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Research Focus

Is pollen limited? The answer is blowin' in the wind

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Pollen from wind-pollinated trees has traditionally been assumed to be abundant and to travel long distances, resulting in extensive gene flow. However, recent empirical work by Knapp *et al.*, genetic analysis by Sork *et al.*, and theoretical models by Satake and Iwasa conclude that short-distance dispersal of limited pollen might be common and play an important role in causing the highly variable seed production (masting) frequently observed in such species. Pollen movement might be sufficiently restricted that increased fragmentation could ultimately bring about reproductive failure in some species.

If wind-dispersed pollen were limited, you wouldn't know it from the millions of hay-fever sufferers worldwide. Indeed, in the spring it scarcely seems possible to avoid the stuff if you live in an area that is or used to be a boreal or temperate forest, typically dominated by one or more wind-pollinated species of conifer, such as pines, firs and spruces, or broad-leafed, usually deciduous, trees including oaks and beeches. Nonetheless, recent work on oaks by Knapp *et al.* [1], looking at the relationship between seed production and local density of flowering conspecifics, and that by Sork *et al.* [2], estimating effective pollen dispersal distance, both conclude that pollen flow might be far more limited than was previously suspected. In combination with recent models developed by Satake and Iwasa [3,4], these studies provide the strongest support to date that pollen limitation could be a crucial driving force behind the highly variable and widely synchronous seed crops that are characteristic of wind-pollinated masting species.

Although one's nose can readily portend the presence of pollen in general, pinning down the movement of pollen from a specific source is more of a challenge. Knapp *et al.* [1] took an indirect approach to this problem, relating acorn production of individual trees to the number of conspecifics flowering within a given distance in a stand of blue oak *Quercus douglasii*, which, similar to other oak species, is primarily an outcrosser. Results varied among years but, in years of relatively good acorn production, there was usually a positive correlation between the number of neighboring trees producing pollen and subsequent acorn production, with the strongest associations occurring when considering the number of trees flowering within a radius of 60–80 m. The implication of this finding is that reproduction in this widespread California species might be limited by the availability of pollen produced by trees growing within a strikingly short distance, of the order of as little as 60 m.

Sork *et al.* [2] took a decidedly different approach, combining allozyme and microsatellite analyses with the recently developed TWOGENER model [5–7], a molecular analysis of variance designed to characterize pollination patterns using a relatively small sample of offspring and the inferred 'pollen pool' sampled by the seed parents. Based on a sample of 211 offspring from 21 adult valley oaks *Quercus lobata* in one year, they estimated that the average effective number of pollen donors per tree was less than four and that the average effective distance of pollen movement was only 65 m. Even if the striking concordance of this estimate with the findings of Knapp *et al.* is a coincidence, their findings lend important support for the hypothesis that, contrary to previous assumptions, dispersal of pollen in wind-pollinated trees might be very short, potentially even less than dispersal distances of the far larger seeds, which can be moved hundreds or thousands of meters by avian and mammalian predators [8].

With such surprising support for both pollen limitation and limited pollen dispersal, it is fortuitous that Satake and Iwasa [3,4,9] have focused on the potential role that pollen limitation could play in producing the highly variable but geographically synchronized seed crops (masting behaviour, Box 1) that are characteristic of many wind-pollinated species. In their model, which follows up on earlier work by Isagi *et al.* [10], the effect demonstrated by Knapp *et al.*, whereby reproduction is determined in part by local availability of pollen, is due to what they call 'pollen coupling'. Without it, trees in the virtual forest that they model can produce highly variable seed crops but do so independently of one another, and thus do not mast. By contrast, dependence of seed set on the production of locally produced pollen results in partial or complete synchrony of reproduction among individuals. The authors found that pollen coupling could potentially synchronize reproduction over much longer distances than that over which direct pollen exchange was occurring. Perhaps most surprisingly, pollen coupling was found to be potentially even more important in synchronizing reproduction than were synchronous environmental fluctuations (the Moran effect [11]), which could not produce a high positive correlation in seed production in the absence of pollen limitation.

Taken together, these papers suggest that pollen limitation and limited pollen dispersal, long known to be important in animal-pollinated species [12], might be playing an equally crucial role in the reproductive lives of wind-pollinated species. Selection for masting, for example, has traditionally been thought to come largely, if not exclusively,

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Box 1. Masting behaviour

Mast seeding, or masting, is the intermittent production of large seed crops by a population of plants [24]. The term 'masting' is usually not applied to semelparous species, such as bamboo, that flower only once and die, but rather to iteroparous species, such as boreal conifers and temperate oaks and beeches, which produce highly variable seed crops from year to year. Masting can be a consequence of 'resource matching', whereby plants produce more or fewer seeds depending on the fluctuating resources available in a particular year. However, in some cases, plants apparently switch resources between growth and reproduction, providing evidence that masting is an adaptation to some ecological challenge.

The two most frequently discussed factors that might select for masting are seed predation and wind pollination. The first, known as predator satiation, occurs when a higher proportion of seeds escape predation in years of good seed production, or 'mast' years. The second, pollination efficiency hypothesis, requires some degree of pollen limitation and occurs when wind-pollinated plants, such as many masting temperate and boreal species, achieve greater pollination efficiency by concentrating their reproductive effort in particular years. Support for both these hypotheses exists. Masting might, in many cases, be favoured by a combination of these and, in some cases by additional 'economies of scale' associated with animal dispersal, seed size, or accessory costs of reproduction [14].

Masting can be synchronized over very large geographical areas, sometimes approaching continental scales [25], and has been reported to involve dozens or more sympatric species in the tropical Dipterocarpaceae [26]. Masting is an example of a 'pulsed resource' with potentially dramatic consequences to the communities in which it occurs. In temperate eastern North America, for example, masting by oaks has been shown to initiate cascading effects on the community, affecting population dynamics starting with the mice and deer that eat the acorns, moving on to the ticks living on the mice and deer and both the defoliating gypsy moths *Lymantria dispar* and songbirds whose nests are depredated by the mice, and reaching as far as the bacterium *Borrelia burgdorferi*, which lives in the ticks and is responsible for Lyme disease [27–29].

as a consequence of larger, synchronized seed crops experiencing proportionately lower predation, known as the 'predator satiation' hypothesis [13,14]. The above studies ensure that the alternative 'wind pollination' hypothesis, whereby masting yields higher fitness by allowing species to achieve greater pollination efficiency through synchronization of flowering [14,15], will not be ignored in future work (Box 1).

Knapp *et al.* and Sork *et al.* raise an additional issue regarding the conservation implications of pollen limitation to the species they studied, both of which are threatened and subject to increasing fragmentation because of a combination of landscape conversion and lack of regeneration (Box 2). As stands and individuals of these species become more isolated, the potential exists for neighbourhood sizes to decline to the point where sufficient pollen would not be available to some individuals, leading to additional genetic isolation and reproductive failure and ultimately facilitating the demise of these keystone species. Clearly, a general conservation strategy for California oak is long overdue and will need to include a plan for maintaining densities sufficient to ensure efficient pollen transfer.

In spite of these studies, the importance of pollen limitation in wind-pollinated species is an issue that remains far from closed. For example, the significant relationships between the number of pollen-producing neighbors and subsequent acorn production found by

Box 2. Threats to California's oaks

The eight major species of tree oaks in California cover an estimated 4.5×10^6 ha, or ~10% of the state [30], and provide shelter and food for a vast array of wildlife species, including over 300 vertebrates and an estimated 5000 species of insects [31]. In spite of this, and the fact that California's oak woodlands include some of the largest remaining old-growth forest in the USA [32], relatively little of these woodlands are protected, with >80% in private ownership [31]. Thus, land conversion of oak woodlands for range improvement and development continues to be a major conservation issue, with losses being of the order of 10 000 ha y^{-1} [30].

Beyond this, oak woodlands in California face at least two major threats. First is inadequate regeneration, which appears to be affecting at least three of the eight species (blue oak *Quercus douglasii*, valley oak *Q. lobata*, and Engelmann oak *Q. engelmannii*) throughout much if not all their range. Whether poor regeneration is a result of overgrazing, fire suppression or altered landscape composition, including the almost universal replacement of native perennial grasses with introduced European annual grasses, is unclear, although all probably contribute to the problem at some level [31,33].

A second, more recent threat is from the disease 'sudden oak death', or SOD. SOD was first detected in 1995 and eventually identified as caused by a species of *Phytophthora* – the same genus of fungus-like organism responsible for the Irish potato famine as well as a wide range of other forest and crop diseases. Two widespread species of California oaks, the coast live oak *Q. agrifolia* and California black oak *Q. kelloggii*, are particularly susceptible to SOD, as is tanoak *Lithocarpus densiflorus*, a closely related species that grows primarily in coastal forests. SOD has so far killed thousands of trees in coastal areas of the state both north and south of the San Francisco Bay region. A variety of other species, including coast redwood *Sequoia sempervirens* and Douglas-fir *Pseudotsuga menziesii*, are also susceptible to the disease, but appear to suffer primarily foliar damage and have not yet been reported to suffer significant mortality.

Together, poor regeneration and SOD threaten at least five of eight species and virtually all oak habitats in California. Unless these problems are confronted and solved, a significant fraction of California's unique landscape is likely to be irrevocably altered within the foreseeable future.

Knapp *et al.* was significant in only two out of four years. Furthermore, it was not possible with their data, taken over a relatively limited area, to test whether pollen coupling was restricted to the 60–80-m radii that they examined, or whether it could have been stronger if a larger area, and thus more trees, had been included. Sork *et al.*'s results indicating short-distance pollen flow are comparable to those reported previously for another species of oak (*Q. alba*) in the Missouri Ozarks [5], but both studies rely on the genetic characteristics of relatively few samples massaged by a statistical model that, as Sork *et al.* point out, remains to be 'ground-truthed' using direct paternity analyses along with larger sample sizes taken over more years. Indeed, there exists considerable evidence from a combination of techniques, including direct parentage assignment [16–18], spatial autocorrelation analyses [17–20], and interpopulational F_{ST} comparisons [21,22] to suggest that gene flow in oaks can apparently be much farther than the short distances suggested by both Knapp *et al.* and Sork *et al.*'s work, and thus that pollen is less limited than these studies suggest. Part of this discrepancy could be due to differences in the precise aspect of gene flow being measured by the various techniques [23]. At the very least, however, it is possible that the results found by Knapp *et al.* and Sork *et al.*, studying oaks that usually grow in relatively low-density, savanna situations, might differ considerably from results from other species that grow in denser landscapes.

The good news is that such contrasting results give excellent indications of the potential for a rousing controversy over the role of pollen limitation and limited pollen dispersal in shaping the genetic structure and reproductive ecology of wind-pollinated trees. The answer might be in the wind but, with increasingly powerful molecular and analytical techniques combined with sophisticated models, the time is coming when we will be able to do more than just watch as it blows on by.

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Selection for uniformity: xenophobia and invasion success

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One reason why ants fascinate us is the seemingly bipolar nature of their social interactions: harmonious cooperation within, and extreme aggression across, colonies. Recent work by Giraud and colleagues and by Tsutsui and colleagues explores a behavioral outlier in this dichotomy, the invasive Argentine ant *Linepithema humile*. Introduced *L. humile* often form unicolonial societies in which conflict between colonies is absent.

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