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Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation?

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Abstract

1 Although reproductive success of pollination specialist plants has been predicted to be more sensitive to habitat fragmentation than that of generalist plants, recent results indicate that effects do not differ between plants with different degrees of specialization.
2 We provide an explanation for such unexpected results by linking evidence that specialization of plant–pollinator interactions is asymmetric to observations that generalist pollinators are less affected by habitat fragmentation.
3 Plant specialization cannot therefore be considered in isolation from the degree of specialization of the mutualist partners. Evaluation of both sides of the mutualistic interaction will yield insights into the mechanisms behind species' responses to habitat fragmentation.

Key-words: Asymmetric interactions, extinction risk, habitat fragmentation, mutualism disruption, niche breadth, plant–animal mutualism, plant reproductive success, pollination specialization, reproductive susceptibility

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Most flowering plants depend on animals for effective pollination and sexual reproduction (Buchmann & Nabhan 1996). Although animal vectors improve pollen transfer to stigmas such evolutionary dependence on mutualists for reproduction has increased plant susceptibility to fragmentation and other forms of habitat disturbance (e.g. Bond 1994; Renner 1998; Spira 2001; Aizen *et al*. 2002). Any change in pollinator species composition, abundance and/or foraging behaviour due to habitat fragmentation is likely to have an effect either on the number of pollen grains deposited or their quality, in terms of degree of outbreeding and total genetic diversity, and thus to have consequences for overall plant fitness (e.g. Murcia 1996; Aizen & Feinsinger 1994; Wilcock & Neiland 2002; Aguilar & Galetto 2004). Thus, in the long term, degradation and disruption of plant–pollinator mutualisms are expected to lead to substantial decreases in the quantity and quality of seeds produced, an early step in the demographic collapse of plant populations (Aizen *et al*. 2002).

The majority of studies conducted so far indicate that insect pollinator guilds are particularly sensitive to habitat fragmentation (e.g. Murcia 1996; Kearns *et al*. 1998; Aizen & Feinsinger 2002). In particular, several reports show consistent decreases in pollinator richness and abundance in fragments compared to continuous areas of natural forest (reviewed by Aizen & Feinsinger 2002; citations therein). Habitat fragmentation is more likely to have an effect on specialist pollinators, which depend exclusively on one or a few plant taxa as food sources, than on generalist pollinators, which are able to feed on a wide array of flower species (Kunin 1993; Bronstein 1995). It is precisely such non-specific foraging behaviour of generalist pollinators that makes them able to predominate and to persist longer in forest fragments (Murcia 1996). Furthermore, since fragmentation can change the composition of the flora, and may cause declines in flower density of certain plant species, any remaining pollinators which cannot emigrate may need to behave as generalists in order to survive (Murcia 1996).

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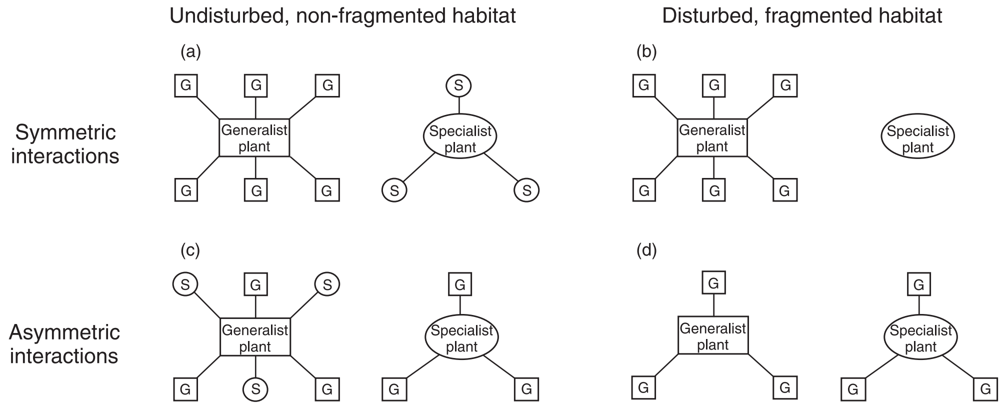

Fig. 1 Schematic representation of specialization in plant–pollinator interactions. In symmetric specialization (a), generalist plants are pollinated by many different generalist pollinators (G) while specialist plants are pollinated by one or a few taxa of specialist pollinators (S), so habitat fragmentation (b) will more strongly negatively affect specialist plants compared to generalist plants. Under asymmetric specialization (c), generalist plants are pollinated by many specialist and generalist pollinator taxa, whereas specialists are pollinated mostly by one or a few taxa of generalist pollinators so that there is similar reproductive susceptibility to habitat fragmentation for specialist and generalist plants (d).

From the plant point of view, however, the extent to which changes in pollinator assemblages translate into lower fruit and seed set, and thus their susceptibility to habitat fragmentation, will be related to their dependence on the pollination mutualism (e.g. Bond 1994; Murcia 1996; Aizen & Feinsinger 2002; Aizen *et al*. 2002). The breeding system of plants is among the ecological traits that determine the degree of their dependence on pollinators, which ranges from independence in self-compatible species that set seed via autonomous, within-flower pollination to obligate in self-incompatible and dioecious plants (Richards 1997). Among those that are either facultatively or obligately dependent, the degree of pollination specialization may determine the response of plant reproduction to disturbance (Renner 1998; Aizen & Feinsinger 2002; Aizen *et al*. 2002). Like the pollinators, plants can be more or less extreme specialists (pollinated by one or a few taxonomically similar animal species) or generalists (pollinated by several to many animal species from different taxa) (Renner 1998). Specialist plants are expected to be more vulnerable than generalists to habitat fragmentation because any decrease in abundance or loss of a single pollinator species from their narrow pollinator assemblages could lead to reproductive failure (Bond 1994; Waser *et al*. 1996; Aizen *et al*. 2002).

Nevertheless, predictions of differential responses to disturbance between plant species with different pollination systems had not been empirically tested until recently. Vázquez & Simberloff (2002), in a study of 12 plant species from the temperate forest of the southern Andes in Argentina, showed that there was no relationship between the degree of pollination specialization and the plant species' reproductive response to habitat disturbance by cattle grazing. Similarly, in a review of 46 plant species representing different life forms, taxonomic origin and distribution, Aizen *et al*. (2002) found that habitat fragmentation negatively affected pollination and reproductive success of a similar proportion of generalist and specialist plant species.

Why do plant species with generalist and specialist pollination systems show such unexpectedly similar responses to habitat fragmentation? We propose that the answer may lie in asymmetry in the degree of specialization of the plants and their pollinators.

The widely accepted prediction that reproductive success of specialist plants should be more affected by habitat fragmentation compared to generalist plants assumes that specialization in plant–pollinator interactions is symmetric (i.e. that generalist plants are pollinated by many different generalist pollinators while specialist plants are pollinated by one or a few taxa of specialist pollinators; Fig. 1a, b). However, in nature asymmetric plant–animal interactions seem more likely to be the rule (Petanidou & Ellis 1996; Bascompte *et al*. 2003; Dupont *et al*. 2003; Vázquez & Aizen 2004). As an example, in the Chaco Serrano forest of central Argentina, *Dolichandra cynanchoides* (Bignoniaceae) is a specialist vine pollinated only by three hummingbird species, although these generalist pollinators visit the flowers of a large number of different plants to fulfil their food requirements throughout the season (L. Ashworth, unpublished data). This trend was recently observed by Vázquez & Simberloff (2002) at the community level in a *Nothofagus* forest. More generally, Bascompte *et al*. (2003) and Vázquez & Aizen (2004) analysed 25 and 18 plant–pollinator networks, respectively, and found that most of these mutualistic webs are highly asymmetric. The asymmetry of the interaction pattern is particularly evident for specialist plants, which tend to be pollinated mostly by generalist animals (well beyond the level expected at random), whereas generalists are pollinated not only by specialists but also by generalists (Fig. 1c).

Generalist plants have a higher number of mutualist partners (i.e. many different specialist and generalist pollinators) than specialists. The loss of many or all of their specialist pollinators therefore places generalist plants in similar conditions (in terms of number and identity of interacting partners) to the specialists, because asymmetry implies that the latter retain their few (generalist) pollinators (Fig. 1d). Decreases in abundance of the remaining generalist pollinators would therefore, potentially, have equal effects on the two groups and the detrimental impact of fragmentation on the reproductive success of specialist plants would not be so dramatic as previously thought.

These differential effects of fragmentation on pollinator assemblages of specialist and generalist plants would equalize, on average, the levels of effective pollination, and therefore their reproductive output. Moreover, these ideas may have implications outside pollination ecology to other mutualistic interaction webs, particularly animal-seed dispersal, where asymmetric relationships have also been demonstrated (Bascompte *et al*. 2003).

Our proposal shows that plant specialization should not be considered in isolation from the degree of specialization of their pollinator partners, and that both sides of the mutualistic interaction must be assessed in order to predict plant reproductive vulnerability to habitat fragmentation. This necessarily involves the study of the pollinators associated with entire local plant communities, or substantial subsets thereof (see Aizen & Feinsinger 2002). Considering two or more ecological traits (e.g. breeding system, pollination and pollinator specialization) may improve prediction of responses to fragmentation because each combination (e.g. self-compatible specialist plant, pollinated by generalists) is likely to respond differently. These factors could be used as continuous variables in multiple regression analyses, but, independently of how these ecological traits are considered, the plant–pollinator interface must be assessed consistently.

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