npg

NEWS AND COMMENTARY

Pollen, seeds and genes: the movement ecology of plants

P Jordano

Plants stand still, but their genes don't. This simple assertion, which provided the title for a special symposium of the British Ecological Society in 2000, captures the essential idea of how plants 'move'. We have seen a tremendous recent advance in our understanding of dispersal processes in plant populations (Levin et al., 2003; Cousens et al., 2008), in parallel with the recent progress on the ecology of the movement of living organisms in general (Nathan et al., 2008). The dispersal of plant propagules, either pollen grains or seeds, pervasively affects genetic patterns because it underpins the demographic regeneration process that depends on successful establishment of new individuals. Harper's (1977, p 29) statement that 'a plant is only the means by which a seed produces more seeds' emphasizes the pivotal role that the seed cohort, produced at the end of each reproductive episode, has in plant demography.

Recent attempts to understand this key role of dispersal processes in plants stem from pioneering work in the late eighties and nineties of the past century, notably Ennos (1994). This highly cited *Heredity* paper was the first to model the relative contributions of seed and pollen movement to the total gene flow in plant populations. Ennos developed his model based on the fact that, for biparentally or paternally inherited DNA, gene flow results from both pollen and seed dispersal events; in contrast, for maternally inherited DNA, only seeds disperse the genes. As a result, levels of population differentiation should vary for markers with distinct types of inheritance. Therefore, if estimates of population differentiation (that is, F_{ST} values) are available for both types of markers, the relative contributions of pollen and seed dispersal to the total gene flow can be derived. Previous attempts in this direction had either failed to distinguish between the two components of dispersal (pollen and seed) or had addressed only one of them (pollen). When mar-

kers obtained from the organelle genomes became widely available for scrutiny, approaches based on Ennos' suggestions were readily applied. Chloroplast genomes, maternally inherited in most angiosperms and paternally derived in gymnosperms, and/or mitochondrial genomes, maternally inherited in most plants, provided a useful instrument to measure the population differentiation and to compare with measures derived from nuclear markers.

The central contribution of Ennos (1994) was therefore to provide a testable model relating the estimated levels of gene flow for the different types of markers to the levels of interpopulation pollen and seed dispersal. This opened new avenues to understand the distinct signals that seed and pollen dispersal events have in plant populations (Petit et al., 2005). For example, the available data for the *Quercus* oak complex evidenced an extreme ratio of ~ 200 between differentiation values for nuclear (biparentally inherited), $F_{st(b)} = 0.037$, vs maternally inherited markers, $F_{st(m)} = 0.884$ (Ennos, 1994). Whereas the pollen flow in outbreeding, wind-pollinated *Quercus* can be extensive, acorn dispersal is likely much more local, either in disturbed stands, wherein the major acorn dispersers are absent or have low abundances, or in closed stands, wherein opportunities for seed establishment are very rare. Most data available until recently were for wind-pollinated and abiotically dispersed seed species, and consequently most evidence indicated that gene flow among established populations tends to occur primarily through the pollen (Petit et al., 2005). However, an increasing number of species with animal-dispersed seeds for which regular long-distance dispersal has been demonstrated (for example, Hardesty et al., 2006; Jordano et al., 2007), or the robust characterization of long-distance wind dispersal of seeds (Bacles et al., 2006), caution against generalization. Most likely, pollen and seed dispersal interact with each other and can poten-

tially determine a variety of situations according to the life-history traits of species and the specific population and landscape settings. In any case, teasing apart their relative contributions is a first step to understanding the factors that determine the effective neighbourhood size (N_b) in plant populations (Wright, 1943) as a function of the variance of parent–offspring dispersal distance (σ^2) and the effective population density (d): $N_b = 4\pi\sigma^2 d$. Given that σ^2 is a function of the dispersal of both haploid (pollen) and diploid (seed) propagules, each dispersal stage will have an influence on neighbourhood size in proportion to their respective variances (Grivet et al., 2009).

Dispersal limitation—that is, the demographic process by which seeds fail to reach and recruit in portions of the forest (Harms et al., 2000; Muller-Landau et al., 2002)—can have far-reaching consequences not only for the demography of plants but also for the fine-scale patterns of genetic structure and the local species composition of forest stands (Vekemans and Hardy, 2004). In particular, dispersal of seeds not only entails the movement of new genotypes, but also determines how these are distributed among different microsites and therefore might have a larger influence on the neighbourhood size and local genetic structure (that is, on the spatial patterns of relatedness among dispersed progeny). For instance, imagine a progeny of 100 seeds, fathered by, say, $N_{ep} = 8$ pollen donors. These seeds can be scattered by animal frugivores among 10 distinct microsites, or be deposited in a clump of all the 100 seeds in a single site. The more clumped dispersal of the latter case could create a genetic bottleneck despite a large effective number of sires in this progeny, given that all new genotypes are dispersed to the same microsite. Thus, the local genetic structure of new recruits can be extremely marked, owing to restricted, clumped dispersal, even when pollen flow has been extensive (Torimaru et al., 2007; Grivet et al., 2009). The approach outlined by Grivet et al. (2009) attempts to dissect N_e, the effective number of parents for a given patch of new recruits, into the numbers of pollen (N_{ep}) and seed parents (N_{em}) computed from kinship coefficients. Their analysis of the fine-scale genetic structure of *Quercus lobata* patches indicates that, despite a relatively large contribution of pollen dispersal to gene flow, highly restricted acorn dispersal reduced significantly the

effective number of trees contributing propagules, either by pollen or by seed, to a given patch of seedlings. Given the omnipresence of the seed dispersal limitation in many natural settings (Harms *et al.*, 2000; Muller-Landau *et al.*, 2002), even efficient dispersal of pollen could hardly compensate the short-term effects of highly aggregated seed dispersal. Seed dispersal limitation can therefore pervasively constrain the extent to which male gametic gene flow contributes to local genetic structure.

All the above conceptual and methodological approaches to assess the contributions of pollen and seed movements to the overall gene flow levels in natural plant populations hold great promise for the preservation of natural levels of genetic diversity and for the cohesiveness of plant metapopulations at the landscape level. Contemporary dispersal events underpin the connectedness among isolated patches, fragments or demes occurring in complex landscapes. We are still far from understanding the proximate factors that contribute to such connectedness (Urban and Keitt, 2001; Levey *et al.*, 2008). For example, when animals mediate pollen or seed dispersal, a particular species might be responsible for maintaining this connectedness among certain patches by contributing long-distance dispersal events; other species might be responsible for maintaining the effective *in situ* regeneration needed for a particular patch to persist in time. Thus, extinction of mutualists that significantly and distinctly contribute to these components of pollen and/or seed flow can ultimately collapse the connectedness of the metapopulation.

The contribution of Ennos (1994) pioneered the spatially explicit analysis of movement patterns in plants, as the ability to dissect the pollen and seed contributions to gene dispersal represents a key advance in landscape genetics. Understanding the fundamentals of dispersal and its genetic bases in natural populations represents a

challenge from both theoretical and methodological perspectives. Ennos envisioned these challenges by advocating a more integrative and quantitative analysis of organelle genomic variability, taking advantage of the established fact that different marker types can be used in combination to address the fundamental biological questions about dispersal.

Conflict of interest

Bacles C, Lowe A, Ennos R (2006). Effective seed dispersal across a fragmented landscape. *Science* **311**: 628–628.

Cousens RD, Dytham C, Law R (2008). *Dispersal in Plants: A Population Perspective*. Oxford University Press: Oxford, UK.

Ennos RA (1994). Estimating the relative rates of pollen and seed migration among plant populations. *Heredity* **72**: 250–259.

Grivet D, Robledo-Arnuncio JJ, Smouse PE, Sork VL (2009). Relative contribution of contemporary pollen and seed dispersal to the effective parental size of seedling population of California valley oak (*Quercus lobata*, Née). *Mol Ecol* **18**: 3967–3979.

Hardesty BD, Hubbell SP, Bermingham E (2006). Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecol Lett* **9**: 516–525.

Harms KE, Wright SJ, Calderon O, Hernández A, Herre EA (2000). Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**: 493–495.

Harper JL (1977). *Population Biology of Plants*. Academic Press: London, UK.

Jordano P, García C, Godoy JA, García-Castaño JL (2007). Differential contribution of frugivores to complex seed dispersal patterns. *Proc Natl Acad Sci USA* **104**: 3278–3282.

Levey DJ, Tewksbury JJ, Bolker BM (2008). Modelling long-distance seed dispersal in heterogeneous landscapes. *J Ecol* **96**: 599–608.

Levin S, Muller-Landau HC, Nathan R, Chave J (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annu Rev Ecol Evol Syst* **34**: 575–604.

Muller-Landau HC, Wright SJ, Calderón O, Hubbell SP, Foster RB (2002). Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In:

Levey DJ, Silva WR, Galetti M (eds). *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International: Wallingford, UK. pp 35–53.

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D *et al.* (2008). A movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* **105**: 19052–19059.

Petit R, Duminil J, Fineschi S, Hampe A, Salvini D, Vendramin G (2005). Comparative organization of chloroplast, mitochondrial and nuclear diversity in plant populations. *Mol Ecol* **14**: 689–701.

Torimaru T, Tani N, Tsumura Y, Nishimura N, Tomaru N (2007). Effects of kin-structured seed dispersal on the genetic structure of the clonal dioecious shrub *Ilex leucoclada*. *Evolution* **61**: 1289–1300.

Urban D, Keitt T (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology* **82**: 1205–1218.

Vekemans X, Hardy O (2004). New insights from fine-scale spatial genetic structure analyses in plant populations. *Mol Ecol* **13**: 921–935.

Wright S (1943). Isolation by distance. *Genetics* **28**: 114–138.

Further reading

Ellstrand N (1992). Gene flow among seed plant populations. *New For* **6**: 241–256.

Slatkin M (1985). Gene flow in natural populations. *Annu Rev Ecol Syst* **16**: 393–430.

Editor's suggested reading

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.

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.

Volis S, Zaretsky M, Shulgina I (2010). Fine-scale spatial genetic structure in a predominantly selfing plant: role of seed and pollen dispersal. *Heredity* **105**: 384–393.

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.

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.