CHAPTER 9

# Flower performance in human-altered habitats

**Marcelo A. Aizen[1] and Diego P. Vázquez[2,3]**

[1] *Laboratorio Ecotono, CRUB, Universidad Nacional del Comahue, Río Negro, Argentina*
[2] *Instituto Argentino de Investigaciones de las Zonas Áridas, Centro Regional de Investigaciones Científicas y Tecnológicas, Mendoza, Argentina*
[3] *National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA, USA*

## Outline

The functioning and performance of flowers and their associated pollinators are susceptible to human-driven habitat alteration. Although habitat alteration is increasingly perceived as an important threat to the integrity of the pollination process with practical and economic consequences, the relative importance of the mechanisms mediating the response of plant reproduction to habitat disturbance is not understood clearly. Here we provide a conceptual framework to help identify critical variables and guide the design of more process- and mechanism-oriented studies of the effects of anthropogenic habitat disturbances on flower performance. With a series of qualitative matrices, we summarize the effects of different disturbance types on different plant and pollinator attributes and evaluate how these attributes affect different aspects of pollination and plant reproduction. Although different disturbances can have distinctive immediate effects on plants and pollinators, they mediate their responses by affecting a series of common environmental, plant, and pollinator attributes. Our characterization of disturbance effects and their consequences could be translated easily into a path-analysis or other structural-model-building approach, which can help stimulate a more mechanistic focus for future research. Last, we identify some plant and animal attributes whose roles in different aspects of pollination have been little studied or not addressed directly in the context of habitat alteration. We also discuss the role of plant sexual system and pollination specialization in modulating the reproductive response of plants to habitat alteration, and structural features of plant–pollinator networks that may buffer pollination function against extinction of individual species.

## 9.1 Introduction

The habitats where flowering plants grow and reproduce are increasingly altered to different degrees by human activities. Habitat fragmentation, fire, clearcut and selective logging, invasion by alien species (plants, pathogens, and herbivores), and different types of chemical alteration (herbicide and pesticide use, pollution) are among the most common disturbances associated with humans that can disrupt plant–pollinator interactions (Aizen and Feinsinger 1994a; Kearns *et al*. 1998). Although flowering plants evolve and diversify in an ever-changing world (including, for instance, natural habitat fragmentation, fire, and species exchange), the rate, scale, and intensity of anthropogenic disturbances probably exceed those previously experienced by plants (Kearns *et al*. 1998).

The functioning and performance of flowers in these human-altered, strongly modified landscapes probably differs from that in less modified landscapes. Although considerable empirical evidence has accumulated during the past two decades documenting the effects of different anthropogenic disturbances on pollinator communities and plant reproduction (e.g., Aizen and Feinsinger 1994a; Renner 1998; Steffan-Dewenter and Tscharntke 1999; Cunningham 2000; Vázquez and Simberloff 2004), a unified framework that allows integrated consideration of the mechanisms involved and their relative importance remains elusive. On the other hand, despite analyses of the effects of plant individual, population, or community attributes on pollination and reproductive success, these effects have usually been assessed without consideration of the disturbance context that is likely to modify them (Ghazoul 2005a).

The primary goal of this chapter is to provide a comprehensive framework to aid in identifying the variables and mechanisms that determine the effects of different anthropogenic perturbations on pollination and plant reproduction, as well as organizing and designing studies of disturbance effects on flower function in human-altered landscapes. Fundamental to this framework is the recognition that disturbance can modify either plant or pollinator attributes, which in turn may affect different aspects of plant pollination and reproductive success (Fig. 9.1). Although many studies have addressed the effects of anthropogenic disturbance (particularly habitat fragmentation) on one or more components of plant reproduction, they mostly provide little guidance in understanding the processes and mechanisms behind the cause–effect relationships depicted in Fig. 9.1 (but see Vázquez and Simberloff 2004; Larsen *et al*. 2005). This shortcoming results in part because key variables that can be measured easily and provide critical information (e.g., pollen receipt) are usually overlooked, but more generally because of the lack of a unified conceptual framework that may help in identifying key variables.

To delve deeper into the processes involved, we develop a series of qualitative matrices based on each of the links depicted in Fig. 9.1, which summarize the effects of different disturbance types on plant and pollinator attributes and their consequences for pollination and plant reproduction. Through this systematic exercise we demonstrate that although different disturbance types can have distinctive immediate effects on plants and pollinators, they affect a common set of plant and pollinator attributes through a relatively few environmental parameters. We also emphasize that the magnitude and direction of changes on plants, pollinators, and their interaction differ not only among but also within types of human-induced alterations, depending on disturbance frequency and intensity. We also illustrate how our matrix representation can be translated into a path-analysis or other model-building approach to guide future research focused on mechanisms, rather than on patterns (see Section 9.8). Last, our examination uncovers some plant and animal

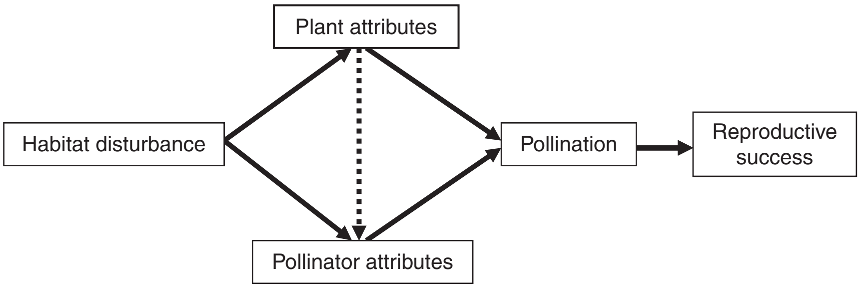

**Figure 9.1** Conceptual diagram showing the links between habitat disturbance, plant and pollinator attributes, and their effects on pollination and plant attributes. Some effects of habitat perturbation on pollinator attributes can be mediated by the effects of habitat perturbation on plant attributes (dotted line).

attributes whose roles in different aspects of pollination have been little studied in the context of habitat alteration. Other attributes, such as sexual system and pollination specialization, are not contemplated in our matrices, because they are not expected to be modified by disturbance, at least in the short term. However, because of their critical importance in the pollination process we discuss their roles as modulators of the response of plant reproduction to disturbance.

Traditionally, studies of floral biology and its response to human-caused perturbations have focused on individual plant species and their associated pollinators, or individual pollinator species and their plant hosts. An emerging perspective adopts a broader focus, centring on entire, or large subsets of, local plant–pollinator interaction networks (see Jordano 1987; Waser *et al*. 1996; Bascompte *et al*. 2003; Vázquez and Simberloff 2003; Vázquez and Aizen 2004). Although this broader view overlooks many of the details revealed by studies of particular pollination interactions, it exposes a deeper understanding of the structure of plant–pollinator interactions (also see Chapter 6) and the effects of disturbance on pollination function. In addition, the study of anthropogenic effects on pollination webs may identify better measures of the integrity of the pollination function than those provided by single-species examples (Aizen and Feinsinger 2003). Within our general conceptual framework, we review recent developments on the effects of disturbance on plant–pollinator webs and highlight new directions in this area of active and promising research.

Like all studies on the effects of disturbance on plant pollination and reproduction, our chapter is based on the unstated assumption that seed production governs the population dynamics of plant populations. When populations are seed-limited, anthropogenic perturbation that impairs pollination function and increases pollen limitation will decrease population growth (Ashman *et al*. 2004; Knight *et al*. 2005). Although populations of short-lived species (Silvertown 1993) and some invasive species (Parker 1997) seem to be seed-limited, seed production does not seem to influence the demography of trees and other long-lived species strongly. However, complete disruption of plant–pollinator interactions may eventually cause the demographic demise of any plant population that depends on sexual reproduction for long-term survival. In addition, pollination-mediated effects of anthropogenic disturbance on progeny quality can erode a plant's evolutionary plasticity (Aizen and Feinsinger 2003).

## 9.2 General effects of disturbance and their reproductive consequences

To characterize the consequences of different disturbance types on pollination and plant reproduction we constructed five matrices, which relate the direct and indirect qualitative effects of disturbance on plant populations as depicted in Fig. 9.1. The first two matrices identify direct effects of disturbance types on plant and pollinator attributes, although we also acknowledge the indirect effects of disturbance on pollinator attributes mediated by changes in plant attributes. The next two matrices relate the effects of the modified plant and pollinator attributes on different aspects of stigmatic pollen deposition, which also mirror aspects of pollen export and thus of male function (e.g., Harder and Barrett 1995; Chapter 4). Finally, the fifth matrix relates pollination success to reproductive output. Each matrix cell contains a symbol indicating the currently understood effect of a row factor or attribute on a column factor or attribute. These symbols include: ↑, a positive relation; ↓, a negative relation; ↑↓, both positive and negative effects are possible; 0, no expected net change; Δ, a change that lacks directionality (e.g., flowering phenology) or involves multiple dimensions (e.g., species composition); and ?, a causal relation for which the expected direction of change is uncertain, despite a presumed effect (e.g., invasion by alien plants could change the quantity and quality of flower rewards through, for instance, changes in the resource status of focal native plants). Rather than reviewing the evidence on the effects of disturbance on flower function exhaustively, we present a series of predictions based on the most likely change(s) that we expect.

Our analysis considers the most common types of disturbances that have relatively immediate impacts on pollination and plant reproduction: (1) habitat fragmentation, (2) fire, (3) selective plant harvesting (e.g., selective logging), (4) introduction of herbivores (e.g., cattle, defoliating insects), (5) introduction of plants (e.g., crops, invasive plants), and (6) chemical disturbance (e.g., contamination with heavy metals, use of pesticides and herbicides). We did not include global-scale disturbances, such as climate change, because their pollination impacts are probably subtle and long term. We recognize that many of the disturbances listed above can be interrelated (e.g., fire may cause habitat fragmentation, or habitat fragmentation could foster invasion of aliens), but they have distinctive impacts on landscapes and individual plant features and so can be studied in isolation.

## 9.3 Effects of human-caused perturbations on plant attributes

Anthropogenic disturbances modify diverse attributes of individual plants, their populations, and communities. In our analysis and discussion, we consider the following features of individual plants: (1) display size (i.e., number of open flowers), (2) flower morphology (including flower size and shape), (3) flower rewards (mainly pollen and nectar), (4) flower physiology (including aspects of floral metabolism that could influence flower lifespan, pollen viability and performance, etc.), and (5) flowering phenology (including onset of flowering, duration, and intensity). The population attributes that we consider include (6) abundance, (7) density, and (8) relative density (i.e., the ratio of number of flowering individuals of a focal species to the number of individuals of other species that flower simultaneously). Finally, we consider the following community attributes: (9) plant species diversity (including both species richness and relative abundance) and (10) plant species composition (Table 9.1).

Except for the introduction of exotic plant species and pesticide application, the perturbations that we consider primarily change local environmental conditions by removing plant biomass, immediately increasing light availability, diurnal temperature, and evapotranspiration and changing nutrient pools. However, the graininess and spatial heterogeneity of the changes in environmental conditions depend on disturbance type. For instance, fragmentation of forest habitats increases light availability by increasing the edge:interior ratio (Fahrig 2003), whereas fires increase light availability by reducing the cover of fire-susceptible species (Waltz and Covington 2004).

Increased light availability and a sudden release of nutrients caused by massive disturbance could in turn trigger immediate physiological changes in remaining and newly recruited individuals (Table 9.1). For instance, higher insolation can increase flower production and display (e.g., Cunningham 1997), which could occur at the expense of, or be accompanied by, increased flower size (e.g., Sato and Yahara 1999), altered flowering phenology (Rathcke and Lacey 1985), enhanced nectar secretion (Rathcke 1992), and

**Table 9.1** Predicted effects of different disturbance types on the attributes of individual plants (floral display, flower morphology, rewards, flower physiology, and flowering phenology), plant populations (size, absolute density, and relative density) and plant communities (species diversity and composition).

| | Individual | | | | | Population | | | Community | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Disturbance type** | **Floral display** | **Flower morphology** | **Rewards** | **Flower physiology** | **Flower Phenology** | **Size** | **Absolute density** | **Relative density** | **Diversity** | **Composition** |
| Fragmentation | ↑ | ? | ↑ | ? | Δ | ↓ | ↑↓ | ↑↓ | ↑↓ | Δ |
| Fire | ↑ | ? | ↑ | ↑ | Δ | ↑↓ | ↑↓ | ↑↓ | ↑↓ | Δ |
| Selective harvesting | 0/↑ | ? | 0/↑ | ? | 0/Δ | ↓ | ↓ | ↓ | ↑↓ | Δ |
| Herbivores | ↑↓ | ↓ | ↓ | ↓ | Δ | ↓ | ↓ | ↑↓ | ↑↓ | Δ |
| Exotic plants | ↓ | ? | ↓ | ↓ | Δ | ↓ | ↓ | ↓ | ↑↓ | Δ |
| Chemical agents | ↓ | ↓ | ↓ | ↓ | ? | ↓ | ↓ | ↑↓ | ↑↓ | Δ |

changes in pollen production (e.g., Etterson and Galloway 2002). Changes in environmental conditions caused by disturbance can also affect paternal reproductive success through changes in pollen quality. For instance, pollen grains produced by water-stressed plants have a lower capacity for siring seeds than grains from plants in benign conditions (Young and Stanton 1990).

Generalist herbivores could also increase light availability; however, because they may affect flowering directly by eating flowers, or indirectly by eating vegetative tissues and reducing photosynthetic capacity, their net effect on floral display depends on the relative effects of tissue removal and increased light availability on plant performance (Chapter 7). Sometimes, herbivores may increase floral display by stimulating meristem production (Paige and Whitham 1987). Herbivory may also affect flowering phenology (Brody 1997) and reduce flower size (Strauss *et al*. 1996; Mothershead and Marquis 2000), nectar secretion (Krupnick *et al*. 1999), and pollen quantity and quality (Quesada *et al*. 1995; Strauss *et al*. 1996; Aizen and Raffaele 1998).

The effects of plant harvesting depend on the abundance of the target species. For instance, if harvesting focuses on a relatively rare species whose removal has limited impact on habitat structure, then attributes of individual plants in the remaining vegetation will be little affected. However, when harvesting causes substantial habitat destruction or targets an abundant species (e.g., logging of a dominant tree species), the resulting widespread habitat modification could induce all the physiological changes associated with increased light availability (e.g., Ghazoul and McLeish 2001; Table 9.1).

Other disturbances are more likely to have negative effects on individual plant attributes, but through different mechanisms (see also Chapter 7). Invasion of exotic plants may have an overall negative effect on plant performance by increasing competition for either light or resources, whereas chemical agents such as herbicides may have similar effects through their direct effects on plant metabolism.

Table 9.1 also identifies some influences of disturbance on individual-level attributes which are difficult to predict, primarily because they have been little studied. For instance, recent studies demonstrate that flower symmetry and shape can influence pollination (Neal *et al*. 1998), but almost nothing is known about how different types of disturbances modify these floral traits. Developmental stability, expressed as fluctuating asymmetry (Palmer 1996), may indicate the degree of environmental stress experienced by an organism. Although much research has addressed this topic for a variety of organisms and organs (including flowers; see Møller 2000), the evolutionary significance of fluctuating asymmetry remains controversial (Palmer 2000).

The clearest and most consistent predictions involve the population consequences of disturbance. For instance, disturbance immediately decreases plant abundance, because of either reductions in the size and number of habitat patches (fragmentation) or increased individual mortality (other perturbation types), although in frequently disturbed areas the abundance of light- or fire-tolerant species might increase in the long term. Population density also probably decreases through increased mortality caused by most perturbation types, except fragmentation and fire (Table 9.1). For instance, in the case of fragmentation the net effect on population density depends on complex indirect effects relating the magnitude and scale of habitat fragmentation to different life-history traits of focal species (e.g., light tolerance). The effect on relative population density (i.e., density of the focal plant species relative to that of simultaneously flowering plant species that share pollinators) depends on both the change in absolute density of the focal species and the response of other species to perturbation (Ghazoul 2005a). Thus, if fragmentation, fire, herbivores, introduced plants, and chemical agents favour perturbation-resistant species, the relative density of the focal species should decrease, whereas if the focal species is itself perturbation-resistant, its relative density could actually increase (Table 9.1). Selective harvesting should decrease the relative density of the focal species as long as it does not affect the density of other species substantially.

Community effects of disturbance depend on the individual responses of the focal and other plant species. The community response depends strongly on the intensity, frequency, and spatial scale of perturbations (Sousa 1984; Chesson and Huntly 1997), and so it is difficult to predict. However, a decrease in species diversity and a relative increase in dominance by one or a few disturbance-resistant species are expected under the intense, frequent, and large-scale disturbances characteristic of many anthropogenic habitat alterations.

## 9.4 Effects of human-caused perturbations on pollinator attributes

Pollination of most plant species depends, to different degrees, on flower visitation by animals, so we consider three aspects of pollinator visits that disturbance can modify independently of changes in plant attributes: (1) total visit frequency, (2) pollinator diversity, and (3) the composition of the pollinator fauna (Table 9.2). Although this list is not exhaustive, these plant and pollinator attributes are discussed most commonly in the pollination ecology literature and are probably most susceptible to anthropogenic perturbations.

Habitat disturbance can strongly affect pollinator assemblages. Most pollinators are short-lived insects with a fine-grained perception of their environment and are thus quite susceptible to local changes in resource supply and habitat structure (Didham *et al*. 1996; Aizen and Feinsinger 2003). Changes in the abundance of individual pollinator species and the composition of pollinator assemblages can result directly from altered environmental and structural characteristics of the habitats (e.g., Ghazoul and McLeish 2001; Burgess *et al*. 2006) or be mediated by changes in plants which provide their food (indicated by a dotted line in Fig. 9.1). For instance, invasion of alien plants, which provides accessible and abundant floral resources, can facilitate the invasion of alien flower visitors independent of habitat disturbance (Morales and Aizen 2006).

**Table 9.2** Predicted effects of different disturbance types on the overall abundance, diversity, and composition of pollinator communities.

| Disturbance type | Abundance | Diversity | Composition |
|---|---|---|---|
| Fragmentation | ↑↓ | ↑↓ | Δ |
| Fire | ↑↓ | ↑↓ | Δ |
| Selective harvesting | ↑↓ | ↑↓ | 0/Δ |
| Herbivores | ↑↓ | ↑↓ | Δ |
| Exotic plants | ↑↓ | ↑↓ | Δ |
| Chemical agents | ↓ | ↓ | Δ |

In general, all disturbance types can decrease total pollinator abundance through increased mortality and habitat destruction, including a reduction in nesting sites. However, pollinator abundance may also increase in the short term, because some perturbations can increase individual plant floral display and promote the encroachment of mass-flowering, light-demanding species (Table 9.2; Westphal *et al*. 2003). All else being equal, a change in pollinator abundance should cause a change of the same direction and magnitude in pollinator visitation frequency. However, the net effect of disturbance on visitation frequency to flowers of the focal species depends on a complex interplay among direct effects of disturbance on pollinator abundance, changes in plant population size and absolute and relative density, the degree of pollination specialization, and other plant traits that determine the interaction with pollinators (Ghazoul 2005a). Thus, excluding cases such as intense, large-scale anthropogenic perturbations (e.g., urbanization) or the use of chemical agents for biological control (e.g., insecticides), disturbances may not affect either total pollinator abundance or visitation frequency (see also Ghazoul 2005b).

Net effects on the diversity and composition of pollinator assemblages depend on three factors: the structural complexity of habitats, which can be greatly simplified by human-driven disturbances; nectar and pollen availability (Westphal *et al*. 2003); and the diversity and composition of flowering species (Morales and Aizen 2006). For instance, mass flowering of an invading plant species with a generalist pollination system could sustain a pollinator community as rich as, or richer than, a plant assemblage composed of several, relatively specialized native plants. However, changes in habitat structure, light and temperature, resource availability, and plant community composition should be, and usually are,

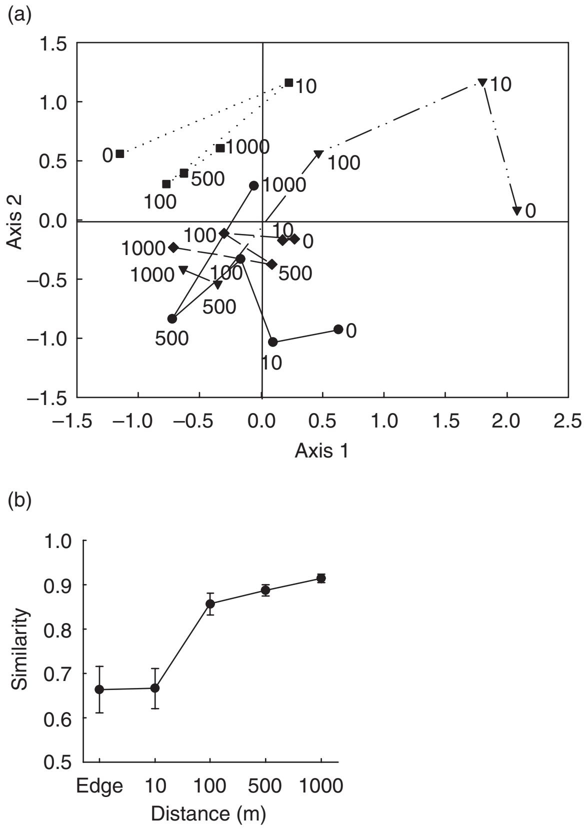

**Figure 9.2** Effects of distance from native vegetation on pollinator species richness at 0, 10, 100, 500 and 1000m from premontane subtropical forest in four grapefruit (*Citrus paradisi*) plantations in northwest Argentina, based on a 1 Bray–Curtis distance coefficient. (a) Non-metric multidimensional scaling (NMDS) ordination of the pollinator assemblages. Axes 1 and 2 explain 43.7 and 25.3% of total variance in pollinator assemblage composition, respectively. The NMDS is based on a matrix of 50 species per 20 site × distance classes. Line segments link flower-visiting faunas at increasing distances from the forest edge within the same plantations. The four plantations are represented by different symbols. (b) Mean (±SE) similarity (averaged over all plantation pairs) versus distance to the edge. Reproduced with permission from Chacoff and Aizen (2006).

accompanied by strong changes in the composition of pollinator faunas (e.g., Potts *et al*. 2001). In many instances, anthropogenic disturbance increases the dominance of one or a few pollinator species (Aizen and Feinsinger 1994b; Morales and Aizen 2006). The most striking example is the increasing domination of disturbed pollinator communities by Africanized *Apis mellifera* throughout most of the Neotropics (Goulson 2003). This bee has become the dominant visitor to the flowers of many native plants that previously sustained rich assemblages of many pollinator species (e.g., Aizen and Feinsinger 1994b).

In addition to impoverishing pollinator faunas, intense and frequent disturbances can homogenize faunas over space, thus decreasing $\beta$-diversity. For instance, bee assemblages in grapefruit plantations in northwest Argentina become increasingly similar with distance from the forest edge (Fig. 9.2). Similarly, disturbed forest areas of northwest Patagonia tend to sustain convergent pollinator assemblages, independent of disturbance type (Morales and Aizen 2006).

## 9.5 Relation of pollination to modified plant attributes

Modification of individual, population, and community attributes of plants mediate indirect pollination responses to anthropogenic disturbance

**Table 9.3** Predicted effects of the individual, population, and community-level attributes of plants listed in Table 9.1 on pollination variables.

| Attribute level | Attribute | Quantity | Quality | Purity |
|---|---|---|---|---|
| Individual | Floral display | ↑ | ↑↓ | ↑ |
| | Floral morphology | ↑ | ↑↓ | ↑ |
| | Rewards | ↑ | ↑↓ | ↑ |
| | Reproductive physiology | ↑ | ↑ | ? |
| | Phenology | Δ | ? | Δ |
| Population | Size | ↑↓ | ↑ | 0 |
| | Absolute density | ↑↓ | ↑ | 0 |
| | Relative density | ↑ | ↑ | ↑ |
| Community | Diversity | ? | ? | ? |
| | Composition | ? | ? | ? |

(Table 9.3). We consider three specific pollination outcomes: (1) pollen receipt; (2) the quality of received conspecific pollen, including genetic aspects, such as the proportion of self-pollen and the diversity of pollen donors, and/or physiological status affecting pollen viability; and (3) the purity of pollen deposition (i.e., number of conspecific versus heterospecific pollen grains). All of these outcomes can strongly influence reproductive success, including seed quantity and seed quality (e.g., seed size, germination rates, seedling vigour). Although these pollination components explicitly involve female function (i.e., seed set), they parallel male performance (i.e., seed siring), because poor cross-pollen receipt results from limited pollen export, self-pollination may limit pollen export and siring success on other plants (pollen discounting), and heterospecific pollination also causes lost siring opportunities (Chapter 4).

Changes in floral display and floral traits affect pollination success through various mechanisms. Indeed, much work during recent decades has considered the consequences of individual phenotypic variation in various floral attributes on pollinator attraction and pollination quantity and quality, mostly in an evolutionary context (e.g., Nilsson 1988; Herrera 1993; Neal *et al*. 1998; Chapters 2, 6, 14, and 15). Some of these studies show that variability in floral traits, including flowering phenology, often has contrasting effects on different pollination components. For instance, increased floral display or nectar production may enhance pollen removal and deposition by increasing pollinator attraction to attractive and rewarding plants. However, these traits may also increase self-pollination and pollen discounting by increasing the number of flowers visited per plant by individual pollinators (geitonogamy) and, in the case of nectar, the time that each pollinator spends visiting individual flowers (autogamy) (Harder and Barrett 1995; Eckert 2000). Thus, whereas these individual-level attributes may initially enhance both pollination quantity and quality by increasing pollinator attraction, they may eventually decrease pollination quality through the transfer of self-pollen while still increasing pollen deposition (Table 9.3).

Effects of perturbation on plant population attributes may also influence pollination quantity. Pollen receipt increases in a decelerating manner with population size or density, because of increasing pollinator attraction, until it decreases because of competition between neighbouring conspecifics and heterospecifics for a limited pollinator pool (Rathcke 1983; Kunin 1997; Brown *et al*. 2002; Table 9.3). Thus, perturbation effects on pollination quantity mediated by population size and density will depend on the pre- and post-perturbation levels of these attributes. However, this curvilinear relation indicates that two populations with contrasting sizes or densities could experience similar low pollination for contrasting reasons: limited attraction in small or low-density populations and intraspecific competition for pollinator service in large, high-density populations.

Population size and density may also affect pollination quality. Larger or denser populations may experience improved pollination quality (Table 9.3), if an increase in the number of conspecific individuals enhances either the genetic diversity represented in the pollen loads or the intensity of competition among male gametophytes (Mulcahy *et al*. 1996). Pollination quality commonly declines in fragmented populations of different tree species due to increased inbreeding (e.g., Aizen and Feinsinger 1994a; Cascante *et al*. 2002). These changes result principally from reduced population size or density, but more direct tests that account for the confounding effect of changing pollinator assemblages would be valuable.

Perturbations are likely to affect pollination quality and purity through changes in relative population density, particularly when generalist pollinators also visit other co-flowering plant species (Rathcke 1983; Kunin 1997; Brown *et al*. 2002). In this case, pollinators visit flowers of other species more frequently as the relative density of the focal species decreases, thus depositing proportionally more heterospecific pollen grains (Table 9.3). In extreme cases, the deposition of a large amount of heterospecific pollen could usurp space on the stigma, interfering with either the germination or tube growth of conspecific pollen. In addition, foreign pollen can have allelopathic effects on germination and tube growth of conspecific pollen (e.g., Murphy and Aarssen 1995). Although the deposition of heterospecific pollen is highly variable in nature, usually representing a low fraction of all pollen deposited (McLernon *et al*. 1996), it might become important when disturbance involves, or is accompanied by, the invasion of an alien flowering plant (Brown *et al*. 2002).

Effects of plant diversity and composition are important to the extent that they affect the relative density of co-flowering plant species that share pollinators with the focal plant species, although these effects are difficult to predict (Table 9.3). The hypothesis that increased floral diversity sustains richer pollinator assemblages which provide more efficient and predictable pollination services in terms of both quality and quantity (Aizen and Feinsinger 2003) awaits formal testing. However, co-flowering species can facilitate each other's pollination at low population densities (Rathcke 1983; Moeller 2004; Chapter 6), and the mere presence of flowering plants of a few rewarding species can facilitate the pollination of rewardless species (Johnson *et al*. 2003).

## 9.6 Relation of pollination to modified pollinator attributes

Pollinator attributes usually have direct and strong implications for pollination (Table 9.4). The effectiveness of a pollinator species, or its quantitative contribution to the pollination of a given plant species, is the product of its visit frequency and the amount of pollen deposited per visit. Although both factors are important, visit frequency predicts total pollinator efficiency most closely, because its variation overwhelms that of per-visit effectiveness (Vázquez *et al*. 2005). This result indicates that quantitative aspects of pollination (both pollen removal and pollen deposition) depend strongly on pollinator abundance, provided that abundance and visit frequency vary positively. Pollinator abundance could also influence the quality of pollination, because large stigmatic pollen loads increase genetic diversity and opportunities for selection among germinating pollen grains (Mulcahy *et al*. 1996).

**Table 9.4** Predicted effects of the attributes of pollinator communities listed in Table 9.2 on pollination variables.

| Attribute | Quantity | Quality | Purity |
|---|---|---|---|
| Abundance | ↑ | ↑ | 0 |
| Diversity | ? | ↑↓ | ↑↓ |
| Composition | ↑↓ | ↑↓ | ↑↓ |

Pollinator diversity and composition can also influence quantitative and qualitative aspects of pollination. For instance, coffee fruit production is enhanced by increases in bee species richness, particularly that of solitary bees, independent of pollinator abundance (Klein *et al*. 2003). For a given visitation frequency, the effects of increased pollinator diversity or changes in its composition on pollination could range from negative to positive, depending on both plant characteristics and pollinator traits (Table 9.4). For a highly outcrossing plant species pollinated efficiently by a large-bodied, mobile bee, increased pollinator diversity or changes in assemblage composition could degrade pollination quantity and quality. However, the opposite trend could be quite common. For instance, *Apis mellifera* usually forage preferentially on highly localized nectar and pollen sources, despite being able to fly several kilometres from their nests. Thus, the replacement of diverse pollinator assemblages by the Africanized honeybee throughout the Neotropics (Goulson 2003) could decrease cross-pollination and increase self-pollination without net changes in total pollination (Aizen and Feinsinger 1994a). Another benefit of a diverse pollinator guild is the more predictable pollination service that it provides through time (Pettersson 1991). This is an issue that deserves more attention in the context of ecosystem services (e.g., Kremen *et al*. 2002; Larsen *et al*. 2005).

## 9.7 Relation of plant reproduction to modified pollination

All attributes of pollination loads, including their quantity, quality, and purity, should affect seed quantity and quality. Although Table 9.5 seems trivial (positive effects are predicted for all cause–effect relationships), it stresses the role of post-pollination processes that might be altered by habitat perturbation, but which are typically overlooked in the context of the effects of anthropogenic disturbance on plant reproduction (Aizen and Feinsinger 2003). Through these effects, increases in pollination quantity and quality can enhance both seed quantity and quality (Ramsey and Vaughton 2000).

The relation of seed production to pollen receipt is straightforward: increased pollen receipt usually enhances fruit and seed set until a threshold is reached at which resource, rather than pollen, availability limits fecundity. Two recent reviews demonstrate that pollen-limited reproduction is more the rule than the exception in nature (Ashman *et al*. 2004; Knight *et al*. 2005), in contrast to theoretical expectations (e.g., Chapter 4). The authors of these reviews proposed that pollen limitation is becoming increasingly common, because most plants currently live in human-disturbed environments where pollinators have become scarce or their abundances vary extensively. This conjecture is supported by Aguilar's (2005) meta-analysis of the reproductive response by 85 plant species to fragmentation, which found an overall negative effect on both pollination and seed output, despite heterogeneous responses by individual species (Fig. 9.3a). Most interesting, species showing strong pollination decreases in habitat fragments were also likely to exhibit sharp declines in seed output, suggesting that the reproductive decline of plants in disturbed environments can be explained largely by pollen limitation (Fig. 9.4).

**Table 9.5** Predicted effects of pollination variables on quantitative and qualitative aspects of plant reproductive success.

| Pollination attribute | Quantity | Quality |
|---|---|---|
| Quantity | ↑ | ↑ |
| Quality | ↑ | ↑ |
| Purity | ↑ | ↑ |

Although pollen limitation is usually interpreted in terms of reduced visit frequency due to a scarcity of efficient pollinators, it can also arise from poor pollen quality, including pollination with either self-pollen, or cross-pollen loads with low genetic diversity that pre-emptively fertilize ovules that fail to mature into seeds (Ramsey and Vaughton 2000). Regrettably, the common protocol to evaluate pollen limitation, involving supplemental pollination with cross-pollen, does not allow discrimination between limitation from pollen quantity and quality (also see Chapter 4). These alternatives could be distinguished, and the magnitude of each of them measured, by knowing (1) the response curve of seed number to pollen receipt under natural conditions, which allows the estimation of the quantitative component of pollen limitation, and (2) the number of seeds produced by virgin flowers receiving unlimited, pure cross-pollen, which allows the estimation of the qualitative component of pollen limitation (M. A. Aizen and L. D. Harder in press).

In addition to determining fecundity, the amount of pollen deposited on stigmas and its genetic diversity, composition, and physiological status affect seed quality, including seed size and germination potential, and seedling and plant performance. Increased stigmatic pollen loads may enhance competition for access to ovules among pollen tubes growing in the style. Because of overlap in gene expression between the paternal sporophyte and the male gametophyte, fast-growing pollen tubes may sire vigorous seedlings (Mulcahy *et al*. 1996). Although conditions for gametophytic competition may be erratic (Herrera 2002), the potential effects of this phenomenon on both ecological and evolutionary time scales may

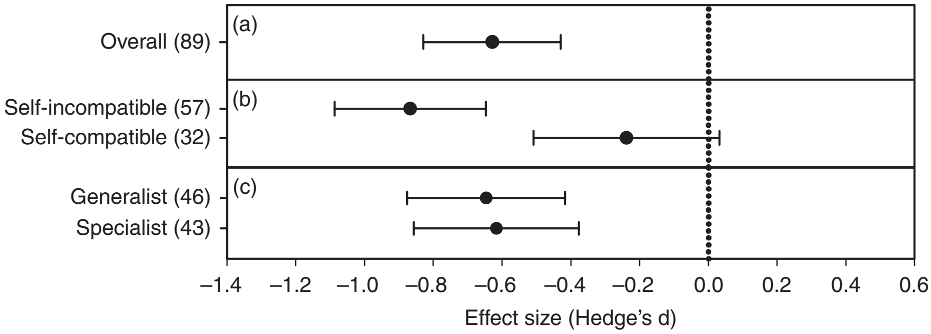

**Figure 9.3** Weighted mean (±95% confidence interval) effect size (Hedge's *d* coefficient) from a meta-analysis of plant reproductive success (either fruit set, seed set, or total seed output) in habitat fragments and more continuous expanses of the same habitat type. Panel (a) shows the overall response, panel (b) depicts the comparative response between self-incompatible and self-compatible plant species, and panel (c) illustrates the comparative response between plant species with generalized or specialized pollination systems. Numbers in parentheses indicate the number of plant species included in each subgroup. The dotted line indicates effect size = 0. Redrawn from Aguilar (2005).

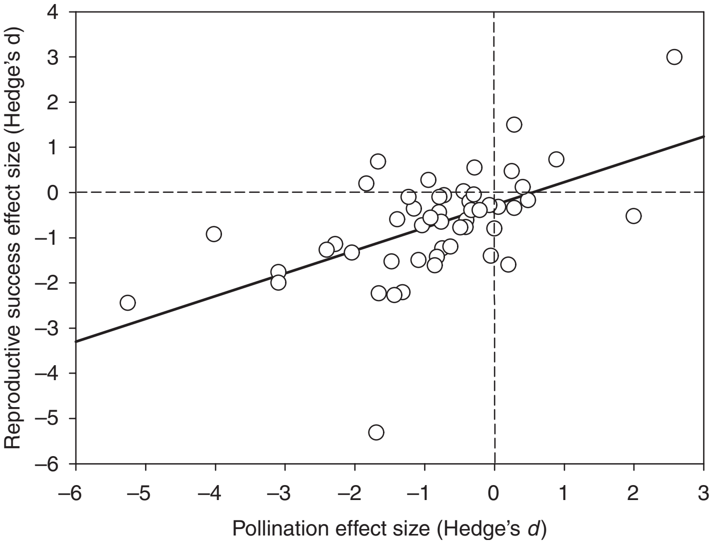

**Figure 9.4** Mean effect sizes (Hedge's *d*) for the relation of reproductive success (either fruit set, seed set, or total seed output) to pollination (either number of pollen grains of pollen tubes) of plants in habitat fragments and more continuous expanses of the same habitat type ($r = 0.55$, $n = 50$ species, $P < 0.001$). The horizontal and vertical dotted lines indicate effect sizes = 0. Redrawn from Aguilar (2005).

be great (Niesenbaum and Casper 1994). In addition to pollen-tube competition, the extent of inbreeding, including selfing, can impact fecundity and seed quality directly (Charlesworth and Charlesworth 1987). As a general rule, inbreeding depression in outcrossing species is commonly expressed early during seed development, whereas in mostly selfing species those effects are expressed much later in mature plants, if at all (Husband and Schemske 1996).

## 9.8 Translation into a path-analysis framework: an example

It is useful at this point to consider an example of how our general matrix approach can be translated into a statistical modelling framework that can be used to evaluate specific causal hypotheses relating human-caused perturbations with floral biology. We base this discussion on work conducted by Vázquez and Simberloff (2004) evaluating the effects of introduced ungulates (cattle) on the pollination and reproduction of an understory herb, *Alstroemeria aurea*.

To consider the effects of particular perturbation types on specific systems, the general matrices (Tables 9.1–9.5) must be adapted to the problem at hand. This process necessarily involves selecting a subset of candidate variables thought to cause the hypothetical effects. Ideally, such variable selection should be based on existing biological knowledge of the system (Shipley 2000; Mitchell 2001). In our example, we first identify the type of perturbation in Table 9.1, namely "herbivory." Vázquez and Simberloff hypothesized that the effects of cattle on pollination and reproduction were mediated entirely by population-level plant attributes, particularly the absolute and relative density of the focal plant species. Using these variables, we characterize a "path diagram," as shown in Fig. 9.5a. In this diagram, variables connected with one-headed arrows are hypothesized to be linked causally; for example, the "browsing index" (a surrogate of the general perturbation caused by cattle) is hypothesized to affect the absolute and relative population densities of the focal plant species (Fig. 9.5a). According to Table 9.1, herbivory is expected to reduce absolute density, so we add an arrow with a dashed line (in path analysis, dashed lines represent negative effects, whereas solid lines represent positive effects). In contrast, the effect of herbivory on relative density could be either positive or negative (Table 9.1), so we tag that arrow with a question mark.

Vázquez and Simberloff's study did not include pollinator responses to perturbation explicitly in the causal model; however, it did include responses of pollinator visitation frequency to absolute plant density, so we add that link in Fig. 9.5a. Vázquez and Simberloff hypothesized that pollinator visitation frequency could be influenced by

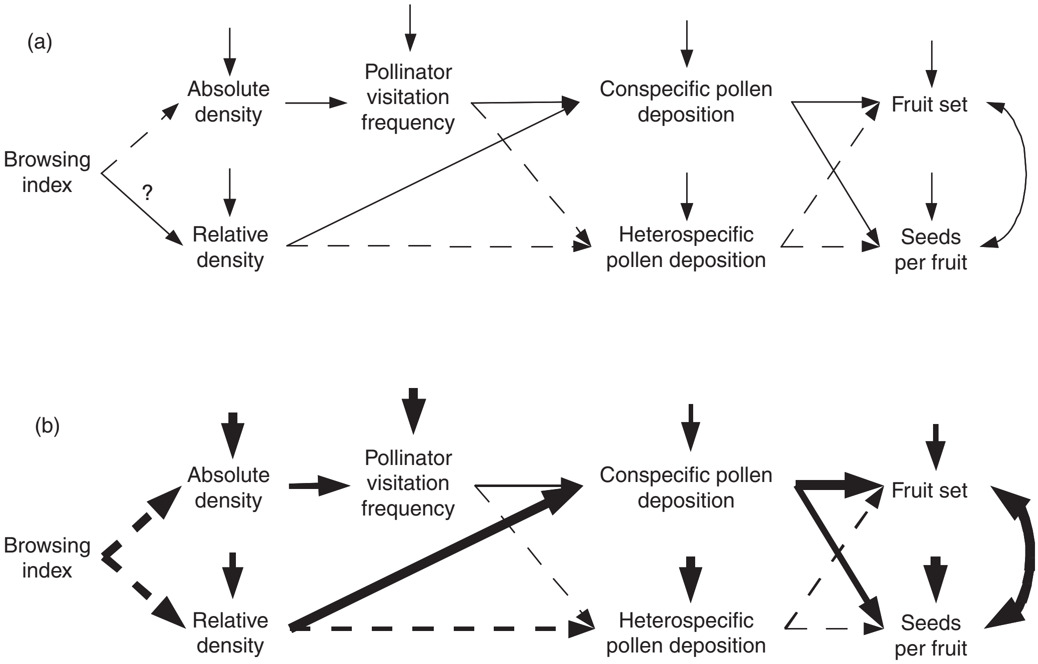

**Figure 9.5** Path diagrams structured on the general framework outlined by Tables 9.1–9.5 depicting (a) hypothesized and (b) observed effects of cattle-caused perturbations on pollination and reproduction of the herbaceous understory plant *Alstroemeria aurea*. One-headed arrows linking variables represent unidirectional causal effects, the two-headed arrow represents bidirectional (i.e., correlational) effects between the two reproductive variables, and vertical one-headed arrows represent unexplained variation in the endogenous (dependent) variables. Line dashing indicates the direction of effects (solid, positive; dashed, negative); line thickness in (b) represents effect magnitude. Modified from Vázquez and Simberloff (2004).

cattle only through an effect on absolute population density, but not through an effect on relative density (see their Fig. 1), so we construct our path diagram to reflect this hypothesized mechanism. Vázquez and Simberloff predicted that this effect is positive, so we add a solid arrow.

We now move on to Table 9.3, which relates plant population attributes with pollination variables. Vázquez and Simberloff included two pollination variables, the numbers of conspecific and heterospecific pollen grains, representing the components of pollination quantity and purity. Notice that the effect of absolute density on pollen deposition is mediated by visitation frequency, which comes from Table 9.4. Here, greater absolute and relative density should promote increased conspecific pollination (solid line), but decreased heterospecific pollination (dashed line).

Moving on to the last matrix, we now relate reproductive outcomes to pollination variables. Vázquez and Simberloff included two such variables, fruit set (proportion of flowers producing fruit) and seeds per fruit. Both variables are quantitative, but seeds per fruit can also be used as a rough estimate of the ''quality'' of reproduction (see Vázquez and Simberloff 2004). Finally, we must account for both unexplained variability, which in path analysis is represented by vertical arrows pointing to all endogenous (''dependent'') variables, and the likely correlation between the two reproductive outcomes (represented by a two-headed arrow). Again, line characteristics reflect the predicted direction of effects, so that conspecific pollen increases reproduction, whereas heterospecific pollen reduces it. This model can be assessed and compared with alternative models following the methods outlined in Shipley (2000) and Mitchell (2001).

The resulting path diagram represents a specific hypothesis depicting the impact of a particular perturbation type on plant reproduction through its effects on pollination. Figure 9.5b presents an evaluation of this causal hypothesis, adapted from Vázquez and Simberloff (2004). The general direction of effects matches predictions, but some effects (represented by arrow thickness) are weaker than expected. For example, pollinator visitation frequency affects pollen deposition weakly, indicating that cattle affect pollen deposition primarily through their effects on the relative density of *A. aurea*, rather than on absolute density. Similarly, whereas conspecific pollen deposition affects both reproductive outcomes strongly, the effect of heterospecific pollen deposition is rather weak. Thus, these data suggest that cattle affect the pollination and reproduction of *A. aurea* by decreasing its density relative to other species in the community, which in turn reduces conspecific pollen deposition and decreases reproductive success.

## 9.9 Modulators of plant reproductive response

The sensitivity of plant reproduction to the negative effects of habitat disturbance may depend on several plant traits. However, traits linked most directly to a plant's pollination and reproductive systems are expected to be most influential (Bond 1994; Aizen *et al*. 2002). In particular, two traits have been identified as primary modulators of the pollination and reproductive responses of plants to anthropogenic disturbance: sexual system and pollination specialization.

Plant sexual systems range from those that enforce outbreeding to those that ensure sexual reproduction via autonomous, within-flower selfing and autogamous seed set (Lloyd 1992). The most common outbreeders include species with hermaphroditic flowers and a genetically based self-incompatibility system and those with distinctive male and female individuals (i.e., dioecy). On the other hand, many self-compatible hermaphroditic species can set seed via selfing (Goodwillie *et al*. 2005). In animal-pollinated species, this inbreeding–outbreeding gradient establishes, beyond its genetic consequences, the overall dependence on the pollination mutualism for plant reproduction (Bond 1994; Chapter 10). Whereas reproduction of obligate outbreeders requires other mates, that of inbreeders can occur mostly independently of other plant individuals and pollinators. Plants also differ in their pollination specialization, from extreme specialists to extreme generalists. Pollination specialists are pollinated by one or a few ecologically similar animal species, whereas generalists are pollinated by several to many species, usually of diverse taxonomic affinities (Renner 1998). The yucca/yucca moth and fig/fig wasp mutualisms are classic cases of extreme specialization. However, flowers of most species are pollinated by a few to more than 100 animal species (Waser *et al*. 1996). This gradient in pollination specialization may relate to the likelihood of mutualism failure: pollination specialists should be more vulnerable than generalists, because the loss of one pollinator species could cause complete plant reproductive failure (Bond 1994).

Figure 9.6 portrays a graphical model showing the predicted differential responses of pollination and plant reproductive success with increasing disturbance (assuming that the range of disturbance frequency or intensity affects these variables negatively) in relation to sexual system and pollination specialization. All else being equal, the pollination and reproductive success of a self-incompatible species (i.e., an obligate outbreeder) is more likely to decline with increasing habitat disturbance than that of a phylogenetically related self-compatible species (i.e., a facultative inbreeder) (Fig. 9.6a). Similarly, but based on the likelihood of the disruption of the plant–pollinator link, pollination and reproduction of a specialist plant species should be more sensitive to the effects of habitat disturbance than that of a generalist plant (Fig. 9.6b).

Two recent reviews explored the effects of habitat fragmentation on pollination and reproductive success on the differential response of species to anthropogenic disturbance. A survey of 45 species (Aizen *et al*. 2002) found no evidence that either plant sexual system or degree of specialization influences the probability of negative responses to habitat fragmentation in terms of either pollination or reproductive success. Also, this probability was independent of whether species occupied tropical or temperate areas, or their growth form. In contrast, Aguilar's (2005) more detailed and complete meta-analysis supported one of our predictions (Fig. 9.6a). Whereas reproduction by self-incompatible species declined significantly in fragmented habitats, the pollination and reproduction of the self-compatible species were, on average, not particularly impaired (Fig. 9.3b). However, this meta-analysis agrees with Aizen *et al*.'s (2002) conclusion that the degree of pollination specialization does not affect a species' differential reproductive response to habitat fragmentation (Fig. 9.3c). This apparent contradiction between expectations and reality may reflect the structure of plant–pollinator interaction webs (Vázquez and Simberloff 2002; Ashworth *et al*. 2004), a subject that we develop in the following section.

## 9.10 Anthropogenic disturbance and the structure of pollination interaction networks

As discussed in preceding sections, human-caused perturbations can alter the structure and

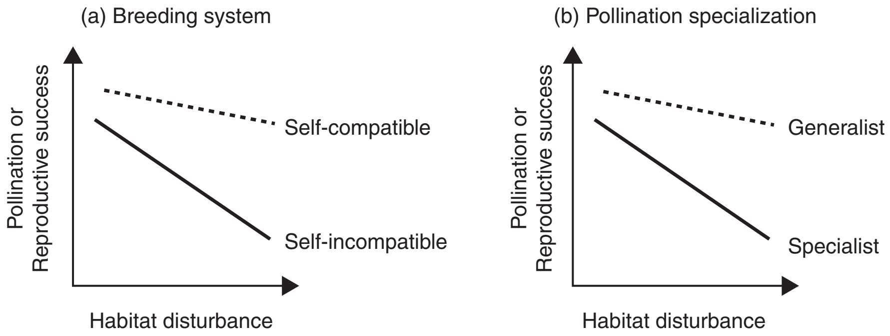

**Figure 9.6** Expected pollination and reproductive responses by plants to increasing habitat disturbance as influenced by (a) plant sexual system and (b) pollination specialization. Although sexual systems and pollination specialization vary continuously, they are each divided into two contrasting categories for simplicity.

functioning of pairwise interactions between a plant and a pollinator species through a variety of mechanisms. However, these effects occur within a community context, rather than in isolation, thus having the potential to impact many pairwise interactions simultaneously (also see Chapter 6). Therefore, the magnitude and direction of the effects of perturbations will be determined partly by community structure.

Interactions among a set of species that coexist in a local environment are frequently represented as networks or ''webs'' in which species or populations are represented as nodes and interspecific interactions are represented as links. Studies in community ecology have long sought to identify regularities in network topology and the underlying mechanisms (Cohen and Newman 1985; Jordano 1987; Williams and Martinez 2000; Dunne *et al*. 2002; Jordano *et al*. 2003). These structural patterns may have dynamic implications for the populations that compose the network and thus may influence the responses of interacting species to perturbations (Dunne *et al*. 2002; Melián and Bascompte 2002; Memmott *et al*. 2004).

Recent studies have identified some apparently pervasive structural features of plant–pollinator interaction webs. First, whereas the classical view assumes that specialist plants interact differentially with specialist pollinators, and generalist plants with generalist plants (i.e., symmetric interactions), specialist plants actually interact with generalist pollinators more frequently than expected by chance, whereas generalist plants interact with a mix of generalist and specialist pollinators (i.e., asymmetric interactions; Bascompte *et al*. 2003; Vázquez and Aizen 2004, 2006). Thus, even if an intense perturbation caused the differential loss of disturbance-sensitive, specialist pollinators, most plants would be buffered against this loss, because of their tendency to interact with some generalized pollinators independently of their degree of pollination specialization (Vázquez and Simberloff 2002; Ashworth *et al*. 2004: Fig. 9.7). Second, generalists form a network ''core'' consisting of a densely connected subset of diffusely interacting species (Bascompte *et al*. 2003). This structural trait may buffer networks against extinctions, because high connectivity and abundance may increase the

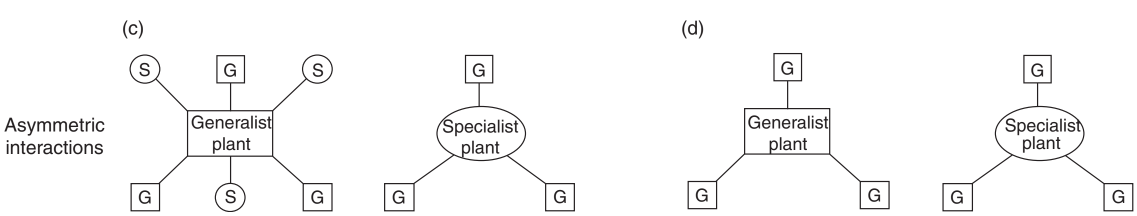

**Figure 9.7** Schematic representation of specialization in plant–pollinator interaction webs. With (a) symmetric specialization, many different generalist pollinators (G) pollinate generalist plants, whereas a few taxa of specialist pollinators (S) pollinate specialist plants, so (b) habitat fragmentation has a stronger negative effect on specialist plants than on generalist plants. Under (c) asymmetric specialization, many specialist and generalist animal taxa pollinate generalist plants, whereas one or a few taxa of generalist pollinators serve specialist plants, resulting in (d) similar reproductive susceptibility to habitat fragmentation for specialist and generalist plants. From Ashworth *et al*. (2004).

probability of persistence of generalists, and many species depend on generalists. Third, a small subset of pollinator species may be sufficient for a plant to achieve reproductive success, and this importance is strongly, positively related to pollinator visitation frequency (Morris 2003; Vázquez *et al*. 2005) and a pollinator's degree of generalization (Vázquez and Aizen 2006). Therefore, this skewed distribution of pollinator effects on plants may further buffer networks against perturbations.

A few studies have explicitly examined the interaction between the structure of plant–pollinator networks and human-caused perturbations. These studies addressed two major classes of questions: whether perturbations affect structural features of plant–pollinator interaction networks, and how some of the above structural features of plant–pollinator networks may determine species' responses to perturbations.

Among the first class of questions (i.e., whether perturbations affect network structure), Vázquez and Simberloff (2003) found systematic changes in network structure resulting from cattle grazing in the understory of native forests. This effect resulted mainly from the modification of a few very frequent interactions, which are probably functionally important (see Morris 2003; Vázquez *et al*. 2005a). Unfortunately, this study did not identify which structural aspects of networks were affected by perturbations. This issue is important, because some structural feature of a network (e.g., nestedness or degree of asymmetry) could remain unchanged despite strong changes in the absolute and relative participation of species in the network.

A few studies provide tentative answers to whether network structure influences species' responses to perturbations. Memmott *et al*. (2004) simulated pollinator extinctions in two of the largest plant–pollinator networks available in the literature to date. Assuming that plants depend entirely on pollinators to reproduce (which is arguable; Bond 1994), they simulated secondary extinctions of plants as a result of extinctions of their pollinators. Memmott *et al*. found that when pollinators went extinct in decreasing order of generalization (i.e., from the most generalized to the most specialized), secondary extinctions of plants occurred earlier and faster than when pollinator extinctions occurred randomly or in increasing order of generalization. This result was explained by the highly nested structure of the networks analysed. Thus, the interaction of a few extremely generalized pollinators with most plant species in the community prevents their extinction, which in turn prevents the secondary extinction of the many plants that depend on these pollinators for reproduction (see also Renner 1998; Vázquez and Simberloff 2002; Ashworth *et al*. 2004). Furthermore, highly connected species tend to be more abundant than species with few connections (see Vázquez and Aizen 2006), and rare populations tend to suffer greater extinction risks than abundant populations (Lawton and May 1995), so that highly connected species may be particularly resistant to extinction, further enhancing the robustness of plant–pollinator networks.

Memmott *et al*.'s (2004) study was unrealistic in that they assumed complete dependence of plants on pollinators and did not include information about pollinators' effectiveness, so they implicitly assumed that all pollinators are equally effective. Morris (2003) attempted to overcome this limitation by explicitly incorporating data on pollinator effectiveness. Based on published data on pollinator effectiveness for 24 plant species, he simulated the loss of total pollinator service (i.e., the added contribution of pollinator species to plant reproductive success) as pollinator species went extinct. Morris' results indicated that a large proportion of pollinator species could be lost before substantial reproductive service to plants was lost. This result was explained by the highly uneven distribution of interaction frequency and of per-interaction effectiveness among pollinator species: frequent pollinators tend to contribute most to plant reproduction, regardless of their per-interaction effectiveness (see Section 9.6 above; Vázquez *et al*. 2005a). The findings of Memmott *et al*. (2004) and Morris (2003) suggest that plant–pollinator networks are highly resistant to perturbations because (1) plant–pollinator networks tend to be organized in a nested, asymmetrically specialized fashion, (2) the most frequent pollinators tend to contribute most to plant reproduction, and (3) the most frequent pollinators are probably highly connected and rather resistant to extinction due to their abundance.

## 9.11 Prospects

Pollination is an essential service in both natural and agricultural ecosystems, so understanding pollination mechanisms and their susceptibility to different habitat disturbances is of paramount importance in different applied fields (e.g., Kremen *et al*. 2002, 2004). Despite considerable progress during the past two decades, much remains to be done. Many studies assume unidirectional effects of anthropogenic disturbance on plant and pollinator attributes and flower function (reviewed in Aizen *et al*. 2002; Ghazoul 2005a). However, many matrix cells (ca. 25%) in Tables 9.1–9.4 were filled with ↑↓, implying that those effects could be positive, negative, or represented by a modal function such as a quadratic. Furthermore, the effects of anthropogenic disturbance are complex, because they modify many environmental variables simultaneously. In general, these effects do not differ qualitatively from those triggered by natural disturbance, although they may differ in frequency and intensity (Sousa 1984; Chesson and Huntly 1997).

The question marks in Tables 9.1–9.4 (∼15% of all matrix cells) also identify particular unresolved issues whose predictions are elusive and await research. For instance, despite many studies considering how variation in floral morphology affects pollination and reproductive success (particularly in the context of phenotypic selection), few have examined how different types of disturbances modify flower traits. Relevant questions in this area include how and to what extent a given environmental disturbance (e.g., fire) modifies floral morphology (including flower size, shape, and symmetry) and its role in pollen dispersal and reproductive performance. Also, although some studies have focused on how certain disturbances, such as herbivory and fire, affect the reproductive physiology of flowers (e.g., post-pollination pollen performance), the relations of these aspects of flower performance to other kinds of disturbances remain unknown. For example, can resource competition with invasive plants affect the physiological status of flowers of native plants, and can this in turn affect pollination?

Another key group of largely unexplored questions concern whether changes induced by habitat disturbance on pollinator community characteristics, particularly diversity and composition, reduce pollination significantly. For instance, will the loss of specialist pollinators due to anthropogenic disturbance decrease pollination quantity and/or quality beyond any effect on overall visit frequency? Also, the replacement of complex pollinator assemblages by Africanized honeybees throughout the Neotropics may have consequences for pollination and patterns of gene flow, which remain largely unexplored. On the other hand, the agricultural service provided by managed or unmanaged populations of native pollinators as an alternative to *Apis mellifera* is a topic of much conservation and economic value, which is still in its infancy (Kremen *et al*. 2002).

Despite evidence for many of the links portrayed in our matrices, understanding the relative importance of the different mechanisms affecting the pollination process in altered landscapes is limited. We advocate the use of path analysis and associated structural equation modelling (Shipley 2000), which allows assessment and comparison of alternative, progressively complex causal models.

Many relevant questions about the structure of plant–pollinator networks and how it is affected by anthropogenic disturbance await answers. For instance, which structural aspects of these webs (e.g., connectance, distribution of specialization, asymmetry, nestedness) change most commonly under disturbance and which are apt to remain invariant? In addition, what consequences have those changes for individual species persistence? Most important, a more direct link between these structural modifications and their consequences for pollination function must be identified.

Geographic information systems also offer increasing opportunities to extrapolate site-specific pollination models to the regional scale (Kremen *et al*. 2004). We expect that this interface between landscape and pollination ecology will be crossed more frequently in the near future, increasing our ability to predict how different aspects of pollination will change in altered habitats with specific landscape configurations.

To conclude, we hope the framework outlined in this chapter will help in developing a more mechanistic approach to the study of anthropogenic perturbations on pollination and plant reproduction. More than providing conclusive answers, our goal has been to show how this approach can be used to identify open questions and future avenues of research, and to aid in organizing and designing studies of disturbance effects on flower function in human-altered landscapes.

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