Effects of Plant Species on Each Other's Pollination: Is Community Structure Influenced?

Peter Feinsinger

Pollination is one of the most important aspects of the life histories of most vascular plants. Until recently, there has been a broad consensus that heterospecific neighbors compete for pollinators, that this competition leads to phenological divergence, and that divergence leads to structured communities. New work is revealing a more complex web of interactions.

Seed production by many flowering plants depends on the efficacy with which animals move pollen from one individual to another. Numerous variables of the plant, the animal and the immediate environment affect pollen transfer and subsequent seed output. One such environmental variable is the species composition of neighboring flowers. Neighboring plants may provide sparse or dense flowers; they may be of the same species (hence, potential mates), or they may be of different species used by the same pollinator. The latter case sets the stage for interspecific competition.

It seems reasonable that plants of different species sharing a limited resource (the pollinator) will decrease one another's pollination success and seed output[1,2]. Thus, natural selection should favor any phenotypic feature of plants that ameliorates competitive effects of neighbors. By this argument, members of a pollination guild (plants using the same pollinators) that coexist for many generations will undergo character displacement[3] analogous to morphological character displacement among competing animal species[4]. Alternatively, intense competition among plants with similar floral characters could extinguish one or another from a site.

This clear reasoning on the role of pollination in plant community structure has, however, become quite muddied in recent years. Ecologists have found that interactions among flowering plants in the field are not always competitive, and have re-analysed purported patterns of character displacement. They have questioned both the premise of environmental stability crucial to the arguments for character displacement, and the universal

Peter Feinsinger is at the Department of Zoology, University of Florida, Gainesville, Florida 32611, USA.

importance of pollination in plant population dynamics. Nevertheless, this reappraisal has created intriguing new questions and new opportunities for research.

Mechanisms for competition

The number of compatible pollen grains deposited on the stigmas of a plant's flowers can influence maternal reproductive success (i.e. the number of seeds produced) and, in some cases at least, the vigor of the resulting seedlings (Fig. 1). The complement to seed production in hermaphroditic plants, or in staminate individuals of dioecious populations, is male reproductive success: fertilization of seeds through the dispersal of pollen grains to receptive stigmas on other individuals.

Neighboring flowers of other species could disrupt both components of reproduction. First, neighbors can influence the frequency with which one another's flowers receive visits from animals. If animals are scarce relative to flowers, an especially nectar- or pollen-rich plant species might draw potential pollinators away from less rewarding flowers that would otherwise receive some attention. For example, Free[6] showed that dandelions can attract bees away from apple blossoms and reduce fruit production in orchards.

Even if the frequency with which pollinators arrive at a particular plant remains unaffected by the presence of heterospecific flowers nearby, the nature of those visits may be affected. When an animal moves among plants of different species in the course of a foraging bout, pollen of one species may rub off on flowers of others. Consequently, in the presence of a mixture of species the number of grains a plant disperses to conspecific flowers may decline[2,3], and paternal reproductive success may suffer. Maternal reproductive success may also decline (Fig. 1) if the average stigma receives fewer compatible grains from pollinators[1–3,7,8]. Recently, Campbell and Motten[9,10]

demonstrated that both mechanisms operated in the interaction between two vernal wildflowers, *Stellaria pubera* (Caryophyllaceae) and *Claytonia virginica* (Portulaceae), in a deciduous forest in North Carolina, USA.

An animal visiting a mixture of flowers might not only transfer pollen ineffectively from one individual to a conspecific but also might deposit pollen of one species on stigmas of another. The presence of other species' pollen can alter maternal reproductive success (Fig. 2). Heterospecific pollen can occupy scarce space on the stigma[1,2] or induce the stigmatic

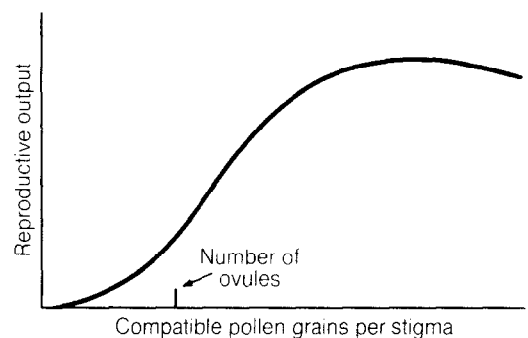Compatible pollen grains per stigma

Fig. 1. A hypothetical relationship between the numbers of compatible pollen grains received on a plant's stigmas, and the maternal reproductive output of the plant. The left-hand portion of the curve is non-linear because many plants abort fruits that receive inadequate pollination. The positive relationship continues to the right of the point where number of grains received equals number of ovules available, for two reasons: (1) many plants require more than one grain per ovule for complete seed set; (2) moderately large pollen loads increase gametophytic competition (among pollen tubes) for access to ovules, which increases the numbers and vigor of offspring[5]. Extremely large pollen loads, however, may result in a 'tangled mess' of pollen tubes and decreased fertilization success.

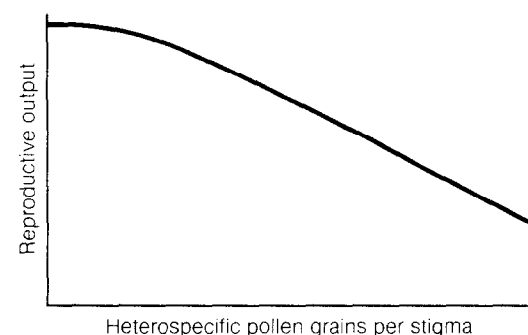Heterospecific pollen grains per stigma

Fig. 2. A hypothetical relationship between maternal reproductive output of a plant, and the loads of heterospecific pollen grains received on its stigmas.
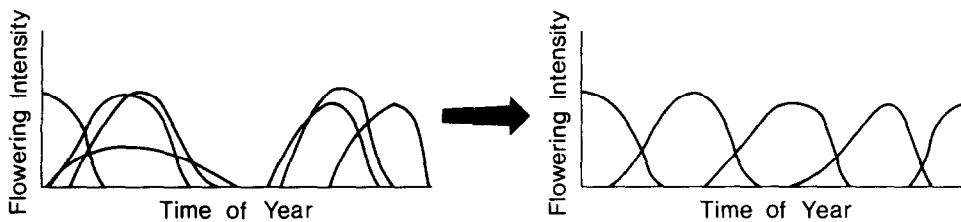
Fig. 3. From chaos to order: a pollination guild whose component species flower at random times with respect to one another is altered, through natural selection within populations or differential colonization and extinction among populations, into a guild with regularly spaced flowering peaks.

lobes to close[11], thereby limiting access by conspecific pollen. In some plants, heterospecific pollen has allelopathic effects on the germination of compatible pollen or inhibits the growth of compatible pollen tubes[12]. Finally, if neighboring plants are of closely related species, interspecific exchange of pollen may lead to production of hybrid seed unlikely to produce vigorous, reproductively successful offspring[3,13].

Character displacement and community structure

If a plant population displays genetically based variation in phenotypic characters of flowers, and if the mechanisms listed above affect darwinian fitness, natural selection could lead to phenotypic divergence of the population from other plants in the same pollination guild.

First, selection might favor phenotypes that bloom at times when those heterospecific plants frequently found as neighbors are not in flower[1,2,14]. Divergent blooming seasons, attributed to such processes of natural selection or to differential immigration and extinction of species on the basis of their flowering times, have been proposed for co-occurring plants pollinated by bumblebees[15,16], by hummingbirds[14,17–19], and by other animal groups[20,21].

Alternatively, natural selection (or differential immigration and extinction) might favor plants with floral structures that deposit pollen on a unique area of the pollinator, minimizing the chance for interference from flowers of other species even if the pollinator is quite catholic in its tastes[3,22]. The end result of competition for pollination, then, may be a pattern of flowering peaks dispersed throughout the growing season (Fig. 3), or a pattern of differently shaped reproductive parts among the species in a pollination guild.

Facilitation

Unlike most animals that share resources, plant species that share pollinators can influence one another in positive as well as negative ways. Flowers of one species may be so sparse that pollinators visit them rarely or never, but flowers of other species growing nearby may contribute to a collective 'lure' that substantially increases the rate of visits by animals (Fig. 4). Interspecific facilitation for pollinator visits may be a common phenomenon when densities of flowers are low[3,8,23], for example in small wildflowers pollinated by bees and flies of the temperate zone[24], or in widely dispersed plants of tropical forest understory[25].

If several plant species that facilitate visits to each other's flowers place pollen at similar locations on their visitors, the positive effects of multiple species on visit rates might be counterbalanced by negative effects on pollen transfer within a particular species. If the plant species place pollen at different sites on their visitors, however, no such negative effects need occur, and heterospecific flowers may actually enhance considerably the maternal and paternal reproductive success of rare plants[26].

Thus, competition and facilitation, operating simultaneously within a diverse guild of plants, would lead over time to a tradeoff in modes of character displacement. Plant species normally producing moderate to high densities of flowers (on single individuals or in the aggregate), and placing pollen at similar locations on animals, would diverge in flowering seasons. Plant species placing pollen at different locations on animals would flower irrespective of one another, or might even converge in flowering times, especially if individuals were widely scattered and produced few flowers each[22,25,26].

Nature isn't that simple

Few of the interspecific patterns once thought to characterize flowering phenology and floral morphology have withstood the onslaught of statistical analysis. Observed distributions of flowering seasons should always be tested against the distributions to be expected were flowering seasons random with respect to one another, i.e. those distributions generated by a biologically realistic null model[27]. Fleming and Partridge[28] found that such tests, when performed properly, revealed that flowering seasons were rarely displaced farther from one another than would be expected by chance alone. Likewise, in some plants that depend simultaneously on a common set of pollinators, floral morphologies are not particularly divergent[25].

Recently, my colleagues and I analysed two diverse guilds of hummingbird-pollinated plants
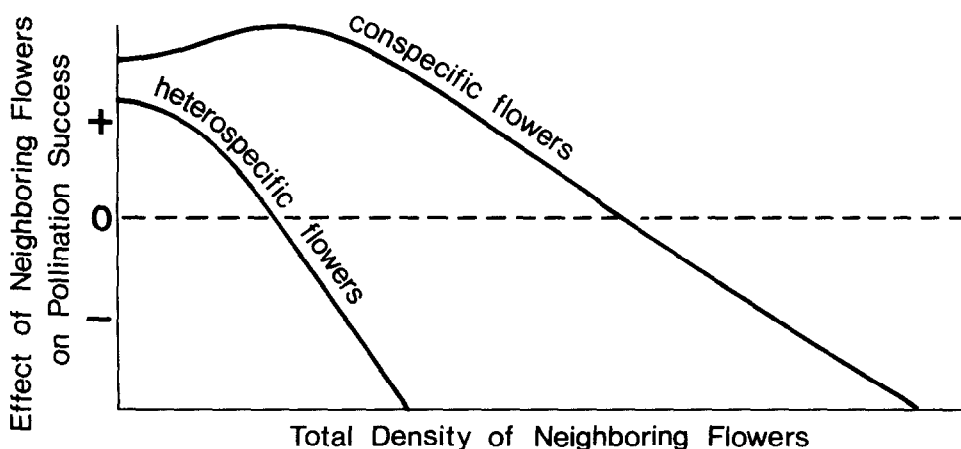

Fig. 4. Possible density-dependent effects of neighboring flowers on the pollination success (both maternal and paternal components) of a hypothetical plant. At very low densities the addition of flowers of any species increases pollination success, but at moderate or high densities the addition of heterospecific flowers inhibits pollen transfer among conspecifics. At high densities, increasing the numbers even of conspecific flowers may lead to declining pollination success, because the pollinator pool may become saturated and per-flower visit rate may decline. Modified from Refs 7 and 23.

from a Costa Rican cloud forest for phenological pattern and for a complementary relationship between phenological and morphological divergence[29]. One guild consisted of plants pollinated by the short-billed Purple-throated Mountain-gem, *Lampornis calolaema* (Fig. 5), the other of plants pollinated by long-billed hummingbirds, principally the Green Hermit, *Phaethornis guy*. In comparisons of observed patterns with those generated by a null model, none of the 12 short-tubed flower species examined, and only 2 of 19 long-tubed species, had blooming seasons that overlapped with the remainder of their guild significantly less than expected by chance alone. On the other hand, 3 of 19 long-flowered species experienced greater phenological overlap from other species than expected by chance – but these were not particularly rare species. Furthermore, in neither guild did species that flowered simultaneously exhibit significantly greater morphological displacement than species with divergent phenologies. In these guilds and others now being critically examined[28], flowering patterns resemble the left-hand portion of Fig. 3 more than they do the right-hand portion.

One reason why clear-cut patterns of character displacement might be scarce is that plants seldom coexist under stable conditions sufficiently long for the competitive demise of particular phenotypes or species. In broad terms, flowering seasons and floral morphologies of species are often quite phylogenetically conservative[30]. Many communities may be in long-term climatic disequilibrium, and plant species may migrate independently over the landscape too rapidly for directional selection at any one site to alter phenotypes dramatically.

Furthermore, the direction of selection itself may be quite inconsistent from generation to generation or year to year. Many pollination guilds experience considerable year-to-year variation in flowering phenologies and interspecific overlaps, thus permitting the coexistence of species (or phenotypes) having traits that would be maladaptive in a stable environment. Pollination within a given plant population may be

Fig. 5. A male Purple-throated Mountain-gem, *Lampornis calolaema*, feeding from a flower adapted for pollination by short-billed hummingbirds, *Cavendishia capitulata* (Ericaceae). Photograph by William H. Busby.

affected by one group of species one year, by another group the next year. Even within a single year, plant species may exert competitive effects upon one another's pollination at some seasons but facilitative effects at other times[8,31]. Similarly, in areas with rapid species turnover in space, different portions of a plant deme or population may interact with different sets of 'guildmates' and thus experience conflicting selection pressures.

Spatial variation in pollinator densities, pollinator behavior or physical conditions may counteract strong effects of neighboring flowers on pollination success. A given array of heterospecific neighbors may enhance pollination of one plant but the identical array may hinder the pollination of another plant a few hundred meters distant. Among the Costa Rican hummingbird-pollinated plants discussed above, we found that species composition and numbers of neighboring flowers rarely exerted consistent effects on the numbers of compatible or heterospecific pollen grains that a plant's stigmas received[8].

Some mechanisms for competition among neighboring plants may be less important than had been supposed. Unless a sudden burst of flowering or inclement weather creates an imbalance in the pollinator-to-flower ratio, plants rarely draw pollinators away from one another[3,19]. Those plant species that commonly face a shortage of pollinator visits, such as wildflowers blooming in early springtime, often have breeding systems

that do not require outcross pollen for seed production[32]. Likewise, floral stigmas undoubtedly receive heterospecific pollen grains, often in quite large numbers[8], but these grains may not always inhibit female reproduction in the ways proposed above. For example, Kohn and Waser[33] found that the presence of *Delphinium nelsonii* (Ranunculaceae) pollen on stigmas of *Ipomopsis aggregata* (Polemoniaceae), a well-studied plant dependent on the same hummingbird pollinators, did not significantly affect seed output by the latter species.

Floral traits and the successful pollination of individual flowers may have a relatively minor impact on the success of genotypes in some plant populations. Seed production by a many-flowered individual whose flowers are poorly pollinated can overwhelm production by a smaller individual achieving excellent pollination success per flower[34]. Selective forces on flowering phenology and flower morphology generated during pollination may be overriden by selective forces generated during other phases of reproduction, such as fruit production or seed dispersal[21]. In some populations, such as understory plants of tropical forests, seed reproduction may play a minor demographic role relative to vegetative propagation, especially when the latter process occurs through broken plant fragments capable of dispersal away from the original site.

Thus, the complexity of pollination events and of plant life histories

suggests that it is unreasonable to expect plants sharing pollinators always to compete intensely or to flower in patterns that minimize overlap, just as analogous expectations for other 'competing' species have often been shown to be unrealistic.

Conclusions: exploring the complexity

The complications discussed above – and others – make the role of neighboring plants in each other's pollination more intriguing than previously conjectured, when the consensus was that heterospecific neighbors must compete for pollination, competition must lead to phenological or morphological divergence, divergence must lead to structured communities. Certainly pollination is one of the most important aspects of the life histories of most vascular plants. Under some circumstances, plant species undoubtedly affect one another's pollination.

A few highly controlled experiments have demonstrated that transfer of compatible pollen between flowers of one species is greatly affected when a pollinator visits intervening flowers of a second species[9,10,14]. It remains to be seen, though, how the severity of this effect varies with the species concerned, for example with the morphology and pollen production of the intervening 'competitors'. Likewise, some studies have shown that receipt of heterospecific pollen grains inhibits seed production[11,12], while others have failed to demonstrate a consistent effect[33]. Under what circumstances are pollen allelopathy or other effects of heterospecific pollen grains important factors in seed output? Only a systematic study will tell.

Mechanisms demonstrated in controlled experiments may vary in their impact on pollination in the field. How do shifts in regional flower densities, for example, affect the role of local conditions (such as the mixture of conspecific and heterospecific neighbors) in the pollination of a plant? Likewise, do self-compatible and self-incompatible plants differ in their sensitivity to the mixture of neighboring flowers?

Treating all species in a pollina-

tion guild as equals, for purposes of statistical analysis, obscures a great deal of important biology, and may be partly responsible for the failure of statistical analyses to distinguish observed flowering patterns from those generated by null models. Multivariate analyses of morphological and phenological overlaps that incorporate variables such as breeding system, size of flower crop, degree of iteroparity, plant growth form, ovules per ovary, and number of pollen grains produced, are the next step to exploring the intricate relationships within a particular pollination guild. Furthermore, the ability of proximate ecological processes to influence community-level patterns undoubtedly varies with the longevity of a plant assemblage. Will statistical analyses of pollination guilds from geologically stable sites with low topographic relief, for example in parts of northeastern South America, reveal more pattern than occurs within guilds occupying spatially and temporally heterogeneous sites in Central America or the western United States?

Finally, researchers need to examine carefully the relationship between pollination and plant population ecology. Under what circumstances does pollination success exert a strong influence on demography, or on darwinian fitness of plants, and under what circumstances are effects of variation in pollination success overwhelmed by other phenomena such as fruit maturation, seed predation, seed dispersal, unpredictable opportunities for seed germination, or vegetative propagation? Are pollination guilds of annual plant species, with a single opportunity for reproduction, more likely to reflect the short- and long-term effects of neighbors on one another's pollination than, for example, long-lived tropical forest trees, or iteroparous forest shrubs whose seeds depend on light gaps for germination and can remain dormant for decades while awaiting suitable conditions?

In short, variation in the nature of pollination-related interactions between plant species – variation over space, over time, and among species with different life history traits or reproductive systems – is a fertile field for exploration.

References

1 Levin, D.A. and Anderson, W.W. (1970) Am. Nat. 104, 455–467
2 Waser, N.M. (1978) Oecologia 36, 223–236
3 Waser, N.M. (1983) in Handbook of Experimental Pollination Biology (Jones, C.E. and Little, R.J., eds), pp. 277–293, Van Nostrand Reinhold
4 Simberloff, D.S. (1983) in Coevolution (Futuyma, D.J. and Slatkin, M., eds), pp. 404–430, Sinauer Associates
5 Mulcahy, D.L. (1987) Am. Sci. 75, 44–50
6 Free, J.B. (1968) J. Appl. Ecol. 5, 169–178
7 Rathcke, B.J. (1983) in Pollination Biology (Real, L.A., ed.), pp. 305–329, Academic Press
8 Feinsinger, P., Murray, K.G., Kinsman, S. and Busby, W.H. (1986) Ecology 67, 449–464
9 Campbell, D.R. (1985) Evolution 39, 418–431
10 Campbell, D.R. and Motten, A.F. (1985) Ecology 66, 554–563
11 Waser, N.M. and Fugate, M.L. Oecologia (in press)
12 Thomson, J.D., Andrews, B.J. and Plowright, R.C. (1981) New Phytol. 90, 777–783
13 Stiles, F.G. (1975) Ecology 56, 285–301
14 Waser, N.M. (1978) Ecology 59, 934–944
15 Heinrich, B. (1975) Evolution 29, 325–334
16 Pleasants, J.M. (1980) Ecology 61, 1446–1459
17 Stiles, F.G. (1977) Science 198, 1177–1178
18 Stiles, F.G. (1985) in Neotropical Ornithology (Buckley, P.A., Foster, M.S., Morton, E.S., Ridgeley, R.S. and Buckley, F.G., eds), pp. 757–787, American Ornithologists' Union
19 Feinsinger, P. (1978) Ecol. Monogr. 48, 269–287
20 Heithaus, E.R. (1974) Ann. Mo. Bot. Gard. 61, 675–691
21 Rathcke, B.J. and Lacey, E.P. (1985) Annu. Rev. Ecol. Syst. 16, 179–214
22 Feinsinger, P. (1983) in Coevolution (Futuyma, D.J., and Slatkin, M., eds), pp. 282–310, Sinauer Associates
23 Thomson, J.D. (1983) in Handbook of Experimental Pollination Biology (Jones, C.E. and Little, R.J., eds), pp. 451–460, Van Nostrand Reinhold
24 Thomson, J.D. (1982) Oikos 39, 241–250
25 Schemske, D.W. (1981) Ecology 62, 946–954
26 Macior, L.C. (1981) Taxon 20, 17–28
27 Harvey, P.H., Colwell, R.K., Silvertown, J.V. and May, R.M. (1983) Annu. Rev. Ecol. Syst. 14, 189–211
28 Fleming, T.H. and Partridge, B.L. (1984) Oecologia 62, 344–350
29 Murray, K.G., Feinsinger, P., Busby, W.H., Linhart, Y.B., Beach, J.H. and Kinsman, S. Ecology (in press)
30 Kochmer, J.P. and Handel, S.N. (1986) Ecol. Monogr. 56, 303–325
31 Waser, N.M. and Real, L.A. (1979) Nature 281, 670–672
32 Motten, A.F. (1986) Ecol. Monogr. 56, 21–42
33 Kohn, J.R. and Waser, N.M. (1985) Am. J. Bot. 72, 1144–1148
34 Heywood, J.S. (1986) Am. Nat. 127, 851–861