

NEWS AND COMMENTARY

Direct monitoring of long-distance pollen and seed dispersals

How fat is the tail?

Olivier J Hardy

Heredity (2009) **103**, 437–438; doi:10.1038/hdy.2009.120; published online 16 September 2009

Seed and pollen dispersals are key parameters in shaping the dynamics and evolution of plant populations, as they affect both colonization processes and genetic exchanges among individuals. Our knowledge of the range of distances crossed by seeds or pollen has been greatly improved during the last two decades by using highly polymorphic molecular markers, such as microsatellites (Smouse and Sork, 2004). By matching genotypes, molecular markers permit the retrospective identification of the fathers of seeds collected from known mothers (pollen dispersal), or even both parents of established seedlings (seed and pollen dispersals), provided that the actual parents are among the tested adults (Jones and Ardren, 2003). With these techniques in hand, ‘molecular ecologists’ have been able to monitor, fairly accurately, pollen or seed dispersal distances in many plant species up to a few tens or hundreds of meters. However, many of these studies have reported a non-negligible fraction of seeds or seedlings with parent(s) lying outside the study area, in which all potential progenitors could be genotyped, an area often smaller than 1 km². Evidence for ‘long-distance’ dispersal was there, but assessing the tail of the distribution in terms of frequency and distances crossed remained elusive (Nathan, 2006). The study by Kamm *et al.* (2009) in this issue sheds light on this question. They performed paternity and parentage analyses over an area of 100 km² in the insect-pollinated tree *Sorbus domestica*, which is scattered in European forests. They observed that ca. 1% of pollen dispersal events occurred over 12 to 16 km and that the fleshy fruits of this tree, dispersed by birds and mammals, can be transported over 10 km. These pollen and seed dispersals events actually connected two sub-populations isolated by an agricultural landscape unsuitable for the species. Obviously, these sub-populations were not isolated genetically and this is consequential for their management and for conservation issues. Most importantly, these results contri-

bute to quantifying the importance of long-distance dispersal both in terms of distance range and frequency for insect-pollinated and animal-dispersed forest trees.

How did this study succeed in detecting long-distance dispersal (>1 km)? The reason does not lie on the molecular side—developing 10 microsatellite loci and 1 chloroplast marker for a species is nothing exceptional nowadays. The reason lies in the near exhaustive sampling of a very low-density population over a large area. This was possible because *S. domestica* has been monitored for 20 years by foresters in a 100 km² area, and Kamm *et al.* (2009) were confident that their sample of 189 adult trees was very near exhaustive. Imagine a species with a density of one individual per hectare. A similar study could not be conducted over such a large scale because inventorying and genotyping ca. 10000 individuals might become unaffordable. Moreover, the same set of markers would not be polymorphic enough to exclude all non-parental potential fathers of a seed (ca. 10000 individuals), or even less all potential parent pairs of a seedling (ca. 10000² individuals). Therefore, to gather more data on long-distance dispersal, new studies should focus on low-density species that can be inventoried over large areas. However, are measures of dispersal obtained on a low-density species representative of a high-density species with the same dispersal vectors?

Density can affect dispersal in two ways. First, it may affect animal behavior, and when density is correlated to landscape structure (for example, under habitat fragmentation), the latter can also alter wind movements. Birds or insects may forage more locally in search of fruits or nectar in a high-density population, thereby reducing the dispersal distances of seeds or pollen. Plant density can affect wind patterns and the aerodynamic properties of pollen dispersal, and open forest often promotes further-ranging dispersal. However, dispersers’ behavioral responses, as well as wind patterns, can be complex and not necessarily predict-

able. Second, pollen dispersal is ‘effective’ (that is, contributes to the next generation) only if pollen reaches a conspecific individual. Therefore, the density and spatial distribution of conspecifics also condition effective pollen dispersal. The mean effective pollen dispersal distance is expected to be lower under high density and/or when individuals are aggregated. Fitting a curve to the distance distribution of inferred pollen dispersal events, as did Kamm *et al.* (2009), is, therefore, of limited interest if one wishes to extrapolate the results to species or populations with other spatial distributions of individuals. However, detected dispersal events can be treated as observations from a probability distribution to fit a dispersal kernel. A dispersal kernel is a model representing the probability density that a pollen grain or a seed lands at a given position away from the source individual, and reflects, therefore, the pattern of primary dispersal. Effective dispersal depends on this kernel and on the spatial arrangement of suitable sites (a conspecific stigma in the case of pollen, a suitable habitat in the case of seeds). Dispersal kernels are precisely what is needed to model the impact of dispersal on population dynamics and gene flow in a landscape. If the behavior of dispersal vectors is not strongly affected by population density, a kernel fitted on a low-density species may be quite representative of the kernel of other species sharing the same dispersal vectors and occurring in the same type of habitat.

Assessing the distance range of ‘long-distance’ dispersal events that represent a minute fraction of all events is not just a habit of maniac investigators in search of ever more accuracy. The important question is how fat is the tail of the dispersal kernel (that is, how leptokurtic; Nathan, 2006). A fat-tailed kernel means that the final fraction of longest dispersal events goes far away, potentially orders of magnitude over the mean dispersal distance, whereas they would be restricted to a few times the mean dispersal distance under a thin-tailed kernel. In a changing environment and/or when suitable habitats are fragmented and populations follow metapopulation dynamics (frequent local extinction/recolonization), whether a seed can ever be transported over more than 10, 100 or 1000 km can strongly affect the population and evolutionary dynamics of the species for at least two reasons. First, because a single seed established in an empty site may

potentially lead to a large population generations ahead. Second, because the longer the dispersal events, the higher the chances that the genetic content of the propagule will be different from the recipient population and the higher the evolutionary impact of the event. Hence, long-distance dispersal events can contribute disproportionately to species persistence in fragmented landscapes and/or under a changing environment (Trakhtenbrot *et al.*, 2005). Reliable data on long-distance dispersal are, therefore, critical to realistically parameterize models predicting how species may respond to a changing environment in terms of their population dynamics and microevolution.

Evolutionary changes resulting from past environmental changes can also be investigated using today's patterns of genetic variation at the species level. The study by Palma-Silva *et al.* (2009) in this issue is a good example of phylogeographic investigation on a tropical plant in a particularly damaged hotspot of diversity—the Brazilian Atlantic Rainforest. Using the same types of genetic markers as Kamm *et al.* (2009), that is nuclear microsatellites and chloroplast DNA sequences, the authors analyzed geographic patterns of genetic variation at the species level. They provide compelling evidence to recon-

struct the biogeographic history of the species, which can reveal how Pleistocene climate changes impacted the distribution of vegetation. Numerous phylogeographic studies have been carried out in temperate zones (notably Europe and North America) and have improved our understanding of species responses to the well-documented environmental changes that have occurred over the past 20000 years. In contrast, most tropical areas are far less well studied while the past climate changes that they have undergone are also less well documented. Given that most hot spots of biodiversity lie in tropical areas, there is an urgent need for more investigations of historical biogeography and phylogeography to assess how species responded to past changes and predict how they might cope with current changes.

Dr OJ Hardy is at the Evolutionary Biology and Ecology Unit, Université Libre de Bruxelles, Faculté des Sciences, CP160/12, 50 avenue F. Roosevelt, B-1050 Brussels, Belgium.

e-mail: ohardy@ulb.ac.be

Jones AG, Ardren WR (2003). Methods of parentage analysis in natural populations. *Mol Ecol* **12**: 2511–2523.

Kamm U, Rotach P, Gugerli F, Siroky M, Edwards P, Holderegger R (2009). Frequent long-distance gene flow in a rare temperate forest tree (*Sorbus domestica*) at the landscape scale. *Heredity* **103**: 476–482.

Nathan R (2006). Long-distance dispersal of plants. *Science* **313**: 786–788.

Palma-Silva C, Lexer C, Paggi MG, Barabá TT, Bered F, Zanettini BM-H (2009). Range-wide patterns of nuclear and chloroplast DNA diversity in *Vriesea gigantea* (Bromeliaceae), a neotropical forest species. *Heredity* **103**: 503–512.

Smouse PE, Sork VL (2004). Measuring pollen flow in forest trees: an exposition of alternative approaches. *For Ecol Manage* **197**: 21–38.

Trakhtenbrot A, Nathan R, Perry G, Richardson DM (2005). The importance of long-distance dispersal in biodiversity conservation. *Divers Distrib* **11**: 173–181.

Editor's suggested reading

Bacles CFE, Ennos RA (2008). Paternity analysis of pollen-mediated gene flow for *Fraxinus excelsior* L. in a chronically fragmented landscape. *Heredity* **101**: 368–380.

de-Lucas AI, Robledo-Arnuncio JJ, Hidalgo E, González-Martínez SC (2008). Mating system and pollen gene flow in Mediterranean maritime pine. *Heredity* **100**: 390–399.

Krauss SL, He T, Barrett LG, Lamont BB, Enright NJ, Miller BP *et al.* (2009). Contrasting impacts of pollen and seed dispersal on spatial genetic structure in the bird-pollinated *Banksia hookeriana*. *Heredity* **102**: 274–285.

Lourmas M, Kjellberg F, Dessard H, Joly HI, Chevallier M-H (2007). Reduced density due to logging and its consequences on mating system and pollen flow in the African mahogany *Entandrophragma cylindricum*. *Heredity* **99**: 151–160.

Nakanishi A, Tomaru N, Yoshimaru H, Manabe T, Yamamoto S (2009). Effects of seed- and pollen-mediated gene dispersal on genetic structure among *Quercus salicina* saplings. *Heredity* **102**: 182–189.