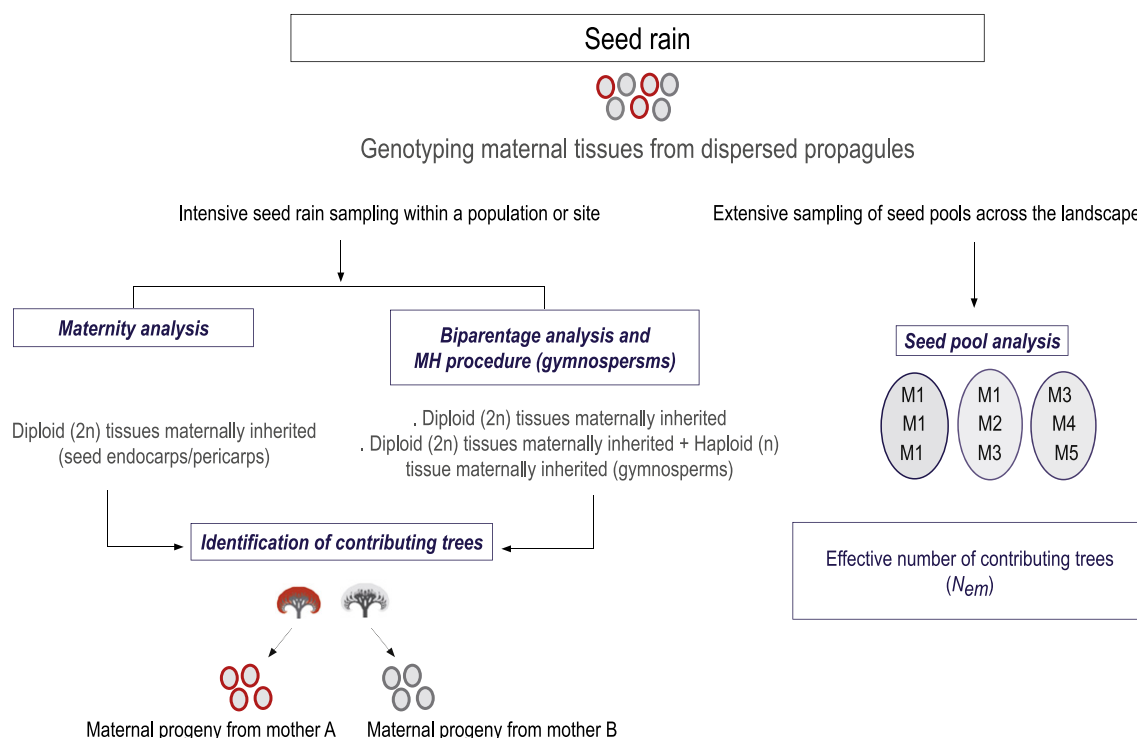


Fig. 2. Two main methodological approaches to track dispersal progenies in the seed rain based on highly polymorphic molecular markers. Grey and red colours represent maternal progenies from different fruiting trees. Left side depicts the use seed maternal tissues to identify maternal progenies in the seed rain on individual basis. By doing so maternal genetic correlations can be straightforwardly estimated. Right side highlights seed pool approach where sets of propagules are genotyped from different seed pools to estimated the effective number of contributing trees (N_{em}). This is a key genetic parameter readable by population genetic models. Both methods provide valuable and complementary insights to investigate the evolutionary outcomes of dispersal mutualisms. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

gymnosperms have maternally-derived diploid tissues generally referred as seed coats, such as pericarps or endocarps. Gymnosperms, additionally, have a haploid maternal tissue, known as the megagametophyte, covering the embryo. Highly polymorphic DNA based markers generally provide sufficient variability to identify each fruiting tree in a small- to medium- sized population and to assign dispersed propagules in the seed rain to their maternal source tree.

If we obtain multilocus genotypes from each fruiting tree in the study site and from maternally inherited tissues of dispersed propagules we can then search for matching genotypes by performing maternity analysis; a fruiting tree is designated as the source tree of those propagules with multilocus matching genotypes (Godoy and Jordano, 2001). If we do not have access to an exhaustive survey of local source trees, genotyping maternal tissues still provide us the identity of contributing trees to the seed rain. By doing so, this method provides a direct and reliable identification of maternal progenies in the seed rain. Once we have identified maternal progenies in the seed rain, we can straightforwardly estimate the maternal genetic correlations across the landscape.

If we genotype maternally inherited tissues from dispersed propagules we can have an additional valuable genetic insight by applying the seed pool approach. This approach decomposes the genetic variance among different strata by applying an AMOVA (Analysis of MOlecular VAriance) (Sork and Smouse, 2006). Thus, seed or seedling clumps act as strata that can be hierarchically grouped according to some ecological factor, such as being below or away from the maternal canopy (Grivet et al., 2009) or being located within a lek territory or outside the lek (Karubian et al., 2010). This analysis yields a statistic that gauges the magnitude of the genetic structure among strata easily translated into an

effective number of contributing trees (N_{em}) (Grivet et al., 2005). Furthermore, the same statistical tools can be used to assess the scale of propagule movement by assuming a given seed dispersal curve (Austerlitz and Smouse, 2001). Note that the seed pool approach does not aim at identifying the maternal progenies on an individual basis, but rather, it is a suitable technique to gauge N_{em} , a key demo-genetic parameter in genetic population models. Ideally our sampling design should cover most of the ecological heterogeneity perceived by dispersal agents across the landscape. In doing so, we straightforwardly translate foraging movement patterns across the landscape into genetic connectivity patterns among sites or populations mediated by seed dispersal mutualisms.

When maternally inherited tissues are not available, biparentally inherited tissue from seedlings or saplings can be collected. In this case, a pair of most likely parents are designated by applying parentage analysis (Jones et al., 2010). Then, with the parent pair in hand for each seedling, the challenge is to ascertain who is the mother and father for a monoecious species. Here ecological information such as gender expression, flowering or fruiting phenology, and location become extremely useful to maximize assignment success. As an example, Hardesty et al. (2006) applied parentage analysis to assign a parent pair to a set of seedlings sampled in a 50-ha plot on Barro Colorado Island, Panama, within which all adult trees were located and genotyped. First of all, those trees positively known to be males or non-fruiting trees were excluded from the analysis. Then, they set two different criteria to identify the mother tree in the parent pair by assigning: i) the closest tree to the seedling as the mother (providing a conservative estimate of dispersal movement); and ii) one parent from the pair randomly chosen regardless of its location as the mother. The actual scenario is unknown, but because the observed immigration rates

and seed dispersal distances did not dramatically differ between scenarios the method provided an accurate sense of the magnitude of the effective dispersal scale (Hardesty et al., 2006). Note that tracking the maternal contribution to the seed rain does not require the location of the mother trees: only their genotypes are strictly needed. Maternity or parentage analysis requires information on the location of the source tree only if you are to assess the spatial dimension of the dispersal, i.e., how do seeds move in terms of distance and direction (Dow and Ashley, 1998; García et al., 2007). Finally, it would be worth noting that this technique estimates realized dispersal (i.e., dispersed seeds subsequently recruited) and not the actual seed dispersal directly attributable to the action of mutualistic frugivores. We probably need both estimates to fully understand the relevance of endozoochory in mediating recruitment dynamics. Both maternity/parentage analyses and seed/seedling/pollen pool approaches are complementary analytical methods useful in assessing maternal genetic correlations in the framework of frugivore-generated seed rains, and their use will depend on the data available, the spatial scale, and on the objectives of the study (Smouse and Sork, 2004; Sork and Smouse, 2006).

When dealing with gymnosperms, a two-step biparentage assignment can be applied based on: i) the megagametophyte haplotype, a maternally inherited haploid tissue; and ii) the embryo genotypes, that combine both maternal and paternal gametic phases. This method is called the megagametophyte haplotype procedure (“MH procedure”) (Iwaizumi et al., 2007). Candidate parents within a population or study plot are sampled and genotyped along with a collection of dispersed seeds that provide embryo genotypes and megagametophyte haplotypes. First, the megagametophyte haplotype is used to discriminate the maternal parent, and secondly, once we know the mother, we can apply parentage analysis to identify the most likely father based on parentage analysis (Jones et al., 2010). This two-stage parentage analysis dramatically increases assignment success and accuracy since the megagametophyte tissue allows us to discriminate between the maternal and paternal haplotypes.

Finally, an alternative to the assessment of maternal contribution is the use of Maximum-Likelihood methods for modelling female and male reproductive success based on the multilocus genotypes and locations of all adult trees and a set of seeds or seedlings within a study plot (Burczyk et al., 2006; González-Martínez et al., 2006; Oddou-Muratorio and Klein, 2008). This approach is well suited to estimate seed and pollen immigration levels, to infer the scale of gene movement, and to estimate the effective number of fathers and mothers in a seedling population, but it does not allow parental assignment on individual basis among recruits; rather, they are useful to quantify selection gradients and to assess the effect of ecological correlates of gene flow patterns, such as female and male fecundity or pair distance.

5. The spatial distribution of the maternal progenies in frugivore-generated seed rains: empirical evidences

By collecting an exhaustive sample of dispersed seeds after one dispersal season and applying molecular markers (microsatellites) and maternity or seed pool analysis a handful of studies explored the spatial distribution of maternal progenies in a frugivore-generated seed rain (García et al., 2009; Grivet et al., 2005; Karubian et al., 2010; Scofield et al., 2010). These studies illustrate that the spatial distribution of maternal progenies in the seed rain reflects the selective foraging behaviour of dispersal agents. One documented consequence of these non-random movement patterns is a highly clumped seed rain, where most dispersed propagules are aggregated in a relatively few large seed clumps (Howe and Smallwood, 1982; Schupp et al., 2002). Additionally,

molecular data provides evidence that frugivore-generated seed rains are not random mixtures of maternal progenies, but rather, seed clumps are aggregates of distinctive subsets of mother trees that only slightly overlap with the maternal pool of nearby seed clumps (García et al., 2009; Grivet et al., 2005; Karubian et al., 2010; Scofield et al., 2010). Two types of aggregates have been found for endozoochorous species: i) large seed clumps frequently contributed by a single (or few) mother tree(s), even in the presence of long distance movements; and ii) hotspots of maternal progenies contributed by numerous mother trees located across the landscape. The genetic environment set by the dispersal agents strongly differs between both scenarios, so do their expected demographic outcomes.

Strong spatial aggregation of seeds from a single mother tree have been documented when frugivore agents recurrently move from the same fruiting tree to the same deposition site creating a kin-structured seed rain (Torimaru et al., 2007), even when seed dispersal is mediated by long distance movements. As a consequence, subsequent recruitment stages would present strong spatial genetic patterns similar to those observed for species with no dispersal agents. Hence, spatial aggregation of maternal progenies in endozoochorous species does not always involve spatial aggregation around the mother tree; caution should be taken when inferring seed dispersal patterns from spatial genetic structure without some knowledge of the dispersal ecology of the study species. The opposite scenario is observed when frugivores enhance seed shadow overlapping in locations in the population that they use to nest, mate, or gather and process food (Gómez, 2003; Jordano and Schupp, 2000; Karubian et al., 2010). As an example, Karubian et al. (2010) reported that lek territories of long-wattled umbrellabirds (*Cephalopterus penduliger*) act as hotspots of seed shadow overlapping: plots within the lek sites had five-times higher effective numbers of source trees compared to plots outside (but close) to the lek areas (27.0 vs. 5.2).

In another study, García et al. (2009) documented great variation in the number of contributing trees among microhabitats within a population of *Prunus mahaleb* due to strong differences in the use of microhabitats by different frugivore guilds (Jordano and Schupp, 2000). Most of the frugivorous bird species frequently visited patches with high density of fleshy-fruited species whereas only a few bird species visited low shrub and open areas and they did so infrequently. As a consequence, 95 fruiting trees contributed progeny to microhabitats dominated by fleshy-fruited species, while only 16 fruiting trees contributed progeny to the microhabitats covered by low shrub. Furthermore, distinctive subsets of maternal trees contributed to different microhabitats. As a result, fruiting trees fail to reach all microhabitats in the population whereas microhabitats only contained a subset of maternal progenies among all available in the population. This effect is referred as genetic limitation associated to seed dispersal (García et al., 2009). In other words, a large mobilization of propagules by dispersal agents does not always involve an extensive movement of genotypes; rather, when only few maternal progenies are involved effective parental size decreased in the seed rain. Molecular insights into dispersal patterns additionally show us that non-random dispersal patterns might promote strong spatial genetic patterns in endozoochorous species at very fine scale.

An important issue to address is the demographic and genetic outcomes of kin-structured seed rains across the demographic cycle. Two studies by Torimaru et al. (2007) and Grivet et al. (2009) provide evidence on the genetic imprint set in the seed rain by vertebrates endures through the recruitment cycle. The first study used seed rain data documenting dispersal patterns of multi-seeded fruits of *Ilex leucoclada* by vertebrates to simulate different recruitment dynamics for different relatedness levels

among seed clumps and infer the subsequent spatial genetic patterns of established recruits. Long distance dispersal of multi-seeded fruits (entailing maternal half-sibs and frequently full-sibs) resulted in highly maternally structured seed rains and strong spatial genetic structure at very fine scale among seedlings, even in presence of long distance dispersal. Interesting enough, the observed structure arose in a single generation. But, does the observed structure persist over time or is it ephemeral? Grivet et al. (2009) investigated this question and they documented that sites with higher seed shadow overlapping (seed caches away from canopy trees) doubled the number of effective contributing trees in the seedling stage compared to sites under canopy trees in a Californian oak population (*Quercus lobata*). On average, seedling clumps away from canopy trees were mothered by 2.8 effective source trees whereas seedling clumps under canopy trees were mothered by 1.1 source trees.

In summary, evidence from current studies illustrates that selective and idiosyncratic social, foraging, and mating behaviour of dispersal agents might create a genetic imprint with a strong maternal structure in the seed rain. Frugivore-generated seed rains are not random mix of unrelated array of propagules from all fruiting trees in the population, nor are they strictly shaped by dispersal distances. Rather, complex feeding behaviour coupled with dispersal distances and heterogeneous landscapes shape maternally structured seed rains with some microhabitats having a high degree of seed shadow overlapping (hotspots of mother trees) while others have a strong aggregation of maternal progenies (hotspots of kin propagules). This highly structured organization of the maternal progenies in the seed rain mediated by frugivores provides opportunities for evolutionary change to happen provided that recruitment cycle proceeds on heritable characters modulating plant performance.

6. Expected demographic outcomes of kin-structured seed rains

Different assemblages of frugivores coupled with the spatial distribution of fruiting trees generate distinctive seed rain patterns due to differences in their body sizes, foraging preferences, and postfeeding movements (Jordano and Schupp, 2000; Schupp et al., 2010; Wenny and Levey, 1998; Westcott and Graham, 2000). Similarly, we can expect maternal genetic correlations to vary according to the assemblage of frugivores generating the seed rain (Fig. 3). For example, small-sized and highly territorial vertebrates might tend to yield short dispersal distances. If additionally, fruiting trees are sparsely located, distance among nearby fruiting trees may exceed seed dispersal distances. If the mean distance among neighbouring adults is roughly twice the maximum dispersal distance or greater, we would expect non-overlapping seed shadows with maternal progenies aggregated around each the mother tree, i.e., a single mother contributes most of the dispersed seeds in nearby seed clumps. Consequently, high correlated maternity within seed clumps and high genetic structure (due to little overlapping) among seed clumps is expected (Fig. 3A). If germination is enhanced by increased local relatedness (kin selection), the highest frequency of recruited individuals would be located beneath or nearby the mother tree where density of half-sibs or full-sibs is high. If, alternately, germination was to increase with the number of contributing trees, recruitment would virtually fail or it would remain steadily low with distance since limited mobility of dispersal vectors hamper seed shadow overlapping.

Seed shadows begin to overlap when dispersal distances exceed half the distance between mother trees, more typical of temperate than tropical systems. This overlap might happen because dispersers have a relatively large home range or due to increased

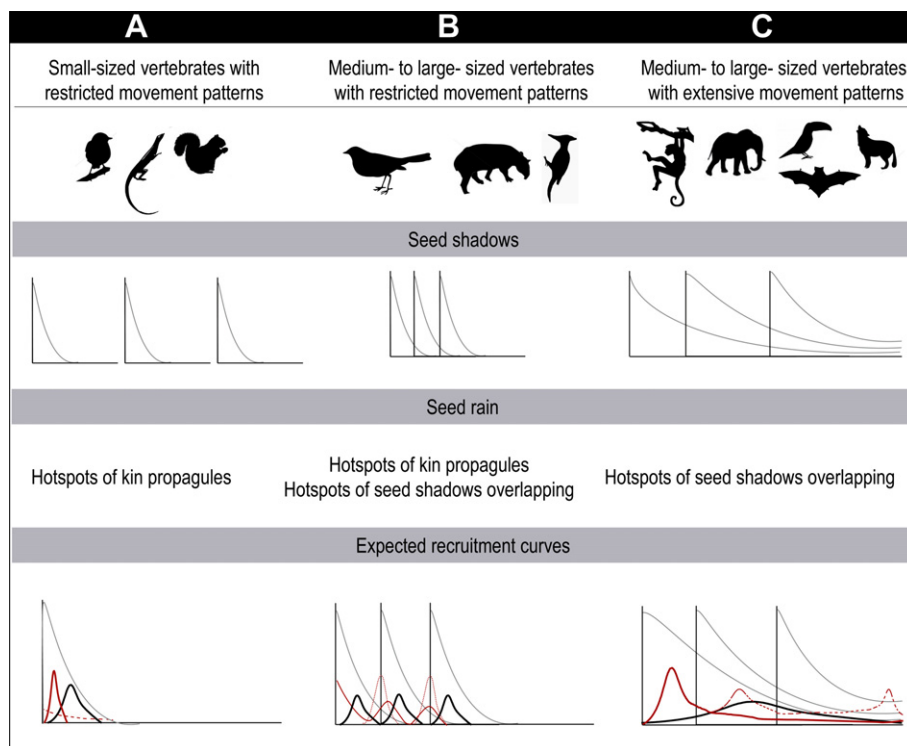


Fig. 3. Scheme depicting the role of different frugivore guild types (top) on shaping seed dispersal kernels and maternal genetic correlations (middle), as well as recruitment patterns (bottom). Graphs below represent expected recruitment curves under a Janzen and Connell (JC) model (black lines). The continuous red line represents predicted recruitment curves under a kin selection scenario, whereas the dotted red lines represent predicted recruitment curves under a scenario where decreased genetic relatedness would enhance recruitment. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tree density and/or marked neighbourhood effects (Kwit et al., 2007). In such a case, correlated maternity and the relatedness among dispersed seeds would decrease as the maternal diversity increases due to some level of seed shadow overlapping. This pattern would be the case for small- to medium- sized vertebrates able to move seeds several tens to hundreds of meters from maternal trees. It is worth noting that some invertebrates also move seeds within that range (e.g. crabs or ants), whereas some small vertebrates with fast gut passage times move quickly over long distances yielding short dispersal distances. If kin selection underlies recruitment patterns, we still expect a single peak of recruits nearby mother trees. However, if recruitment was enhanced by decreasing genetic relatedness, we would expect a multi-peak recruitment curve with distance from the source tree (Fig. 3B). These peaks would be located in those sites with high seed shadow overlapping such as forest gaps, water sources, patches with high densities of fruiting trees (García et al., 2009), or lek territories (Karubian et al., 2010). Finally, when frugivore guilds include large vertebrates able to disperse seeds several kilometers, we would expect an extensive seed shadow overlapping, especially in the tail of the dispersal curve (Fig. 3C). Under this scenario, if high relatedness favours germination and survival, the recruitment curve would peak near/under source trees. However, if decreased relatedness and increased maternal diversity enhance germination and survival, we will expect several recruitment peaks. Interestingly, recruitment far away from the mother trees would significantly exceed recruitment near the mother tree, since seed shadow overlapping would increase with distance. This would be the case for plant species dispersed by medium to large birds or mammals such as jays (*Garrulus glandarius*) and cassowaries (*Casuarius casuarius*) or foxes (*Vulpes vulpes*) that disperse large amounts of seeds away from the mother tree raising secondary peaks in the dispersal curve (Gómez, 2003; Jordano et al., 2007; Westcott et al., 2005).

7. Conclusions and future venues

Integrative approaches launched an intense research agenda on dispersal ecology in the last decades by merging plant population ecology, behavioural ecology of dispersal agents, ecology of movement, population genetics, and spatial ecology (Damschen et al., 2008; Jordano, 2007; Sork et al., 1999). This synthesis provides novel insights as to how (and how much) propagules move across the landscape assisted by vertebrates in a wide range of ecosystems (Dennis et al., 2007; Levey et al., 2002). As frugivores disperse propagules they also move the genotypes harboured in their seeds, and yet, their joint genetic and demographic effects for plant populations are still poorly understood.

In this article, we highlighted the importance of seed dispersal mediated by vertebrates in setting the spatial distribution of maternal progenies in the seed rain. This aspect could have pervasive consequences for plant performance that might explain natural regeneration success (or failure) patterns across the landscape. The incorporation of highly polymorphic molecular markers based on DNA becomes a reliable approach to identifying maternal progenies in frugivore-generated seed rains on an individual basis. From the existing literature, we can derive the following generalizations:

- (1) Frugivore-derived seed rains capture the selective foraging movements mediated by dispersal agents that deliver different subsets of maternal progenies among microhabitats or sites across the landscape;
- (2) Frugivore activity results in demographic, spatial, and numerical limitations. Molecular data revealed that non-random

foraging movements also resulted in genetic limitations in the seed rain;

- (3) Maternally-structured seed rains combine microhabitats with a high degree of seed shadow overlapping (hotspots of mother trees) with microhabitats with a strong aggregation of maternal progenies (hotspots of kin propagules);
- (4) Scarce empirical evidence available so far document that the genetic imprint set by frugivores in the seed rain endures through subsequent demographic stages, at least through the early recruitment.

In spite of these advances, we still lack a comprehensive picture of how dispersal agents (or the lack of them) drive the genetic aspects of the regeneration patterns in plant populations. It is widely accepted that recruitment success relies on distance- and density- dependent processes as envisioned by the JC model. However, recruitment might also depend on the genetic relatedness among neighbouring seeds. How this unexplored facet of dispersal mutualisms explains natural regeneration patterns within the JC framework remains to be understood in order to make accurate predictions on the role of different frugivore guilds on plant population fate.

It is critical to keep the momentum gained in seed dispersal and dispersal mutualism studies in the last decades going. As this field moves forward integrating different ecological and evolutionary disciplines, it is time to develop clear definitions and expectations for genetic consequences of dispersal mutualisms beyond distance- and density-effects.

Future work might address some of these key questions:

1. *How do different demographic processes interact to modify the genetic footprint set by frugivorous vertebrates?* Other ecological processes play an important role in the non-random distribution of recruits and/or in their genetic structure in plant populations. For example, mating patterns and pollen movement (Ashman et al., 2004), secondary dispersal (Vander Wall and Longland, 2004), seed predation (Forget et al., 2005), pathogens and herbivory activity (Antonovics and Ellstrand, 1984) and landscape features (Damschen et al., 2008). The interplay of ecological factors combined with evolutionary forces (gene flow, genetic drift, selection) sets the seed rain on the ground and shapes the genetic footprint, ultimately leading to recruitment patterns in plant populations. Experimental studies should complement field data in order to estimate the relative importance of each relevant process.
2. *What is the temporal variability in seed dispersal processes?* All studies discussed above present an accurate picture of how dispersal agents distribute maternal progenies across the landscape after one or few fruiting seasons. Studies entailing temporal variability are required to quantify how these patterns change across years in response to temporal variation in foraging resources that dictate the movement of dispersal agents.
3. *Which dispersal agents have the most significant impact on the genetic and demographic outcomes?* Ideally we should be able to tease apart the genetic and demographic consequences of each dispersal agent comprising the frugivore guild of plant communities. Currently, one of the most difficult tasks in dispersal ecology consists in tracking the differential contribution of different frugivores to set maternal correlations in the seed rain (Jordano et al., 2007). This analysis will provide robust predictions on the demo-genetic consequences of gaining or losing seed dispersal agents in plant populations communities. While the seed dispersal effectiveness concept (Schupp, 1993; Schupp et al., 2010) is designed to address the demographic

outcomes, there is presently no similar framework that integrates the genetic with the demographic aspects.

4. *How can we integrate tools from plant population ecology and genetics to more effectively address these questions in a population genetic framework?* Genetic tools and the population genetic framework provide valuable tools for plant ecologists to gain a quantitative understanding of the role of dispersal mutualisms in shaping ecological and evolutionary features in plant populations. They offer a straightforward means to link foraging movements by dispersal agents with genetic connectivity patterns across the landscape (Broquet and Petit, 2009). More interestingly, genetic estimates of dispersed propagules can be converted into genetic variables (N_{em}) readable for genetic models. This will provide us with valuable insights into the role of dispersal vs. other evolutionary forces such as drift, selection and mutation.
5. *What are the demo-genetic consequences for plant populations of disrupting dispersal mutualistic interactions?* It is a timely goal to evaluate to what extent human-induced changes in the landscape (such as forest fragmentation, defaunation, or species introduction) alter seed shadows, seed rain patterns and importantly the distribution of maternal progenies in the seed rain across the remaining landscape e.g. Wang et al. (2007).

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