

Habitat fragmentation and plant–pollinator interactions

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Habitat fragmentation is one of the most apparent forms of environmental degradation and is often considered to be one of the greatest threats to terrestrial biodiversity. We examine plant–pollinator relationships as one example of a vital interaction that may be affected by fragmentation. All available evidence shows that pollinator abundance and diversity decline with fragmentation. For some plants, this decline causes reduced pollination and seed set. For both pollinators and plants, specialization for mutualistic partners appears to be a key characteristic that increases their risk of local extinction in fragments. For more generalized species, substitutability of available partners will be necessary for their success. However, relatively little evidence exists for evaluating the importance of these or other characteristics in causing species loss in fragments. Potentially, the loss of one mutualistic partner could cause cascading extinctions, but this process remains to be documented for plant–pollinator communities. More studies on the biologies of key plant–pollinator mutualisms would be valuable for habitat management and would also provide insights into how plant–pollinator interactions influence demographic and genetic processes.

HABITAT fragmentation immediately reduces the sizes of species populations, increases their isolation, surrounds them in a matrix consisting of a new environment such as agriculture fields or development, and commonly changes their abiotic environment. Much of conservation biology in the last two decades has been concerned with the loss of biodiversity due to fragmentation. However, we still have little information about the causes of species loss in fragments, or how these losses may affect species interactions within communities. Here we examine plants and their pollinators as one example of a vital mutualistic interaction that may be affected by fragmentation.

Because pollination by animals is a necessary (but not sufficient) first step for long-term population persistence for the majority of angiosperm species, understanding the effects of fragmentation on plant–pollinator interactions may be essential for predicting the long-term persistence of populations and communities in fragmented habitats. For example, a plant population may show no immediate effect of fragmentation if individuals are long-lived, but a study of its pollination may predict future extinction if seed set is pollination-limited and greatly reduced. The extinc-

tion of a plant species may also cause the loss of its pollinators. The loss of plants or pollinators could subsequently cause cascading extinctions throughout the community^{1–3}.

Here we review studies that have addressed the effects of fragmentation on patterns of pollinator diversity and plant pollination. Habitat fragmentation could disrupt plant–pollinator interactions for many reasons⁴, but little data exist with which to evaluate possible causes of species loss in plant–pollinator systems. Therefore, we suggest how particular characteristics of pollinators and plants could influence the extinction or persistence of these species in fragmented landscapes. An understanding of how different species will respond to fragmentation would be valuable for future habitat management and would also provide insights into how plant–pollinator interactions can influence demographic and genetic processes in plant and animal communities.

Changes in pollinator communities

Studies focusing on the population dynamics of pollinators in fragments have only recently begun, but thus far all relevant data show that the abundance and diversity of insect pollinators decrease as habitat area decreases. These studies encompass a wide variety of habitats and insect pollinators, suggesting that the results are quite general. In a study of 20 sub-alpine meadows, Bowers⁵ found that the number of bumblebee queens and diversity of queen species were positively correlated with meadow area. Shreeve and Mason⁶ found that the number of butterfly species was positively correlated with woodlot area in England. In lowland dry meadows, Jennersten⁷ found that flower-visiting insect species were fewer in two fragments than in a continuous 'mainland' habitat.

Powell and Powell⁸ utilized the Biological Dynamics of Forest Fragments Project in Brazil to study the effects of fragmentation of wet tropical forest on male euglossine bees. They found that the number and density of bees visiting chemically scented baits were lower in fragments than continuous forest and were positively correlated with fragment size. In Argentinian dry thorn forest, Aizen and Feinsinger⁹ found that the number of small bee species caught in traps was lower

in two small forest fragments than in continuous forest. In addition, flower visitation by native bees to two predominant tree species was lower in fragments, whereas visitation by introduced Africanized honeybees increased.

The specific reasons for pollinator decline in fragments are unknown and are probably varied, because fragment area, isolation distance, isolation time and the environment of the intervening matrix all differ among these study sites. Below we propose how fragmentation could differentially affect pollinator species depending upon specific characteristics, such as resource requirements and dispersal ability.

Pollinators that are specialists on one or few plant species, like euglossine bees⁸ and solitary bees^{10,11}, may be especially vulnerable to habitat fragmentation for many reasons. Because specialist pollinators often exist in small, patchy populations^{10,12,13}, small fragments are more likely to exclude them, and environmental or demographic stochasticity¹⁴ is more likely to cause their extinction. For a specialist, the loss of its host plant will cause extinction. For specialists that exploit sparse, scattered floral resources, a reduction in floral abundance caused by fragmentation could also be threatening. Bronstein *et al.*¹⁵ present a striking example from figs and their specialist fig wasp pollinators. Because a tree releasing wasps must be synchronized with another tree receptive to wasps in order to be pollinated, tree density is critical to wasp success and to tree pollination. The authors estimate that at least 95 tree individuals are necessary to maintain wasp populations for four years. Because figs can act as keystone species that provide food for many frugivores during periods of resource scarcity, the loss of figs could generate cascading extinctions throughout the animal and plant community far beyond the fig-pollinator wasp populations³.

In contrast, generalist pollinators may be less vulnerable to fragmentation than specialists. Generalists often originally exist in widespread populations^{5,16,17} and thus are less likely to be excluded in small fragments. Furthermore, because many plant species can act as substitutable, or interchangeable resources for these pollinators⁹, the loss of one or few plant species should not directly threaten their survival. However, Bowers⁵ found that floral composition of meadows was a major component determining the probability of local extinction of bumblebees which are generalized floral visitors.

On the other hand, many floral-species generalists are actually specialists for high-density resources. If fragmentation reduces the abundance of these resources, these generalists may be highly vulnerable and experience high extinctions rates as Pimm and Pimm¹⁸ have suggested for Hawaiian honeycreepers. Even if species do not become locally extinct, the composition

of the pollinator community could change if floral densities or distributions are altered with fragmentation. For example, Sowing¹⁹ found that long-tongued bumblebees were more common in large, dense patches of flowers whereas short-tongued bumblebees were more common on plants in small, scattered patches.

Many generalist species are superior competitors for food on high-density or mass-flowering plants, and these species could reduce the diversity of other pollinators over time. Eusocial bees^{17,20} and large species of hummingbirds²¹ and bats²² can exclude smaller species from these resources^{16,20-23}. Competition with honeybees may partly explain the lower visitation by native bees at mass-flowering trees in fragments⁹. Whether competition with honeybees can also explain the lower diversity of native bees in fragments remains to be demonstrated^{9,16,23}.

The risks arising from dependence upon particular plant species or resource densities within fragments can be reduced if pollinators are long-range foragers that can accumulate resources from many fragments for their food needs⁹. But this benefit will depend upon distances between fragments relative to foraging ranges. Large bats can fly 100 km a night for food²², and honeybees can travel 20 km to forage¹⁷. However, for many other pollinators isolation distances from 100 m to 1 km would preclude inter-fragment foraging^{10,13,16,17}. Even when distances are relatively small, other factors may act as barriers to pollinator movements. Powell and Powell⁸ found that males of four euglossine bee species did not cross 100 m pasture clearings from continuous forest to forest fragments, even though males can fly >20 km in a day from a release point²⁴.

Pollinators that are long-lived may be at risk in fragmented habitats because they require extended periods of resource availability. If a keystone plant species, i.e. one that provides food during periods of resource scarcity³, fails to flower or goes locally extinct, pollinators may not survive^{1,25,26}. Many different pollinators migrate seasonally to different habitats to follow abundant floral resources. Seasonal migration is common within tropical areas and has been reported for bats²², hummingbirds²¹, butterflies²⁷, sphinx moths²⁸, and honeybees¹⁷. Haber²⁷ estimates that >80% of the butterfly species in Costa Rica migrate during the dry season from dry lowland tropical forest to wet tropical forest. Although one habitat may be adequately preserved, the loss of another keystone habitat could cause the extinction of such species over large areas. Because habitat destruction is often concentrated in certain habitat types in a particular region, many migrating species could be threatened⁴.

Long-distance dispersal will be necessary for colonization of fragments which can be important for species persistence over the long term^{5,29}. For long-ranging foragers and migrants, colonization of fragments should

be assured. An exception may be eusocial bee species that must move many workers with the queen and therefore have restricted dispersal for colonization^{16,17}. The average long-distance dispersal rates of other species are not well known, but for many of these a single fertilized female could potentially colonize a fragment.

The risks posed by fragmentation will also depend upon other non-food requirements and interactions with other species. For example, small bee species often have specialized nesting requirements^{10,16}, whereas most honeybee species have relatively generalized requirements¹⁷. Aizen and Feinsinger⁹ suggest that the prevalence of honeybees in fragments may partly reflect their ability to nest in the matrix area between fragments. Butterflies and moths have specific larval host plant requirements^{30,31} which may partly account for their observed decline in fragments^{6,7}. Changes in other species, such as predators or parasites, in fragments could also influence the survival of pollinator species, but no information is available on these effects.

Effects on plant pollination and plant reproductive success

Because fragmentation commonly reduces pollinator abundance and diversity, it seems likely that pollination and seed output may also be reduced. Indeed, both the studies that specifically address pollination in habitat fragments, show some reduction in pollination as well as pollination-limitation of seed set. Jennersten⁷ found that the perennial herb *Dianthus deltoides* showed pollination-limitation of seed set in meadow fragments but not in continuous habitat. In their study comparing two forest fragments with continuous forest, Aizen and Feinsinger³² found significant or marginal declines in pollen tube numbers per flower in 9 of 16 plant species, in fruit set for 5 of 15 species, and in seed set for 3 of 14 species in forest fragments.

The specific reasons for these reductions in pollination are varied and often ambiguous. Some key plant characteristics that may contribute to reduced pollination success in fragments are: (i) dependence on pollinators for seed set, (ii) specialization for one species or type of pollinator, (iii) self-incompatibility, and (iv) inbreeding depression^{4,32,33}.

Dependence upon pollinators and pollination specialization can account for much of the observed reproductive decline in plants in fragments. For *Dianthus*, Jennersten⁷ showed that although pollinator dependence varied seasonally, seed set typically decreased when pollinators were excluded. In addition, this species is specialized for butterfly pollination and was visited mainly by butterflies for nectar and by small flies

for pollen⁷. Aizen and Feinsinger³² documented that all their species largely depended upon pollinators for seed set. The role of pollinator specialization is less clear. The plant species that showed the greatest reduction in pollination in fragments were those that were infrequently visited regardless of habitat unit³² and hence were somewhat specialized for scarce pollinators. In contrast, no species that was commonly visited by introduced honeybees as well as native bees showed reduced pollen deposition³². Evidence from oceanic islands also indicates that plants having specialized pollinators show pollination-limitation of seed set more commonly than plants with more generalized pollinators^{34,35}. The risk of pollinator specialization may be especially high for orchids that are obligatorily pollinated by only one particular species of euglossine bee³⁶. These orchids may be severely threatened by the loss of their euglossine pollinators in fragments⁸.

Generalized plant species that are visited by a spectrum of pollinator types may be less likely to suffer from the loss of one or a few pollinator species than specialized species, but they could experience reduced pollination success if pollinators are not substitutable. Pollinator species can vary greatly in the quantity and quality of pollen they transport to flowers^{24,37}. In temperate floras, many solitary, oligolectic bees are poor pollinators, and most pollination is probably effected by bumblebees or honeybees^{10,11}. Honeybees appeared to be substitutable for small bees on the two tree species studied by Aizen and Feinsinger³². However, honeybees can be poor pollinators for other plant species^{23,38}, and they may be reducing the pollination success of many plants in Australia where they have been introduced³⁸.

The importance of self-incompatibility and inbreeding depression in the pollination declines in fragments among the species studied. Aizen and Feinsinger³² found no correlation between self-incompatibility and pollination reduction, but they present evidence that inbreeding depression may account for reduced fruit or seed set in several of the species. *Dianthus* is self-compatible and showed no evidence that inbreeding depression reduces seed set⁷. In a study of *Silene regia* in prairie fragments, Menges³³ found that germination success was lower for plants from small populations (<150 plants) than from larger populations. He suggests that this reduction most likely reflects higher inbreeding depression resulting from small population size and possibly from shorter pollen dispersal distances caused by hummingbirds foraging in small patches.

The pollination success of one plant species can also be influenced indirectly by the presence of other plant species that maintain pollinators. Waser and Real³⁹ documented that a failure in flowering of an early-flowering species caused migrating hummingbirds to leave the area; as a result, a later-flowering species

experienced lower visitation rates and lower seed set. The disruption of such sequential mutualisms by fragmentation could cause cascading extinctions through the community^{1,40,41}.

Fragmentation can also modify microclimates and the availability of abiotic resources⁴² which may directly or indirectly change the patterns of plant reproduction. Abiotic conditions can directly affect the production of flowers and seeds and can indirectly affect seed production by changing floral resources for pollinators. Changes in the availability of nectar or pollen can alter pollinator behavior and determine pollination success^{41,43}. For example, Zimmerman⁴⁴ found that watering plants of *Delphinium nelsonii* not only increased nectar production, but also pollinator visitation and seed set.

Summary

Habitat fragmentation can clearly disrupt plant-pollinator interactions and threaten the local persistence of plants and pollinators. Pollinator abundance and diversity typically decline in fragments⁵⁻⁹, and this decline can result in lowered seed set for some plants^{7,32}. Fragmentation can also restrict pollinator movement⁸ which may reduce gene flow and result in increased inbreeding^{4,33}. Inbreeding depression could further lower the reproductive success of plants in fragments. Lowered seed set or viability could reduce the regeneration of species in fragments. However, whether reduced pollination will be as important as other factors, such as herbivory or microclimate, in determining local extinctions in fragments remains to be determined³².

For pollinators, many characteristics could increase their likelihood of becoming extinct in fragments. Many pollinator losses may occur because they originally existed in small, patchy populations and were excluded in single, small fragments. However, restricted dispersal between fragments is the only characteristic that has been demonstrated to cause species absence in fragments⁸. Specialization for floral hosts should also increase risk of extinction, but no documented examples were found. Other characteristics that could increase species vulnerability to fragmentation effects are restricted foraging range, the need for extended periods of floral availability, requirements such as nesting sites, and poor colonization ability. The relative contributions of these characteristics to species extinctions in fragments remain to be tested.

For plants, their reproductive success may be more likely to decline in fragments if they possess one or more of the following characteristics: dependence upon pollinators for seed set, specialization for one species or type of pollinator, self-incompatibility, or high inbreeding

depression. Evidence is currently too limited to evaluate the relative effects of these factors on reproduction in fragments, but plants that are specialized for pollination appear more likely to experience pollination reduction in fragments than more generalized plants^{7,32}. Because certain types of pollinators may be more sensitive to fragmentation than others, plants specialized for these pollinators would have a greater risk of reproductive failure^{9,32}.

Pollinator and plant species that are more generalized in their requirements for mutualistic partners may be more successful than specialists in fragments. However, their success will depend upon the substitutability of the partners available. For example, honeybees can be substituted for solitary bees for some plants³² but not for others²³.

The loss of one species in a plant-pollinator mutualism can indirectly cause the loss of other species in the community. In particular, keystone plant species for long-lived pollinators or keystone habitats for migrating pollinators may be crucial for the maintenance of these mutualistic communities. The importance of such indirect effects in causing species declines in fragments needs to be tested. In general, many more studies are needed before we can identify the causes of species declines in fragments or predict the effects of fragmentation on plant-pollinator interactions.

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India's buzzy biodiversity of bees

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The historical background of research on the bees or Apoidea of India is reviewed. Current knowledge of these important pollinating insects is compared with that in other parts of the world. Recommendations for further research in India are made, with suggestions regarding the conservation of bee species and the management of their populations to benefit both agriculture and wildlife in India.

A millennium ago, India was a place of floral bounty, where people relaxed in beautiful public gardens. At that time, bees were extolled in Sanskrit poetry, especially the *bhramara* (*Xylocopa*, or carpenter bees). These big, acrobatic, noisy bees symbolized virile male lovers, voluptuously kissing the dainty, fragrant, feminine flowers¹. In religious poetry, bees represented seekers of knowledge or wisdom, which is symbolically hidden in flowers (usually the lotus, which may nocturnally close, to trap any lazy bees). Bees were admired and cherished for their musical humming, their persistent attraction to beauty, their epicurean taste in food, their love of fragrances, their dynamic and far-ranging flights, and their preference for fair weather. In the Ramayana, when Hanuman found Ravana's

beautiful ladies asleep, 'On their soft limbs, the marks of their ornaments sat like bees...'. They were '... like garlands of flowers attended by lovesick bees, ... like the intertwined branches of great forest trees, full of clouds of swarming bees ...'. The behavior of bees was related to the seasons¹: 'With tumbled hair of swarms of bees, and flower-ropes dancing in the breeze, with sweet, unsteady lotus-glances, intoxicated, Spring advances.' Also, 'This season of erotic fragrance, of wistful love, has maddened the sporting bees.' Bee sport, or *bhramara vilasita*, evidently refers to the territorial hovering, courtship and fighting of male *Xylocopa*, which happens during Spring. Sri Guru Granth Sahib states: 'In Chet, agreeable is the Spring, and beautiful the *bhowra*'. (= *bhramara*). However in the rainy season (*Bhadon*), 'The bees have forgotten all about honey and the fragrance of flowers, and are hiding themselves in heaps'. Male solitary bees often cluster together to sleep in nooks.

Although the ancients romanticized carpenter bees, they also found two unusual practical uses for them. The *bhramara* were apparently used to carry messages, as homing pigeons are used today. These bees can return to their nests when released as far away as 4 km