Towards the theory of pollinator-mediated gene flow

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I present a new exposition of a model of gene flow by animal-mediated pollination between a source population and a sink population. The model's parameters describe two elements: (i) the expected portion of the source's paternity that extends to the sink population; and (ii) the dilution of this portion by within-sink pollinations. The model is termed the portion-dilution model (PDM). The PDM is a parametric restatement of the conventional view of animal-mediated pollination. In principle, it can be applied to plant species in general. I formulate a theoretical value of the portion parameter that maximizes gene flow and prescribe this as a benchmark against which to judge the performance of real systems. Existing foraging theory can be used in solving part of the PDM, but a theory for source-to-sink transitions by pollinators is currently elusive.

Keywords: foraging theory; pollen; pollination

1. INTRODUCTION

Pollen-mediated gene dispersal is an important influence on the genetic structure and evolution of plant populations (Fenster 1991; Ellstrand & Elam 1993; Ennos 1994). For example, gene dispersal among populations (gene flow) counteracts the effects of natural selection or genetic drift and can thus prevent population divergence (Slatkin 1985). Recently, the study of pollen-mediated gene flow has become an imperative because of concern over the spread of engineered genes from genetically modified crops into conventional agriculture by cross-pollination (Lutman 1999; Hails 2000).

In a seminal paper, Bateman (1947) proposed that animal-mediated pollen dispersal could be predicted by compounding models of pollinator movement and pollen transfer. Bateman's approach has been elaborated (Morris 1993; Harder & Barrett 1996) and modified to predict the dispersal of genes (Cresswell *et al.* 2002). The model of Cresswell *et al.* (2002) encapsulates the conventional view of animal-mediated pollination and can therefore provide a foundation for the theory of pollinator-mediated gene flow.

2. DERIVATION OF A MODEL FROM THE CONVENTIONAL VIEW OF ANIMAL-MEDIATED POLLINATION

A pollinator that visits a series of monomorphic, cosexual flowers as part of its foraging bout typically picks up friable pollen from a source flower and then deposits it on stigmas during subsequent flower visits. Diminishing amounts of source pollen are deposited during successive flower visits in a process termed 'pollen carryover' (Lertzman & Gass 1983; Morris *et al.* 1994). Carryover

dwindles as the pollen on the pollinator's body is exhausted by deposition on stigmas and by the pollinator's grooming activities (Thomson 1986).

Deposition of the source flower's pollen may yield paternity. Consider that the source flower's pollen fertilizes a fraction of the ovules at the first recipient flower, denoted f_1 , and a lesser fraction at the second recipient, denoted f_2 , and f_v of the ovules at the v th-visited recipient flower (figure 1). This paternity-versus-visits relationship is termed the flower's 'paternity shadow' (Cresswell *et al.* 2002).

Let a source flower's paternity shadow extend to m recipient flowers. When the pollinator visits enough flowers in a source population to become saturated with pollen (i.e. $\geq m$ flowers) followed by enough flowers in a sink population to exhaust source paternity (i.e. $\geq m$ flowers), inspection of figure 2 reveals that when the fertilization of sink flowers is completed the paternity attained by the source population is $\Psi = \sum_{v=1}^m f_v v$, which is the portion of the source population's paternity that extends to the sink in units of fruits full of seed.

When the likelihood that a pollinator arrives at the sink population via the source population is E , the expected source paternity is $E\Psi$. During each bout in the sink, pollinators visit and fertilize an average of $\bar{b}$ flowers, which is termed the pollinators' mean 'residence' (Cresswell *et al.* 2002). During the residence, the source's paternity portion is diluted by within-sink pollinations. When the fertilization of flowers is completed, the amount of source paternity per fertilized sink flower, ξ , is given by $\xi = E\Psi/\bar{b}$, which quantifies the relative contribution of gene flow to seed set (Cresswell *et al.* 2002). This model is here termed the PDM. An example portion-dilution curve for *Brassica napus* (oilseed rape or canola) is given in figure 3.

3. APPLICABILITY OF THE PDM

The exposition of the PDM is straightforward when it is assumed that a sink flower is fertilized completely by a

Figure 1. Paternity shadow of a source flower (darkened) at a series of recipient flowers. The height of the bars indicates the fraction of available ovules that are fertilized by the source flower, f_v . The arrow shows the direction of pollinator movement. The height of the bars diminishes over successive visits and, here, paternity extends over $m = 3$ flowers.

single pollinator visit. The PDM nevertheless applies when fertilization requires multiple pollinator visits (Bell & Cresswell 1998). Consider the scenario in which flowers receive visits from more than one pollinator and the earlier pollinators fertilize more of the ovules than the later ones. Specifically, assume that the proportion of ovules fertilized by the q th-arriving pollinator is given by a monotonically declining function, $\gamma(q)$, whose nature will be determined by the dynamics of inter-pollinator arrival times and post-pollination processes. The q th-arriving pollinator will deliver an expected $\gamma(q)E\Psi$ fruits of source paternity and fertilize $\gamma(q)\bar{b}$ fruits during its residence in the sink population. When these two quantities are each summed across the q pollinators that precede the completion of fertilization, the PDM emerges in its original form uncomplicated by multiple pollinator visits.

It is inconvenient to apply the PDM when the paternity shadow varies. The paternity shadow is most reasonably assumed to be constant in systems of monomorphic, cosexual flowers, but even these may present complications. For example, the intensity of pollinator grooming responds to pollen availability and may affect the paternity shadow (Thomson 1986), but the extent to which grooming varies in time and space is not known. In principle, the PDM also applies to plants with either polymorphic, cosexual flowers (e.g. heterostylous plants) or plants with unisexual flowers, but the characterization of the expected paternity shadow will be complex because it will depend on the frequencies of the different flower types. A similar complexity attends studies of plants with self-incompatibility systems. The requirement for a paternity shadow to be characterized may seem to exclude plants that package their pollen into pollinia from application of the PDM, but it applies nevertheless because although any one pollinator will deposit each pollinium on a particular recipient flower, an *expected* paternity extends across a series of recipient flowers. Overall, therefore, the PDM applies to animal-pollinated plants in general, but the model may be inconvenient to solve in certain instances.

The PDM can be applied to individual plants, where an individual's display serves as the source population. The preceding formula for Ψ is adjusted when the mean residence on a source display is less than m , however. It is thus possible to compound the paternity shadow as shown in figure 2 to derive expressions for the levels of autogamy (Cresswell *et al.* 2002), geitonogamy and outcrossing.

Figure 2. Consequences of pollen carryover from a source population (darkened flowers) caused by a pollinator's subsequent visits to a series of recipient flowers in the sink population. The dark bars indicate the portion of source paternity that extends to the sink population, Ψ . The lightly shaded bars indicate the portion of source paternity that does not reach sink flowers.

Figure 3. An example of a portion-dilution curve. The level of gene flow into a sink population declines as the portion of extrinsic paternity is diluted by within-population pollination. The PDM solution shown here (Cresswell *et al.* 2002) is for bumble-bee-pollinated oilseed rape (*Brassica napus*), where $\Psi = 1.22$ and it is assumed that all pollinators make the source-to-sink transition (i.e. $E = 1$). The number of flowers visited by bees during bouts in the sink population is indicated by 'residence'.

4. IMPLICATIONS OF THE PDM

The three parameters of the PDM expose the influences on gene flow and each is considered successively below.

The shape of the paternity shadows from which it is compounded determines the value of Ψ . What kind of paternity shadow will maximize Ψ and, hence, the level of gene flow? If we exclude shadows in which the fraction of ovules fertilized increases over successive flower visits and those whose shape is non-monotonic, then gene flow is maximized when a source flower fertilizes $1/m$ of the available ovules at each of the m recipient flowers to which the shadow extends. In this case, there is no autogamy because $1/m$ of each recipient flower's ovules is fertilized by each of the m previously visited flowers. The maximum portion of paternity is given by $\Psi_{\max} = (m + 1)/2$ for all $m > 0$, which shows that $\Psi_{\max}$ increases with m . No natural paternity shadow will attain this ideal shape because of the nature of pollen carryover, but $\Psi_{\max}$ provides a benchmark for evaluating real systems.

Natural selection can act on paternity shadows because they affect the level of outcrossing among individuals. Selection for enhanced outbreeding may therefore adapt features that modify pollen carryover, such as floral architecture (Waser & Price 1984), display size (Klinkhamer & de Jong 1993) and floral rewards (Galen & Plowright 1985). Specifically, we should expect selection for features that extend pollen carryover and in this way there may be indirect evolutionary influences on Ψ , which may thereby tend towards $\Psi_{\max}$.

The expected length of pollinator residences in the sink population, $\bar{b}$, is determined by the behavioural responses of the pollinators to patches of plants. Typically, pollinators collect floral rewards and so the length of the residence will be shaped by the economics of foraging. There is a trivial limit to $\bar{b}$ in that a pollinator will not visit more flowers than are present in the patch unless it is willing to entertain revisits to depleted flowers. However, pollinators often visit no more than a minority of the flowers in a patch (Ohashi & Yahara 2002). Theory suggests (Charnov 1976) that a forager is disposed to short residence when it rapidly discerns that the rewards in a patch are lower than elsewhere, perhaps because of its own depletion activities, and when travel is cheap. The combination of the PDM and foraging theory therefore implies that small populations of plants that are adjacent to other conspecific populations are most exposed to pollinator-mediated gene flow.

Solving E , the probability that the pollinator makes the source-to-sink transition, presents the greatest current challenge. The effect on pollinator movements of patchiness in plant dispersion has been studied at a small scale (Cartar & Real 1997; Cresswell 1997, 2000), but solving E requires knowledge of animal movements at the landscape scale. Logistically, this is inconvenient because many pollinators have an extensive foraging range and can therefore fly between widely separated plant populations. For example, honeybees fly up to 10 km from their hive to forage (von Frisch 1950, p. 73) and bumble-bees may have a similar range (Cresswell *et al.* 2000). To investigate E , it would be helpful to invoke theory for guidance, but this is rudimentary at present. What will the theory of E look like? The diffusion–advection approach (Morris 1993; Cresswell *et al.* 1995) offers the prospect of characterizing each landscape by a permeability coefficient that predicts the extent of inter-patch movements by pollinators. However, many pollinators are central-place foragers or adopt traplines (Thomson 1996) and will not diffuse across a landscape in a simple way, which may invalidate this approach. Alternatively, economic models of forager movements (Cresswell *et al.* 2000) eventually may be adapted to patchy landscapes by including a mechanism for solving the ‘travelling salesman’ problem, a mathematical chestnut (Ausiello *et al.* 2000) whose solution is the shortest route around a set of spatially discrete points, or plant populations in this case. Any economic approach will, however, require a description of floral rewards at the landscape scale, which is daunting. At present, it has proved expedient merely to calculate maximum levels of gene flow by assuming that all pollinators make the source-to-sink transition (Cresswell *et al.* 2002).

5. CONCLUSION

The PDM is a parametric restatement of the conventional view of animal-mediated pollination. In principle, it can be applied to plant species in general. The PDM exposes the influences on pollinator-mediated gene flow. It is possible to propose theoretical values of its parameters that maximize gene flow and to use these as benchmarks against which to judge the performance of real systems. Existing foraging theory can be used in solving part of the PDM, but a theory for source-to-sink transitions by pollinators is currently elusive.

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GLOSSARY

PDM: portion-dilution model