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Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter?

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Abstract. This paper explores whether plant breeding system and pollination specialization influence the reproductive response of plants to habitat fragmentation. It is meaningful for conservation to predict a plant species' extinction risk. We found 25 studies in the literature assessing the effects of habitat fragmentation on either pollination or reproductive success of 46 plant species to answer the following questions: 1. Are pollination and reproductive success of self-incompatible species more likely to decline with habitat fragmentation than the pollination and reproductive success of self-compatible species? Although most of the species showed statistically significant negative effects, the pollination and reproduction of self-incompatible species were as likely to decline with fragmentation as those of self-compatible species. 2. Are pollination and reproductive success of specialist plants more affected than the pollination and reproduction of generalist plants? Comparisons of fragmentation-related changes in pollination and reproductive success between specialists and generalists do not support the hypothesis that specialization in pollination increases the risk of plant extinction. 3. Can self-incompatible species offset their expected higher vulnerability to fragmentation by being, on average, more pollination generalist than self-compatible species? In a larger data set on 260 species, we did not find significant differences in either the mean number or frequency distribution of numbers of flower-visiting species or orders between self-compatible and self-incompatible species. Our review suggests that no generalizations can be made on susceptibility to fragmentation based on compatibility system and pollination specialization.

Keywords: Breeding system; Habitat fragmentation; specialization; Reproduction; Self-compatible; Self-incompatible.

Introduction

It is largely accepted that habitat fragmentation has distinctive effects on plant and animal populations. Particularly, a reduction in population size and an increase in isolation related to fragmentation may be linked to increased inbreeding, decreased individual fitness, the loss of genetic variation, and consequently to increased risk of population extinction (Murcia 1995; Jules & Rathcke 1999; Jacquemyn et al. 2002 and citations therein). In addition to its direct consequences, fragmentation may alter interactions among species (Kattan & Alvarez-López 1996; Murcia 1996). More than 80 % of the extant flowering plants depend, to different degrees, on animals for their pollination and sexual reproduction (Bawa 1990; Buchmann & Nabhan 1996). Although the evolutionary acquisition of animals as pollen vectors boosted pollen transfer efficiency, dependence on mutualists for reproduction could have increased plant susceptibility to fragmentation and other forms of habitat disturbance (e.g. Bond 1994; Spira 2001).

Disruption of plant-pollinator interactions can occur because of the sensitivity of many flower visitors to the changes in habitat quantity and quality triggered by fragmentation (Kearns et al. 1998; Aizen & Feinsinger in press). As a result, the degradation of this plant-animal mutualism may provoke sizeable decreases in seed number and quality, and even constitute the first step towards the demographic collapse of many plant populations. There are a few examples of plant taxa on the verge of extinction due to a lack of sexual reproduction associated with the loss of their original pollinators (e.g. Buchmann & Nabhan 1996; Renner 1998; Cox & Elmqvist 2000; Paton 2000). However, plant species can differ in their vulnerability to habitat fragmentation according to their dependence on pollination mutualism. In particular, two reproductive traits could be important in determining the degree of reproductive responsiveness of plants to habitat fragmentation: breeding system and pollination specialization (Bond 1994; Murcia 1996; Renner 1988; Aizen & Feinsinger in press).

Plant breeding systems range from those that enforce outbreeding to those that ensure sexual reproduction

via autonomous, within-flower selfing and autogamous seed set (Lloyd 1992). Among the most common outbreeders are plant species with distinctive male and female individuals (i.e. dioecy), and those which produce hermaphroditic flowers but possess a genetically-based self-incompatibility system. On the other hand, there are many self-compatible species that can set seed via selfing. In animal-pollinated species, this inbreeding-outbreeding gradient will dictate, beyond its genetic consequences for plant populations and individual fitness, the overall degree of dependence on the pollination mutualism for plant reproduction (Bond 1994). Whereas reproduction of obligate outbreeders will require the presence of other mates and a pollen vector to transfer pollen between them, reproduction of inbreeders will be mostly independent of the presence of mates and animal mutualists.

Plants can also vary in their degree of pollination specialization, from extreme specialists to extreme generalists. Pollination specialists are defined as plants pollinated by one or a few ecologically similar animal species, whereas generalists are plants pollinated by several to many species, usually of diverse taxonomic origin (Renner 1998). The yucca/yucca-moth and fig/fig-wasp mutualisms are well-studied cases of extreme specialization. However, flowers of most species are usually visited – and presumably pollinated – by animal visitors that can vary from a few, to more than 100 species (Feinsinger 1983; Herrera 1988; Waser et al. 1996). This gradient in pollination specialization may be related to the likelihood of mutualism failure. Pollination specialists are expected to be more vulnerable than generalists because the loss of only one pollinator could lead to a complete reproductive failure (Bond 1994).

Recent reviews (Bond 1994; Murcia 1996; Renner 1998) describe in detail how dependence on the presence of other plant individuals and on particular pollen vectors can make some plant species more susceptible than others. However, mainly because of the lack of much published data, there has not been so far any formal testing of the hypotheses that breeding system and pollination specialization determines a species' reproductive response to habitat fragmentation. Some authors have suggested that single-variable patterns might not be detected because plants could exhibit a suite of compensatory reproductive traits that make them, on average, equally resilient (or susceptible) to the effects of habitat fragmentation (Bond 1994; Jules & Rathcke 1999). Particularly, Bond (1994) argued that extinction may have already removed high-risk specialists with no backup reproductive mechanisms and that self-pollination may have evolved rapidly in response to pollinator failure. Here, we try to answer the following questions: 1. Are the pollination and reproductive success of self-

incompatible species (i.e. obligate outbreeders) more likely to decline with habitat fragmentation than the pollination and reproductive success of self-compatible species (i.e. facultative inbreeders)? 2. Are the pollination and reproductive success of specialist plants more affected by fragmentation than the pollination and reproduction of generalist plants? 3. Can self-incompatible species offset their expected higher vulnerability to fragmentation by being, on average, more pollination-generalist than self-compatible species?

Data sets

We have built a database of > 10 000 references on plant reproductive ecology from the 1991-2001 Current Contents data base. According to the three objectives of this study we selected 406 papers, out of which 25 studies assessed, either explicitly or implicitly, the effects of habitat fragmentation on either pollination or reproductive success of 46 species. Some of these studies assess pollination and reproduction of (1) plants in true habitat fragments (e.g. Aizen & Feinsinger 1994; Cunningham 2000); (2) isolated trees in pastures vs. those in forests (e.g. Aldrich & Hamrick 1998; Rocha & Aguilar 2001); (3) plant patches of different sizes or degree of isolation (e.g. Morgan 1999; Steffan-Dewenter & Tscharntke 1999). We included the third type of studies because many of the mechanisms involved in the so-called 'fragmentation effects' are population-size or -isolation dependent.

For each species, we compiled information on family, location (latitudinal region and continent), habitat type, growth form, breeding system, and type of flower visitors. All 46 species have hermaphroditic flowers. All studies but one (Cunningham 2000) provide information on whether the focal species were self-compatible (SC) or self-incompatible (SI). For self-compatible species and if available, we also computed either the percent fruit or seed set when pollinators were excluded (i.e. capacity for autonomous self-pollination). We classified each species as a pollination-specialist (S) or pollination-generalist (G) based on the taxonomic array of flower visitors mentioned in the reference, pollination mechanism (e.g. buzz pollination), and flower morphology. Although there may be a subjective judgement in the assignment of some plant species to either category, we believe that our dichotomous classification captures a large part of the variation in the specialization-generalization gradient characterizing this species sample.

We also include the effect of fragmentation on pollination and reproductive success. Although many of these studies provide quantitative estimates of fragmentation effects, we consider only the qualitative effect

(negative, neutral, positive) because the range in fragment size and degree of isolation included in these studies were so dissimilar that estimations of the magnitude of these effects were meaningless for comparative purposes. For many species, pollination levels were estimated by counting pollen tubes (Aizen & Feinsinger 1994) or through pollen limitation assays (e.g. Jennersten 1988; Moody-Weis & Heywood 2001). These measures could reflect either quantitative (i.e. related to visit frequency, pollinator efficiency and capacity for within-flower self pollen deposition) or qualitative aspects of pollination (i.e. determined by breeding system and pollen transfer).

However, in a few studies only quantitative estimates of pollination were provided through measuring either pollen deposition (e.g. Rocha & Aguilar 2001) or pollinator visitation frequency (Smith-Ramírez & Armesto in press). In most studies, reproductive success was estimated as fruit set, seed set or total seed output. In a few studies, however, other aspects of reproductive success such as seed germination (e.g. Menges 1991; Ouborg & van Treuren 1995) were considered. Information on the species, habitats, and qualitative fragmentation effects is summarized in Table 1.

To address our third question, we also gathered information on breeding system and pollination specialization of 260 species, from 183 genera and 85 families. This data set (available from the authors on request) includes species that represent most existing growth forms and occur in a wide range of tropical and temperate habitats in all five continents. Based on the qualitative or quantitative information provided, we assigned each species to one of three breeding system categories (dioecious, self-compatible or self-incompatible). We considered the number of either flower-visiting species or orders reported for each particular plant species as a measure of pollination specialization.

Habitat fragmentation and breeding system

Are the pollination and reproductive success of self-incompatible species (i.e. obligate outbreeders) more likely to decline with habitat fragmentation than self-compatible species (i.e. facultative inbreeders)? Ca. 70% and 60% of the species listed in Table 1 experienced statistically significant negative effects on pollination and reproductive success, respectively. However, the pollination and reproduction of self-incompatible species were as likely to decline with fragmentation as those of self-compatible species (Fig. 1).

Despite the fact that Table 1 includes a heterogeneous set of studies that differ greatly in habitat type, fragment sizes, surrounding matrix and response variables this

lack of difference between SC and SI species is surprising. A potential source of bias that might influence the similar response of SC and SI species is that studies dealing with effects of fragmentation (or patch size) on plant reproduction often focuses on species with showy flowers that depend on pollinators for seed set, regardless of their breeding system. Thus, the pollination and reproduction of the self-compatible species included in these studies could be as mutualist-dependent as those of most obligate outbreeders. This subset of self-compatible species, exhibiting a mixed mating system, also express inbreeding depression at early stages of reproduction (e.g. during seed set; Klekowski 1988), particularly in small populations trapped in habitat fragments. However, negative responses of fragmentation at either pollination or seed set stages were also found in self-compatible species with a large capacity to produce seed autonomously (e.g. *Gentianella germanica, Nepeta cataria, Portulaca umbraticola*; Table 1). Considering the available evidence, we can conclude that some selfing capacity does not lessen the probability of a plant species to respond negatively to fragmentation.

Given the lack of information of the compatibility system for a few species (Table 1) and potential wrong assessments for others, we also used variation in growth form as a surrogate of the outbreeding-inbreeding gradient with trees occupying the outbreeding extreme and herbaceous plants the inbreeding extreme (Klekowski 1988). According to Murcia (1996) trees would be the group most susceptible to forest fragmentation, not only due to a high incidence of self-incompatibility but also because of low density.
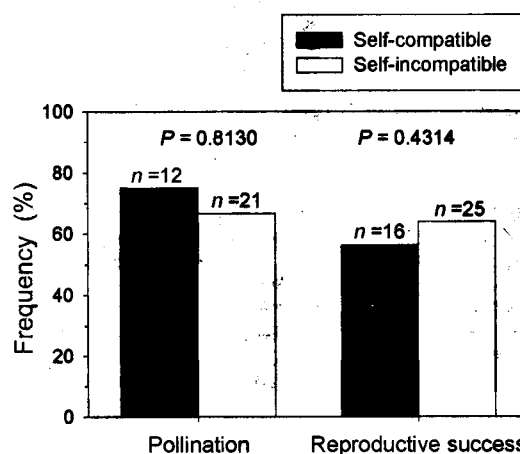
Fig. 1. Relative frequency of self-compatible vs self-incompatible plant species showing negative fragmentation effects on pollination and reproductive success. *P*-values associated with a one-tailed Fisher's exact test (i.e. are self-incompatible species more likely to exhibit fragmentation effects than self-compatible species?) are shown.

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Table 1. Fragmentation or plant-population size and/or isolation effects on pollination and plant reproductive success. − = significant negative fragmentation effect; + = a significant positive effect; 0 = a non-significant effect. FE = Fragmentation effect.

Species	Family	Location[a]	Habitat type	Growth form	Breeding system[b]	Flower visitors[c]	Specialization[d]	FE pollination	FE reprod. success	Reference
Acacia aroma	Fabaceae	Subtropical SA	Dry forest	Tree	SI	Medium-sized to large bees	S	−	−	Aizen & Feinsinger (1994)
Acacia atramentaria	Fabaceae	Subtropical SA	Dry forest	Tree	SI	Bees, beetles	G	0	+	Aizen & Feinsinger (1994)
Acacia brachybotrya	Fabaceae	Temperate AU	Sclerophyllous woodland	Shrub	?	Diverse insects	G	?	−	Cunningham (2000)
Acacia furcatispina	Fabaceae	Subtropical SA	Dry forest	Shrub	SI	Butterflies, bees, wasps	G	0	+	Aizen & Feinsinger (1994)
Acacia praecox	Fabaceae	Subtropical SA	Dry forest	Tree	SI	Bees, wasps	G	0	0	Aizen & Feinsinger (1994)
Atamisquea emarginata	Capparaceae	Subtropical SA	Dry forest	Shrub	SI	Bees, wasps, moths	G	−	−	Aizen & Feinsinger (1994)
Banksia goodii	Proteaceae	Temperate AU	Sclerophyllous woodland	Shrub	SI	Mammals, birds	S	?	−	Lamont et al. (1993)
Brassica kaber	Brassicaceae	Temperate NA	Experimental populations	Herb	SI	Bees, flies	G	0	0	Kunin (1997)
Caesalpinia gilliesi	Fabaceae	Subtropical SA	Dry forest	Shrub	$SC_{3\%}$	Hawkmoths	S	−	0	Aizen & Feinsinger (1994)
Campanula cervicaria	Campanulaceae	Boreal EU	Glade	Herb	SC	Bees, flies	G	?	0	Eisto et al. (2000)
Cassia aphylla	Fabaceae	Subtropical SA	Dry forest	Shrub	$SC_{0\%}$	Large bees (B)	S	−	0	Aizen & Feinsinger (1994)
Centrosema virginianum	Fabaceae	Subtropical NA	Mainland vs island	Vine	SC	Large bees	S	−	−	Spears (1987)
Cercidium australe	Fabaceae	Subtropical SA	Dry forest	Tree	SI	Bees, wasps	G	−	0	Aizen & Feinsinger (1994)
Clarkia coccinna	Onagraceae	Temperate NA	Disturbed road side	Herb	SC	Bees, flies, butterflies	G	−	−	Groom (1998)
Dianella revoluta	Phormiaceae	Temperate AU	Sclerophyllous woodland	Herb	?	Large bees (B)	S	?	−	Cunningham (2000)
Dianthus deltoides	Caryophyllaceae	Temperate EU	Forest and meadow	Herb	$SC_{20\%}$	Bees, butterflies	G	−	−	Jennersten (1988)
Embothrium coccineum	Proteaceae	Temperate SA	Rainforest	Tree	SI	Birds, hummingbirds	S	+	?	Smith-Ramírez & Armesto (in press)
Enterolobium cyclocarpum	Fabaceae	Tropical CA	Dry forest	Tree	SI	Moths, beetles, bees	G	−	−	Rocha & Aguilar (2001)
Eremophila glabra	Myoporaceae	Temperate AU	Sclerophyllous woodland	Shrub	?	Birds	S	?	−	Cunningham (2000)
Eupatorium resinosum	Asteraceae	Temperate NA	Open wetland	Herb	SI	Wasps, bees, flies, moths	G	?	−	Byers (1995)
Eupatorium perfoliatum	Asteraceae	Temperate NA	Open wetland	Herb	SI	Wasps, bees, flies, moths	G	?	0	Byers (1995)
Gentianella germanica	Gentianaceae	Temperate EU	Calcareous grassland	Herb	$SC_{55\%}$	Flies, bees	G	?	−	Fischer & Matthies (1998)
Ipomopsis aggregata	Polemoniaceae	Temperate NA	Open woodland	Herb	SI	Hummingbirds	S	−	−	Heschel & Paige (1995)
Justicia squarrosa	Acanthaceae	Subtropical SA	Dry forest	Herb	$SC_{0\%}$	Butterflies	S	−	−	Aizen & Feinsinger (1994)
Ligaria cuneifolia	Loranthaceae	Subtropical SA	Dry forest	Hemiparasite	$SC_{10\%}$	Hummingbirds	S	+	0	Aizen & Feinsinger (1994)
Mimosa detinens	Fabaceae	Subtropical SA	Dry forest	Shrub	$SC_{5\%}$	Moths, wasps	G	0	−	Aizen & Feinsinger (1994)
Nepeta cataria	Lamiaceae	Temperate NA	Disturbed deciduous forest	Herb	$SC_{64\%}$	Bees, flies, butterflies	G	−	−	Sih & Baltus (1987)
Lychnis viscaria	Caryophyllaceae	Boreal EU	Experimental populations	Herb	SC	Bees, butterflies, flies	G	−	0	Mustajärvi et al. (2001)
Lythrum salicaria	Lythraceae	Boreal EU	Mainland vs island	Herb	SI	Bees, flies, butterflies	G	−	−	Ågren (1996)
Oenothera macrocarpa	Onagraceae	Temperate NA	Glade	Herb	SI	Hawkmoths	S	−	−	Moody-Weis & Heywood (2001)
Opuntia quimilo	Cactaceae	Subtropical SA	forest	Succulent	SI	Medium-sized to large bees	S	0	0	Aizen & Feinsinger (1994)
Opuntia stricta	Cactaceae	Subtropical NA	Mainland vs island	Succulent	SI	Bees	G	−	−	Spears (1987)
Portulaca umbraticola	Portulacaceae	Subtropical SA	Dry forest	Herb	$SC_{61\%}$	Small bees, butterflies	G	−	−	Aizen & Feinsinger (1994)

Table 1, *cont.*

Species	Family	Location[a]	Habitat type	Growth form	Breeding system[b]	Flower visitors[c]	Specialization[d]	FE pollination	FE reprod. success	Reference
Primula elatior	Primulaceae	Temperate EU	Forest	Herb	SI	Bees, other insects	G	?	–	Jacquemyn et al. (2002)
Prosopis nigra	Fabaceae	Subtropical SA	Dry forest	Tree	SI	Bees, flies, wasps	G	–	–	Aizen & Feinsinger (1994)
Raphanus sativus	Cruciferae	Temperate EU	Experimental populations	Herb	SI	Solitary bees	S	–	–	Steffan-Dewenter & Tscharntke (1999)
Rhipsalis lumbricoides	Cactaceae	Subtropical SA	Dry forest	Epiphyte	SI	Butterflies, bees, wasps	G	–	–	Aizen & Feinsinger (1994)
Rutidosis leptorrhynchoides	Asteraceae	Temperate AU	Grassland	Herb	SI	Beetles, flies, moths	G	–	–	Morgan (1999)
Salvia pratensis	Lamiaceae	Temperate EU	Calcareous grassland	Shrub	SC	Bees	S	?	0	Ouborg & van Treuren (1995)
Senna artemisioides	Fabaceae	Temperate AU	Sclerophyllous woodland	Shrub	?	Large bees (B)	S	?	+	Cunningham (2000)
Silene regia	Caryophyllaceae	Temperate NA	Prairie	Herb	SC	Hummingbirds	S	?	–	Menges (1991)
Sinapis arvensis	Cruciferae	Temperate EU	Experimental populations	Herb	SI	Bees, flies, beetles, waps, bugs	G	–	–	Steffan-Dewenter & Tscharntke (1999)
Symphonia globulifera	Buttiferae	Tropical CA	Rainforest	Tree	SC	Hummingbirds, birds	S	+	+	Aldrich & Hamrick (1998)
Spondias mombin	Anacardiaceae	Tropical CA	Moist forest	Tree	.SI	Small diverse insects	G	–	–	Nason & Hamrick (1997)
Tillandsia ixioides	Bromeliaceae	Subtropical SA	Dry forest	Epiphyte	SI	Hummingbirds	S	0	0	Aizen & Feinsinger (1994)
Trillium ovatum	Liliaceae	Temperate NA	Mesic forest	Herb	SI	Beetles, bees, moths	G	?	0	Jules & Rathcke (1999)

[a]AU= Australia, SA= South America, NA = North America, CA = Central America, EU = Europe; [b]SC = self-compatible, SI = self-incompatible. For self-compatible species and when information was available, a subscript indicates % of either fruit or seed set from flowers where pollinators were excluded; [c]B = buzz pollination; [d]S = pollination specialist, G = pollination generalist.

In our sample (Table 1), 50% and 56% of the trees, 50% and 55% of other woody plants (including shrubs, cacti, vines and one hemiparasite) and 92% and 76% of the herbs showed negative fragmentation effects on pollination (Fisher's Exact Test, $P = 0.07$) and reproductive success (Fisher's Exact Test, $P = 0.20$), respectively. This trend is opposite to that expected. Although pollination and reproduction of herbaceous species could be more impaired than in trees due to a more spatially limited pollen flow, this comparison does not support the hypothesis that compatibility system is an important character in predicting reproductive response to fragmentation.

Habitat fragmentation and pollination specialization

Are pollination and reproduction success more affected in specialist than in generalist plants? Comparisons of fragmentation related changes in pollination and reproductive success between specialists and generalists (Table 1) do not support the hypothesis that specialization in pollination increases the risk of plant extinction. The proportion of species showing a decline in pollination and reproduction with fragmentation was similar among pollination specialists and generalists (Fig. 2).

Also, reproductive vulnerability in plants is thought to increase with decreasing latitude, because of a higher frequency of specialized pollination syndromes (e.g. bat, bird) in the tropics compared with temperate zones (Bawa 1990; Renner 1998). With respect to habitat fragmentation, our data do not support this statement. Although non-significant, we found a trend in the opposite direction with 62% and 52% of the tropical-subtropical species vs 83% and 71% of the temperate-boreal species showing pollination (two-sided Fisher's Exact Test, $P = 0.26$) and reproductive ($P = 0.23$) decline with fragmentation, respectively. However, this trend could be explained by a higher number of studies focusing on herbs in temperate than tropical latitudes (76% vs 10%). The herb growth form shows the highest susceptibility to fragmentation (Table 1). In any event, pollination and reproduction of tropical plants do not seem to be more vulnerable to fragmentation than in temperate plants.

One possible explanation for a lack of relationship between specialization and negative fragmentation effects is that pollination specialists rely only on dependable flower visitors. Waser et al. (1996) demonstrated that the most successful plants specialize with efficient pollinators that are relatively abundant and exhibit limited variation in time and space. This would involve
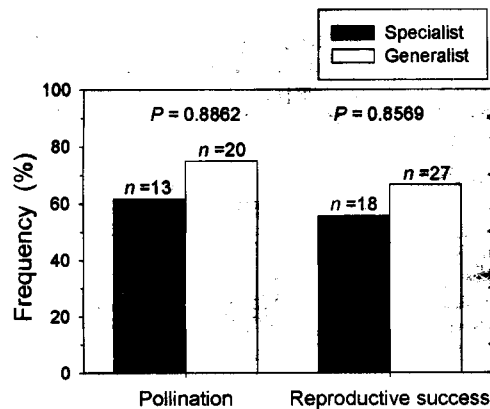
Fig. 2. Relative frequency of pollination-specialist vs pollination-generalist species showing negative fragmentation effects on pollination and reproductive success. P-values associated with a one-tailed Fisher's Exact test (i.e. are pollination specialists more likely to exhibit fragmentation effects than pollination generalists?) are shown.

pollinators that tolerate disturbance and/or are stronger flyers (and are probably less restricted to cross habitat barriers) like many medium and large bees, hummingbirds, bats and hawk moths (Janzen 1971; Stouffer & Bierregaard 1995; Murcia 1996; Aizen & Feinsinger in press), the pollinators usually associated with specialist plants. Also, plants that utilize pollinators may have compensatory reproductive traits that allow them to cope with changes in pollinator abundance. In addition to an increasing selfing capacity, these traits could involve an extended life span, profuse vegetative reproduction (Bond 1994) and staggered flowering phenologies (Bronstein & Hossaert-Mc Key 1995). In any event, our results do not support the widespread assumption that pollination specialization *per se* increases a plant's vulnerability to fragmentation. Of course, this general statement should not be in conflict with the fact that some specialist plants, such as some island bird pollinated species (Cox & Elmqvist 2000), may be on the verge of extinction due to the disruption of their pollination mutualism. However, proximate factors other than fragmentation (e.g. introduced diseases or competitors) are usually involved in the demise of these plants' pollinators (Renner 1998).

Compensatory effects between breeding system and pollination specialization

Can self-incompatible species offset a possible higher vulnerability to fragmentation by being more generalist than self-compatible species? The absence of independent effects of breeding system and pollination specialization on the response of plant pollination and reproduc-

tion to habitat fragmentation might be attributed to a compensatory association between these two factors. After all, extant plant species are the product of millions of years of evolution and should, in general, be relatively adapted to local disturbance and to an ever changing environment. The hypothesis of compensatory effects among reproductive traits was developed by Bond (1994) who showed that, at least in some communities, plants that were severely pollen limited had a low demographic dependence on seeds, whereas pollen limitation was uncommon among plants that reproduce mainly via seed. He also implied the existence of compensatory effects between pollination specialization and degree of reproductive dependence on mutualism (which relates directly to breeding system), but he did not test this idea with empirical data.

The existence of compensatory effects between breeding system and pollination specialization was not clearly supported by species listed in Table 1, although the trend was in the expected direction. Whereas we classified 50% of the self-compatible species as pollination specialists, this proportion decreased to 31% among self-incompatible species (one-sided Fisher's Exact test, $P = 0.18$). Our larger data set provides less support, showing that a similar number of animal species visited the flowers of both self-compatible and self-incompatible species (including dioecious species). In addition, self-compatible and self-incompatible species exhibited a similar frequency distribution in terms of the number of flower-visiting species (Fig. 3A). This figure also shows that extreme specialization and generalization can be found among both self-compatible and self-incompatible species. However, plants with several mutualist species may still be susceptible if these species are all taxonomically closely related (Bond 1994). Furthermore, functional specialization in plants may be better characterized by the number of higher order animal taxa, particularly at the taxonomic level of "orders" (Johnson & Steiner 2000). Our data set showed that the flowers of >70% of plant species are visited by only 1-2 orders of animals, with some flowers being visited up to >6 orders of animals. However, there were no significant differences in the mean number of flower visiting orders or frequency distribution between self-compatible and self-incompatible species (Fig. 3B).

It is possible that associations with other factors, such as growth form or habitat type, could be obscuring a relationship between breeding system and pollination specialization. Although an assessment of all those potentially confounding factors is beyond the scope of this article, the results of our analyses suggest that the relationship between breeding system and specialization, if present, is not clear cut.
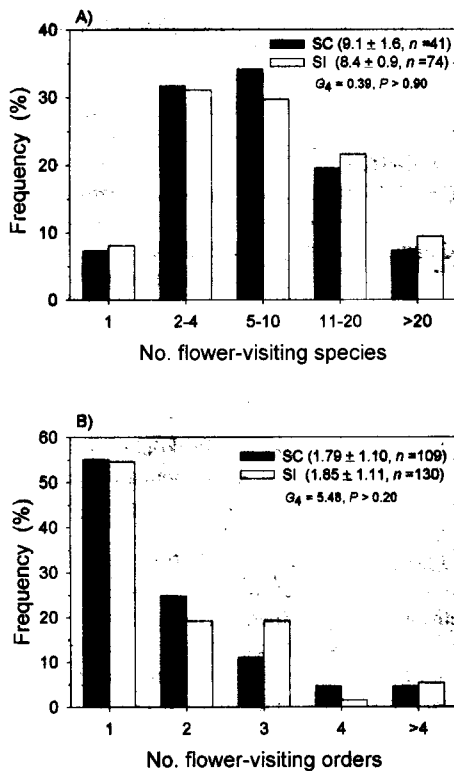
Fig. 3. Histogram of relative frequencies of plant species associated with increasing numbers of (**A**) flower visiting species and (**B**) flower-visiting orders. Separate histograms for self-compatible (SC) and self-incompatible plus dioecious species grouped together (SI) are depicted. In parentheses, means ± 1 s.e. Results of a G-test comparing the frequency distribution of SC vs SI species are shown.

Concluding remarks

The aim of this study was to test common assumptions about how plant reproduction responds to habitat fragmentation. Particularly, whether or not plant breeding system and pollination specialization influence this response. More studies using comparable protocols, looking at whole assemblages of plants, and measuring the same dependent variables are obviously needed for a more formal testing of these ideas. The answer we can provide on extant evidence is that no generalizations can be made on susceptibility to fragmentation based on compatibility system and pollination specialization. However, our results do not mean that these characteristics could not be important in determining the demographical decline of particular species, particularly of extreme outbreeders or specialists (see Renner 1998). Neither do they mean that these traits should not be used in assessing extinction risk or susceptibility of particular plant species, which is significant to conservation (see Bond 1994). However, our results demonstrate that

these two characteristics alone, at least in the way they are usually estimated, cannot predict how the reproduction of plant species will change with fragmentation. Species are characterized by complex suites of integrated traits (Armbruster et al. 1999), which determine a myriad of interactions and thus the relevance of different potential causal mechanisms influencing population growth and persistence (e.g. variation in seed production, seed dispersal, seedling recruitment, seed and seedling herbivory; Jules & Rathcke 1999). Therefore, it is unlikely that one or a few traits and/or ecological processes will be enough to explain why pollination and reproduction decline with fragmentation in many species but not in others.

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