

REVIEWS AND  
SYNTHESES

## Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis

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**Abstract**

The loss and fragmentation of natural habitats by human activities are pervasive phenomena in terrestrial ecosystems across the Earth and the main driving forces behind current biodiversity loss. Animal-mediated pollination is a key process for the sexual reproduction of most extant flowering plants, and the one most consistently studied in the context of habitat fragmentation. By means of a meta-analysis we quantitatively reviewed the results from independent fragmentation studies throughout the last two decades, with the aim of testing whether pollination and reproduction of plant species may be differentially susceptible to habitat fragmentation depending on certain reproductive traits that typify the relationship with and the degree of dependence on their pollinators. We found an overall large and negative effect of fragmentation on pollination and on plant reproduction. The compatibility system of plants, which reflects the degree of dependence on pollinator mutualism, was the only reproductive trait that explained the differences among the species' effect sizes. Furthermore, a highly significant correlation between the effect sizes of fragmentation on pollination and reproductive success suggests that the most proximate cause of reproductive impairment in fragmented habitats may be pollination limitation. We discuss the conservation implications of these findings and give some suggestions for future research into this area.

**Keywords**

Compatibility systems, extinction risk, habitat fragmentation, meta-analysis, mutualism disruption, plant reproductive success, plant–pollinator mutualism, pollination specialization, reproductive susceptibility.

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**INTRODUCTION**

Throughout the last two decades fragmentation studies of plant populations have mainly focused on demographic processes, with particular emphasis in evaluating the effects of fragmentation on plant fecundity (reviewed by Hobbs & Yates 2003; Ghazoul 2005; Honnay *et al.* 2005). Furthermore, because most extant angiosperms need biotic vectors to reproduce sexually, the pollinator fauna and pollination process have equally been studied in relation to habitat fragmentation (Didham *et al.* 1996; Kearns *et al.* 1998; Aizen & Feinsinger 2003). Theoretical arguments about plant reproduction suggest that plants and pollinators possess particular biological attributes that result in differential

ecological responses to the effects of habitat fragmentation (Bond 1994; Waser *et al.* 1996; Renner 1999; Aizen & Feinsinger 2003; Hobbs & Yates 2003; Harris & Johnson 2004). Therefore, sexual reproduction in plants may be differentially susceptible to habitat fragmentation depending on certain ecological traits that characterize the degree of dependence and specialization on their pollinators.

One of the attributes is plant breeding systems, which will determine the degree of dependence on pollination mutualism (e.g. Bond 1994; Aizen & Feinsinger 2003). Plants range from complete outbreeders to those able to ensure sexual reproduction via autonomous, within-flower selfing, and autogamous seed set (Lloyd 1992; Richards 1997; Vogler & Kalisz 2001). In this regard, the compati-

bility system of plants is important to evaluate the degree of pollination mutualism dependence. In general, self-compatible (SC) plants can be considered facultatively autonomous. Although SC species usually require animal pollinators to transport pollen from other conspecific individuals, either self (autogamous or geitonogamous) or outcross (xenogamous) pollination can elicit seed production. Moreover, some species may possess the capability to reproduce via spontaneous autogamy (i.e. without the intervention of pollinators). Therefore, SC plants can be facultatively dependent on pollinators. Conversely, self-incompatible (SI) plants are obligate outbreeders because they can use only outcross pollen (from other individuals) to produce seeds, thus they present high dependence on pollinators for sexual reproduction (Richards 1997). Moreover, due to such exclusive requirement for outcross pollen, changes in the foraging behaviour of pollinators are likely to further affect the reproduction of SI plants. Thus, it is expected that SI plant species will be more susceptible to alterations introduced by habitat fragmentation on pollinator assemblages; i.e. changes in abundance, composition and/or foraging behaviour of pollinator species (e.g. Aizen *et al.* 2002; Wilcock & Neiland 2002; Aizen & Feinsinger 2003). Consequently, their reproductive success should be more impaired by habitat fragmentation than the reproductive success of SC plants.

Another important potential determinant of pollination mutualism disruption in fragmented habitats is the degree of pollination specialization (Bond 1994; Renner 1999; Johnson & Steiner 2000). Plant species vary widely in their degree of pollination specialization, ranging from extreme generalists that may interact literally with hundreds of pollinator species to extreme specialists with just a single pollinator mutualist. In spite of this continuum, in practice plant species are typically considered generalists (G) when pollinated by several or many animal species of different taxa, and specialists (S) if pollinated by one or a few taxonomically related pollinators (Bond 1994; Herrera 1996; Waser *et al.* 1996; Renner 1999). Theory predicts that plant species characterized by a high degree of pollination specialization will be more vulnerable to pollination mutualism disruption induced by habitat fragmentation, because they cannot compensate for the loss of their few specific mutualist partners with other alternative pollinators (Bond 1994; Waser *et al.* 1996; Fenster & Dudash 2001). In contrast, G plants are expected to be more resilient to the changes imposed by fragmentation on their pollinator assemblages because the absence of one or some of their pollinators could be buffered by other pollinators from their wide assemblages (Morris 2003).

The hypotheses detailed above, concerning the differential reproductive susceptibility of plants to habitat

fragmentation in relation to their compatibility systems and degree of pollination specialization, have not been formally tested until recently. Through a literature review, Aizen *et al.* (2002) evaluated the qualitative reproductive response of 46 plant species with different taxonomic origin, life forms and geographical distribution. Contrary to theoretical expectations, their results showed that habitat fragmentation negatively affected the reproductive success of a similar proportion of SC and SI species, and of G and S species. Their review concludes that no generalizations can be made on plant reproductive susceptibility to habitat fragmentation based on either compatibility or pollination systems, thus there would not be any discernible response pattern among animal-pollinated plant species based on these reproductive traits. Similarly, Ghazoul (2005) recently reviewed how the different spatial dimensions of plant distributions (namely population size, density and distance between conspecifics, purity and habitat fragmentation) affect pollination and reproductive output of plants. Specifically, he analysed the frequency with which Allee effects are observed among plants under different spatial conditions and assessed vulnerability of plants according to their breeding system and life form. He arrived at the same conclusion as that of Aizen *et al.* (2002): SI plants do not appear to be more susceptible to Allee effects than SC plants (Ghazoul 2005).

It is important to point out, however, the possible limitations of the qualitative review approach followed by Aizen *et al.* (2002) and Ghazoul (2005). The 'vote counting' method they applied, which has been widely used to summarize results from multiple studies in ecology, calculates the proportion of studies with negative, positive and neutral effects, and evaluates the hypotheses in relation to these proportions (Hedges & Olkin 1985). Unfortunately, this method has poor statistical properties. The results of vote counts can be seriously biased towards finding no effects because of low statistical power. Also, and most importantly, vote counting results fail to provide critical information on the magnitude and range of effect sizes shown by a group of studies (Hedges & Olkin 1985; Gurevitch & Hedges 1999).

Quantitative generalizations such as meta-analysis, on the contrary, offer a different perspective on the results of independent studies. Instead of giving a definite demonstration on a particular phenomenon, individual results are treated as if they were subjected to sampling uncertainty. This kind of quantitative synthesis, where not only the magnitude and direction of the effects are estimated, but also the variability of effects among individual studies, can be a more powerful tool to establish generalizations that answer a wider variety of questions (Hedges & Olkin 1985; Arnqvist & Wooster 1995; Rosenberg *et al.* 2000; Gurevitch & Hedges 2001).

In this paper, we summarize and integrate the accumulated knowledge generated up to now, and evaluate whether compatibility systems and degree of pollination specialization influence the reproductive response of plants to habitat fragmentation. Specifically, we address the following questions: (i) what is the overall direction and magnitude of habitat fragmentation effects on pollination and sexual reproduction in plants? (ii) Is the reproduction of plants with higher pollination–mutualism dependence (SI) or fewer number of pollinator interactions (S) more negatively affected by habitat fragmentation than the reproduction of less pollination–mutualism-dependent plants (SC) or plants with greater number of pollinator interactions (G)? (iii) Regarding this previous question: what is the particular trend among plant species from a single ecosystem where the reproductive response to fragmentation of many species has been studied (i.e. the Argentine Chaco Serrano; Aizen & Feinsinger 1994a; Aguilar 2005)? (iv) What is the relationship between the effects of habitat fragmentation on the pollination process and plant reproductive response? (v) Following Aizen *et al.* (2002), we also analysed two other traits that could be partially associated with compatibility system and pollinator specialization: life form and the typical habitat type where a species occurs. Overall, we ask whether there is any discernable signal that allows the easy identification of ecological characters of plants that determine their reproductive susceptibility to habitat fragmentation and, eventually, to their local extinction risk.

## MATERIALS AND METHODS

### Literature search

We conducted an extensive survey of the literature using different approaches: first, we searched through our own data base (Reference Manager 10.0, 2001) with more than 12 000 updated references using a combination of ‘fragment\*’ and ‘poll\*’ and (seed set or fruit set) as keywords. Internet searches were also conducted using the same keyword combinations through the Science Citation Index and Biological Abstracts data bases as well as through the main editorials (Blackwell Publishing, Springer-Verlag and Elsevier) that gather the most important indexed journals of ecology and conservation biology. This search led to a large number of papers that were subsequently examined for suitability of inclusion in the meta-analysis. For inclusion, an article had to evaluate directly or indirectly, explicitly or implicitly, the effects of habitat fragmentation on the reproduction of animal-pollinated plants. As response variables of plant reproductive success we used either fruit or seed production. In cases where the same author measured both variables for a single species, we considered only seed production as this was the variable most inclusive

and consistently measured among all the studies. We included studies that compared plant reproductive success in: (i) real habitat fragments vs. continuous forests; (ii) natural plant populations of different sizes or degree of isolation; (iii) isolated trees vs. those in forests; and also (iv) experimental artificial plant populations that controlled for population size and/or degree of isolation to evaluate the mechanisms associated with habitat fragmentation. We did not include in this review those papers that exclusively analysed the correlation between population size and reproductive response without any explicit mention of the effects of habitat fragmentation. We only included those studies that correlated reproductive success with population size as an indirect assessment of habitat fragmentation effects. Information about the compatibility and pollination systems was obtained either from the same paper or from other publications on the same species. For both traits, we followed the classification given by the authors in the papers. A few papers did not specify the degree of pollination specialization of the species, but gave the list of pollinators (usually at the order level). In these cases, we considered it a generalist species if pollinated by two or more insect orders and a specialist species if pollinated by only one insect order (Herrera 1996). Similarly, life form (tree, shrub, vine, herb, hemiparasite or epiphyte) and habitat type (summarized in five main natural systems: boreal, temperate and tropical forests, grasslands and shrublands) for each species was obtained either from the same paper or from other publications on the same species. In some cases we contacted the authors to obtain this information.

For those papers in which multiple species were simultaneously studied, we included all the species as if they were independent studies. Due to the different magnitude and direction of the reproductive responses of each species to habitat fragmentation within the same study (cf. effect size values in Table S1), it can be reasonably assumed that the effects are independent for each species, even though they were evaluated in the same system by the same author (Gurevitch & Hedges 1999, 2001). Furthermore, to make sure that any bias resulting from potential non-independence did not undermine the wider and more general results, we statistically compared the effect sizes between those studies evaluating more than one species simultaneously with the rest of the single-species studies. On the contrary, studies with repeated measures in time for a given species cannot be taken as independent observations (Gurevitch & Hedges 2001). Therefore, we did not include all the response values of the same species when evaluated in different years in the same paper. In each of such papers, we decided to consistently work only with the data taken for the latest season. A few plant species were studied by more than one author in different papers, thus we included all those replicates in the analysis.

## Data analysis

The majority of the studies found in the literature search evaluated reproductive success of plants in contrasting conditions (i.e. habitat fragmentation taken as a categorical factor). In most of the papers, response variables were compared between small habitat fragments (or either small populations or isolated conditions) and large fragments or continuous forest (or either large populations or non-isolated conditions). For this reason we used Hedge's unbiased standardized mean difference (Hedge's  $d$ ) as the metric of effect size for the meta-analysis. The effect size  $d$  can be interpreted as the difference between the reproductive response of plants in fragmented habitats versus continuous conditions, measured in units of standard deviations. Thus, large differences and low variability generate the largest effect sizes (Hedges & Olkin 1985; Rosenberg *et al.* 2000; Gurevitch & Hedges 2001). We used Hedge's  $d$  rather than the response ratio (Osenberg *et al.* 1997) because some studies showed zero values of reproductive success in fragmented habitats, making the response ratio difficult to interpret.

To calculate Hedge's  $d$  for each species, we obtained (either from text, tables or graphs) the mean values, sample sizes and some variance measure of reproductive success for each of the two categories (cf. Gurevitch & Hedges 2001 for detailed information on the calculations and equations of Hedge's  $d$ ). Data from graphs were scanned and then obtained using Datathief II software (B. Tummers, <http://www.datathief.org>). If any of these data were not provided in the paper, it was either obtained by contacting the authors or otherwise excluded from the analysis. For those studies exclusively evaluating habitat fragmentation effects with correlations (typically population size or isolation with reproductive success) we either used the data points from the scatter plot of the lowest and highest values of the independent variable (only when each point from the scatter had an associated variance measure and sample size) or calculated the mean value, standard deviation and sample size from the graphs by pooling the data points for the lower-half (used as fragmented condition values) and higher-half values (used as non-fragmented condition values) of the continuous independent variable. Positive values of the effect size ( $d$ ) imply positive effects of habitat fragmentation on the reproductive response whereas negative  $d$  values imply negative effects of fragmentation on plant reproduction.

Within the final list of selected studies, we further searched for those that had also measured variables related to the pollination process (e.g. pollinator visit frequency, pollen loads on stigmas or pollen tubes in the style). With these variables we calculated Hedge's  $d$  as a measure of effect size for each study and carried out a separate meta-

analysis to evaluate the effects of habitat fragmentation on the immediate previous animal-mediated step of plant reproduction: the pollination process.

The analyses were conducted using the MetaWin 2.0 statistical program (Rosenberg *et al.* 2000). Confidence intervals (CI) of effect sizes were calculated using bootstrap re-sampling procedures as described in Adams *et al.* (1997). An effect of habitat fragmentation was considered significant if the 95% biased-corrected bootstrap CI of the effect size ( $d$ ) did not overlap zero (Rosenberg *et al.* 2000). Data were analysed using random-effect models (Raudenbush 1994), which assume that studies differ not only by sampling error (as fixed-effects models do), but also by a random component in effect sizes between studies, which is named 'pooled study variance' (Rosenberg *et al.* 2000). Random-effect models are preferable in ecological data synthesis because their assumptions are more likely to be satisfied (Gurevitch & Hedges 2001).

To examine the heterogeneity of effect sizes we used  $Q$ -statistics (Hedges & Olkin 1985), which are essentially weighted sums of squares that follow an approximately asymptotic chi-square distribution. These statistics allow several tests; the more general one being whether the variance among effect sizes is greater than expected by chance (Cooper 1998). For the categorical comparisons (SC vs. SI, generalists vs. specialists, etc.) we examined the  $P$ -values associated with  $Q_{\text{between}}$  categories, which describe the variation in effect sizes that can be ascribed to differences between the categories. We also used these statistics to compare the effect sizes between experimentally vs. naturally fragmented habitat studies to account for the potential differences in effect sizes produced from the different spatial scales used by these two types of studies.

An intrinsic problem when conducting quantitative reviews of published studies is the potential of publication bias; i.e. studies showing significant results having a greater possibility of publication than those showing non-significant results. We explored the possibility of publication bias (the 'file-drawer problem', *sensu* Rosenthal 1979), graphically (weighted histogram and funnel plot), statistically (Spearman rank correlation test) and also by calculating a weighted fail-safe number, which helps in estimating whether publication bias is likely to be a problem (Rosenberg 2005). If the distribution of a weighted histogram (where the weight is 1/variance of the effect size in each study) is depressed around zero, it suggests that there may be publication bias against publishing non-significant results (Greenland 1987). The funnel plot is a scatter plot of effect size vs. sample size (Palmer 1999). If no publication bias exists, the resulting plot is shaped like a funnel with the large opening at the smallest sample sizes; i.e. the variation around the cumulative effect size should decrease as sample size increases (Rosenberg *et al.* 2000). As a statistical test analogue to the

funnel plot, we conducted a Spearman rank correlation test, which examines the relationship between the standardized effect size and the sample size across studies (Begg 1994). A significant correlation indicates a publication bias where larger effect sizes are more likely to be published than smaller effect sizes. Finally, we used the fail-safe number calculator (Rosenberg 2005; <http://www.public.asu.edu/~mrosenb/lab/softwarehtml#failsafe>) to estimate the number of non-significant, unpublished or missing studies that would need to be added to a meta-analysis to nullify its overall effect size (Rosenthal 1979). This general weighted fail-safe number proposed by Rosenberg (2005) is grounded in the meta-analysis framework and applicable to random-effect models. If the fail-safe number is larger than  $5n + 10$ , where  $n$  is the number of studies, then publication bias (if they exist) may be safely ignored (i.e. the results are robust regardless of publication bias; Rosenthal 1991; Rosenberg 2005).

## RESULTS

### Generalities of sampled species

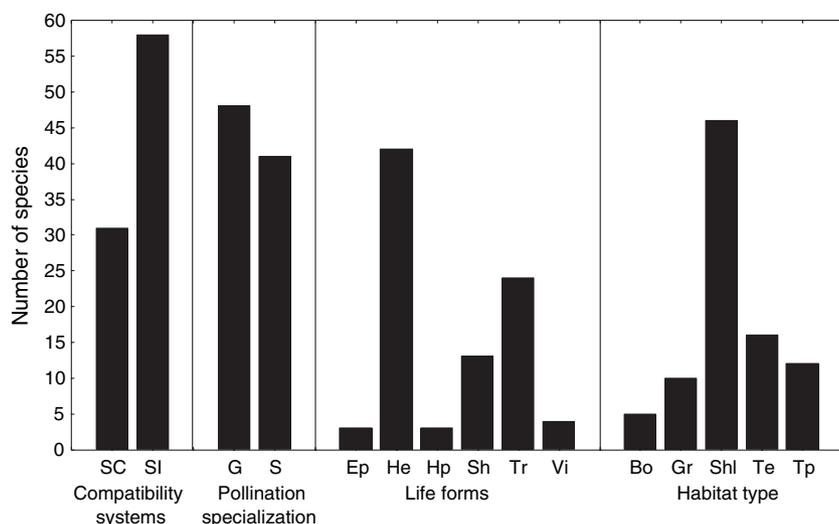
We found 53 published articles (papers and book chapters) and a PhD thesis that evaluated the effects of habitat fragmentation on plant reproduction, comprising the period 1987–2006. These studies yielded 93 data points from 89 unique plant species (Table S1). A summary of the number of species within each of the categories examined in this review is given in Fig. 1. In general, plants with different compatibility systems and a degree of pollination specialization were fairly evenly represented among the different life forms and habitat types. Some exceptions are worth mentioning. Most species studied in grasslands were SI herbs (90%) whereas most species in tropical forests were SI

trees (92%). Most trees, irrespective of habitat type, were also SI. All the species studied in boreal forests were herbs, mostly SC. The vast majority of the species were studied in naturally fragmented habitats (93%). A statistical comparison of the effect sizes between experimentally vs. naturally fragmented habitat studies showed no significant difference ( $Q_{\text{between}} = 1.59$ ,  $P = 0.291$ ).

Six studies evaluated more than one species simultaneously (Aizen & Feinsinger 1994a,b; Steffan-Dewenter & Tscharnkte 1999; Cunningham 2000; Donaldson *et al.* 2002; Quesada *et al.* 2004; Aguilar 2005). The effect sizes of these species varied greatly in magnitude and direction (Table S1), suggesting they can be taken as independent data points. Moreover, there was no statistically significant difference ( $Q_{\text{between}} = 6.31$ ,  $P = 0.178$ ) between the mean effect size of the species included in these studies ( $d = -0.40$ ) and the mean effect size for the rest of the single-species studies in the data set ( $d = -0.83$ ). The lower magnitude of the mean effect size of the multiple-species studies indicates that this subset is unlikely to undermine the wider results. In 25 species from 11 different studies the effects of habitat fragmentation on plant reproduction were evaluated for more than one season. For all these species we only considered the data taken on the last studied season (see Materials and methods). The species *Ceiba grandiflora*, *Primula elatior*, *Pedicularis palustris* and *Viscaria vulgaris* were each studied twice in different papers (*V. vulgaris* was studied by Mustajarvi *et al.* (2001) using its synonymous name: *Lycbns viscaria*).

### Habitat fragmentation and plant reproductive success

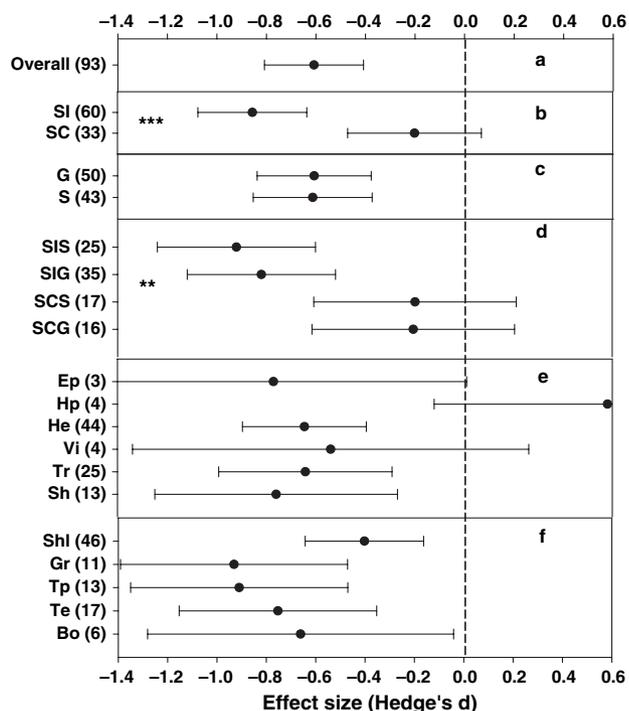
The overall weighted-mean effect size of habitat fragmentation on plant reproduction across all studies was negative ( $d = -0.608$ ) and significantly different from zero according



**Figure 1** Summary of the number of species within each category included in the review: compatibility systems (SI, self-incompatible; SC, self-compatible), pollination specialization (S, specialist; G, generalist), life forms (Ep, epiphytes; He, herbs; Hp, hemiparasites; Sh, shrubs; Tr, trees; Vi, vines), and habitat type (Bo, boreal; Gr, grassland; Shl, shrubland; Te, temperate; Tp, tropical).

to the 95% bias-corrected bootstrap confidence limits (−0.817 to −0.412). The overall heterogeneity of effect sizes was large and statistically significant ( $Q_{\text{total}} = 145.64$ ,  $n = 93$ ,  $P < 0.001$ ; Fig. 2a), indicating that they do not share a common effect. In other words, habitat fragmentation has a significant overall strong negative effect on plant reproduction, and such fragmentation effects differ among different species. Subsequently, we evaluated the categorical variables to determine whether any of them could explain the heterogeneity observed.

Among the categorical variables, the compatibility system of plants explained the highest proportion of variation among species ( $Q_{\text{between}} = 13.23$ ,  $P = 0.0003$ ), and significant differences were observed between the two groups (SI vs. SC; Fig. 2b). On average, SI species showed a strong negative effect of habitat fragmentation on reproduction ( $d_{\text{SI}} = -0.855$ ), and this effect was significantly different from zero (based on 95% biased-corrected bootstrap CI; Fig. 2b). For SC species the weighted-mean effect size was



**Figure 2** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on plant reproduction for the whole sample of species (a), and categorized by their compatibility systems (b), pollination specialization (c), the combination of both, compatibility systems and pollination specialization (d), life forms (e) and habitat types (f). Sample sizes for each categories are shown in parentheses; dotted line shows Hedge's  $d = 0$ . Abbreviations are as specified in Figure 1. Significance levels associated with  $Q$ -values: \*\*\* $P < 0.001$ ; \*\* $P < 0.05$ .

also negative, albeit much smaller ( $d_{\text{SC}} = -0.200$ ) and not significantly different from zero (i.e. the 95% CIs overlapped zero, Fig. 2b). Thus, the reproductive success of SC species is not significantly affected by habitat fragmentation.

On the other hand, the effect sizes of plants with different degrees of pollination specialization did not differ significantly between them ( $Q_{\text{between}} = 0.017$ ,  $P = 0.976$ ; Fig. 2c). For both, pollination specialist and generalist species, the weighted-mean effect sizes were large, negative and significantly different from zero ( $d_{\text{S}} = -0.613$  and  $d_{\text{G}} = -0.607$ , Fig. 2c). Thus, habitat fragmentation equally (and negatively) affects the reproduction of S and G species.

When characterizing the species by the combination of both their compatibility and pollination systems, there were significant differences in their mean effect sizes ( $Q_{\text{between}} = 12.81$ ,  $P = 0.031$ ). However, by examining their mean effect size values and CIs, it is evident that such a difference is mainly due to their compatibility systems and not to the combined effect of both traits (Fig. 2d). SI species, either pollination G or S, were significantly negatively affected by habitat fragmentation, whereas SC species were not.

The heterogeneity of effect sizes of species with different life forms was not significant ( $Q_{\text{between}} = 7.65$ ,  $P = 0.337$ ). Herbs, trees and shrubs showed significantly negative weighted-mean effect size values. For vines and epiphytes the negative effects were not significantly different from zero (Fig. 2e). The exception was the hemiparasite species group that had a positive but non-significant weighted-mean effect size (Fig. 2e). Finally, for the habitat type category there was no significant heterogeneity in their effect sizes ( $Q_{\text{between}} = 6.93$ ,  $P = 0.139$ ). For all the species growing in different habitat types their weighted-mean effect sizes were negative and significantly different from zero (Fig. 2f).

In order to assess whether the differences in the mean effect sizes observed between SI and SC species could be due to the disparity in the sample sizes of each group ( $n = 60$  from 58 SI species vs.  $n = 33$  from 31 SC species), we randomly chose 33 SI species data points from the original sample and re-analysed the data. After equalizing the sample sizes of both groups we still found significant differences between the weighted-mean effect size values of SI and SC species ( $Q_{\text{between}} = 20.60$ ,  $P = 0.001$ ). As observed previously, this analysis showed that SI species had a large negative mean effect size significantly different from zero ( $d_{\text{SI}} = -1.064$ , 95% CI = −1.326 to −0.786), whereas SC species had a smaller negative mean effect size but not significantly different from zero ( $d_{\text{SC}} = -0.203$ , 95% CI = −0.492 to 0.080).

### The subsample of species from the Chaco Serrano

Given the relatively high number of species studied by Aizen & Feinsinger (1994a,b) and Aguilar (2005) in different

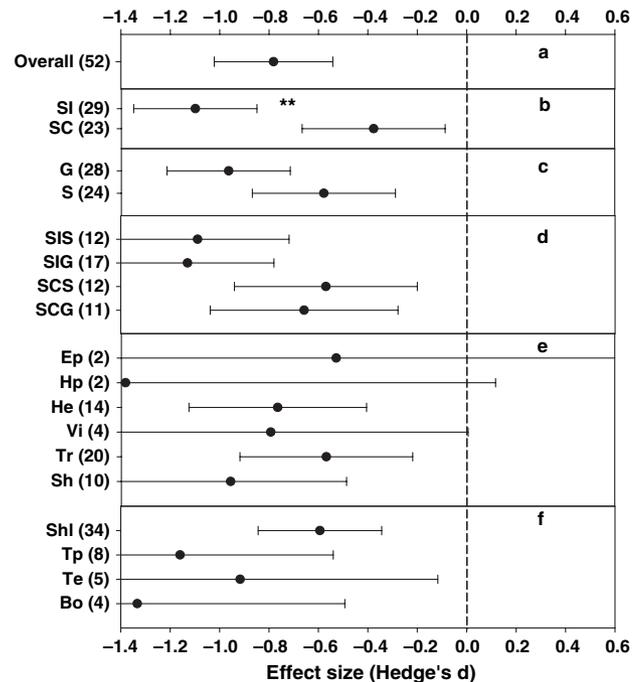
regions of the Chaco Serrano forest, we were interested in determining whether this biogeographically homogeneous subset reflected the trends found for the whole data set. The overall weighted-mean effect size for this subsample was also negative and significantly different from zero but of smaller magnitude compared with the original sample ( $d = -0.463$ , 95% bias-corrected bootstrap CI:  $-0.762$  to  $-0.148$ ; see Fig. S1). In contrast to previous trends, the heterogeneity of effect size values of these species was not significant ( $Q_{\text{total}} = 31.72$ ,  $n = 30$ ,  $P = 0.153$ ); i.e. the individual effect sizes of these species were not significantly different among them. Therefore, none of the categorical analyses showed statistically significant differences, as seen from the non-significant  $Q$ -statistics (not shown) and the overlapping of 95% bias-corrected bootstrap CIs among the different groups for all the categorical variables (Fig. S1). Although non-significant, SI species here also showed a larger negative mean effect size value than SC species ( $d_{\text{SI}} = -0.690$  vs.  $d_{\text{SC}} = -0.238$ ; Fig. S1).

### Habitat fragmentation and pollination

We were able to estimate the effect sizes in 50 species where authors had simultaneously evaluated the effects of fragmentation on pollination and reproductive success of plants. Two of these species (*C. grandiflora* and *L. viscaria*) were evaluated twice in different papers, thus we analysed a total of 52 data points. A comparison of the effect sizes among the three different response variables from which they were calculated (pollinator visits, pollen loads and pollen tubes) showed no significant difference among them ( $Q_{\text{between}} = 5.74$ ,  $P = 0.322$ ), indicating that they are comparable measures of pollination quantity.

The overall weighted-mean effect size of habitat fragmentation on pollination was large, negative ( $d = -0.782$ ) and significantly different from zero, using 95% bias-corrected bootstrap CIs ( $-1.044$  to  $-0.536$ ; Fig. 3a). The overall heterogeneity of effect sizes was statistically significant ( $Q_{\text{total}} = 88.67$ ;  $n = 52$ ;  $P = 0.002$ ), thus we subsequently analysed which categorical variables could account for such heterogeneity.

Weighted-mean effect sizes of SI and SC species were significantly different ( $Q_{\text{between}} = 8.53$ ,  $P = 0.003$ ); where SI species showed a very large negative mean effect size ( $d_{\text{SI}} = -1.102$ ), and SC species showed a much smaller negative mean effect size ( $d_{\text{SC}} = -0.377$ ). Both effects were significantly different from zero (Fig. 3b). None of the other categories showed significant heterogeneity  $Q$  values (not shown); that is, neither pollination specialization, the combination of both compatibility systems and pollination specialization, life forms nor the different habitat types had significant different mean effect sizes within their subcategories (Fig. 3c–f). This can be graphically observed by the



**Figure 3** Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on pollination for 50 plant species (a), and categorized by their compatibility systems (b), pollination specialization (c), the combination of both, compatibility systems and pollination specialization (d), life forms (e) and habitat types (f). Sample sizes for each categories are shown in parentheses; dotted line shows Hedge's  $d = 0$ . Abbreviations are as specified in Figure 1. Significance levels associated with  $Q$ -values, \*\* $P < 0.05$ .

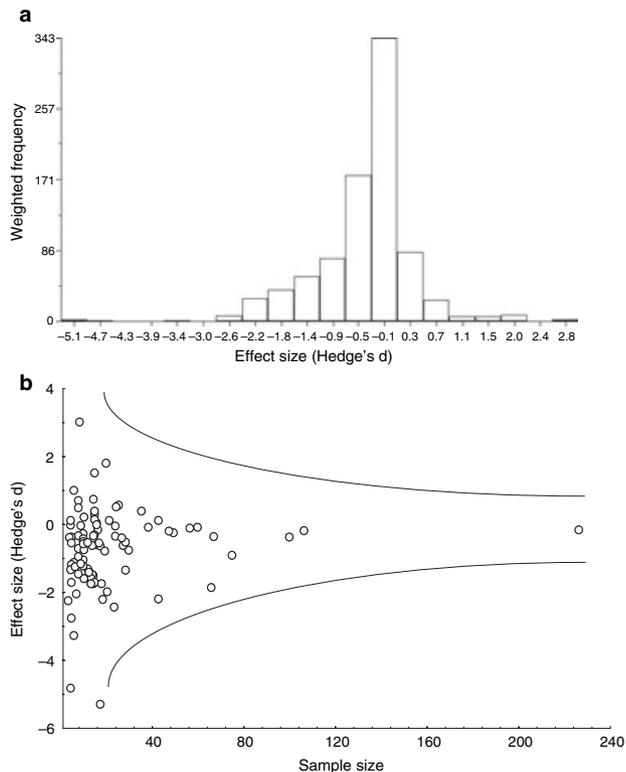
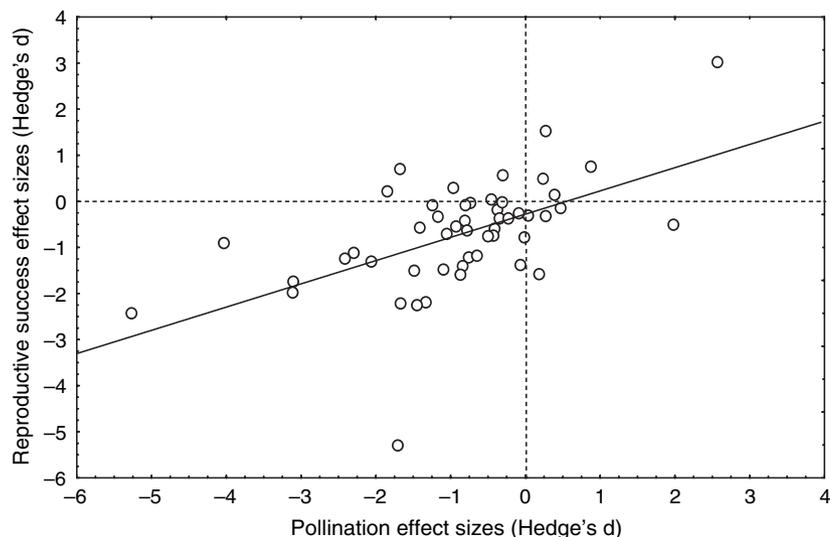
overlapping of 95% bias-corrected bootstrap CIs among the different subcategories of each categorical variable (Fig. 3c–f).

Finally, we conducted a correlation analysis between the calculated effect sizes of pollination and reproductive success. This correlation was positive and highly significant ( $r = 0.55$ ,  $P < 0.001$ , Fig. 4), indicating that for most species whenever habitat fragmentation had an effect on pollination (e.g. pollinator visits, pollen loads or pollen tubes) it was also expressed in terms of fruit or seed-set.

### Publication bias

The weighted histogram of effect size shows no depression around zero. On the contrary, it shows a unimodal distribution with the highest frequency close to zero (Fig. 5a). Similarly, the funnel plot of effect size vs. sample size shows no skewness (Fig. 5b). These two graphical approaches suggest that there was no bias in reporting results from the studies included in this review. These results are further emphasized by a non-significant

**Figure 4** Relationship between the effect sizes of habitat fragmentation on pollination and reproductive success of 50 plant species. Correlation coefficient  $r = 0.55$  significant at  $P < 0.001$ . Dotted lines indicate values of zero for the effect sizes.



**Figure 5** Histogram of effect size values of plant reproductive success weighted by  $1/\text{variance}$  (a), and Funnel plot of sample size vs. effect size values of plant reproductive success (b) based on 93 data points from 89 plant species.

Spearman rank correlation test ( $r = 0.176$ ;  $P = 0.160$ ). Finally, the calculated weighted fail-safe number (924) was much greater than expected (475) without publication bias, which supports the robustness of our results.

As shown for reproductive success, the weighted histogram and funnel plot for the effect sizes of the pollination meta-analysis (not shown) as well as the rank correlation test ( $r = 0.081$ ;  $P = 0.567$ ) indicate no publication biases. Moreover, the fail-safe number calculated for this separate meta-analysis was 871, also much greater than expected (270).

## DISCUSSION

The results of this review indicate that sexual reproduction of flowering plants is considerably negatively affected by habitat fragmentation, regardless of the different ecological and life-history traits and the different types of habitat. Moreover, the only categorical variable that explained the differences among the species effect sizes was their compatibility systems, which expresses their degree of dependence on pollination mutualism. Other traits such as pollination specialization, its combination with compatibility systems, life form or type of habitat, on the contrary, are not useful in identifying reproductive susceptibility of plants to habitat fragmentation.

Within the area of plant reproductive ecology, studies of habitat fragmentation date from the mid-1980s, but have considerably increased in number throughout the 1990s. In the present review, we included the majority of these studies where the information given was appropriate and precise, which resulted in the evaluation of reproductive responses to habitat fragmentation of 89 plant species from 45 families, with diverse life forms and of different natural systems from several regions of the world. This number and diversity of species suggest that the trends found in this review can be generalized; moreover, the fact that no publication bias was detected indicates that these trends would not be modified by increasing the number of published papers on this topic (Hyatt *et al.* 2003). Remark-

ably, most of the studies have evaluated the effects of habitat fragmentation on single species (89%) and on a single flowering season (80%), factors that have limited considerably the ability to find consistent patterns in the past. Furthermore, there is a marked bias in the selection criterion of the species to study the effects of habitat fragmentation. Herbaceous perennial species and trees with self-incompatibility mechanisms, considered rare or threatened, have been the main subject of study. This is less evident in relation to species with different degrees of pollination specialization. This would imply that the overall magnitude of fragmentation effects on the reproduction of angiosperms in general is likely to be smaller than the overall effect size reported here. To verify this, future fragmentation studies on plant reproduction should involve random selection of plant species or the study of common, widespread species. It is important to point out that this type of bias (research bias, *sensu* Gurevitch & Hedges 1999), in which particular ecological traits of the species are likely to be more frequently selected as a study subject by different authors is not detected by the graphical or statistical tests of meta-analysis. That is, the species' selection criterion of each author does not necessarily have any relationship with publication bias, which particularly refers to the higher probability of publication of those papers showing significant results.

### Habitat fragmentation and compatibility systems

The trends found in the present work regarding the reproductive susceptibility to habitat fragmentation of species with different compatibility systems differ from previous results (Aizen *et al.* 2002; Ghazoul 2005). The mean effect size of SI species was large, negative and significantly different from SC species, whose mean effect size also did not differ from zero. This trend was further confirmed when re-analysing the data by randomly taking a number of SI species that would match the number of SC species, so as to equalize the sample size of both groups. The higher reproductive susceptibility to habitat fragmentation of SI species agrees with the originally stated hypothesis. SI species necessarily require pollen from other conspecific individuals to produce seeds, thus are highly dependent on animal pollinators for successful sexual reproduction. Such mutualism dependence makes seed production of SI species more vulnerable to the effects of habitat fragmentation that can modify richness, composition, abundance and/or behaviour of pollinators or the availability of conspecific mates (e.g. Jennersten 1988; Aizen & Feinsinger 1994a, 2003; Didham *et al.* 1996; Kearns *et al.* 1998; Steffan-Dewenter *et al.* 2002). These changes may alter the pollination process and limit the amount of compatible pollen deposited on the stigmas or modify the

patterns of pollen transfer, thus negatively affecting sexual reproduction (Wilcock & Neiland 2002; Quesada *et al.* 2003; Aguilar & Galetto 2004).

In the Chaco Serrano subsample instead, the similar susceptibility observed between SI and SC species could be ascribed to some particularities of the system. The mean effect size of the SI species from this subsample was smaller than that of the SI species from the whole sample, whereas the mean effect size of SC species remained similar in both analyses. Namely, it appears that SI species from the Chaco Serrano would be somehow less affected compared with the total sample of SI species. One particularity of these studies (Aizen & Feinsinger 1994a,b; Aguilar 2005) is the consistently higher presence of introduced honeybees (*Apis mellifera*) registered in the smaller forest fragments, which could at least in part be responsible for the comparatively smaller mean effect sizes observed for these SI species. *Apis mellifera* could partially compensate for the decrease or absence of certain native, legitimate or more effective pollinators in the smaller forest fragments, and thus decrease slightly the mean effect size of fragmentation on the reproduction of some of the SI species of this system. This speculation may, in principle, be non-intuitive, given that the foraging behaviour of *A. mellifera* is not particularly likely to favour the transfer and deposition of outcross pollen, indispensable for SI plants. However, it should be considered given that Aizen & Feinsinger (1994a,b) and Aguilar (2005) found that honeybees were frequent pollinators among SI species, and overall, their visits were detected to different degrees in 75% of the SI species of the Chaco Serrano subsample. It must be mentioned, however, that the interaction of *A. mellifera* with these SI species did not prevent negative effects of habitat fragmentation on fruit or seed set in most of them (Table S1); but it could have ameliorated the magnitude of its effect on these variables. On the other hand, we would have expected honeybees to particularly favour SC species, which instead did not show any change in the magnitude or direction of mean effect size compared with the whole sample (cf. Fig. 2b and Fig. S1). Interestingly, the majority of these SC species, whose effect sizes were negative, are pollinated by particular pollinator guilds (hawkmoths, wasps, butterflies, hummingbirds, etc.) that do not include *A. mellifera* within their assemblages (Aizen & Feinsinger 1994a; Aguilar 2005). The rest of these SC species, which were assiduously visited by honeybees, effectively showed positive or neutral effect sizes (Table S1). A remarkable example of such reproductive rescue effect by *A. mellifera* has also been observed by Dick (2001) in isolated individuals of *Dinizia excelsa*. In conclusion, the high incidence of honeybees in this system together with the particular characteristics of the species from this Chaco Serrano subsample may explain the lack of difference in the effect sizes of SI and SC species.

### Habitat fragmentation and pollination specialization

When evaluating the reproductive susceptibility of species in relation to their degree of pollination specialization no significant difference was found in the mean effect sizes of specialist and generalist species, both being equally negatively affected by habitat fragmentation. These results disagree with the expectations based on the classical theoretical concepts, which hold that reproduction of specialist species should be more negatively affected by fragmentation than generalist species. Because specialist species have a comparatively smaller diversity of mutualist interactions, they must have a higher risk of pollination disruption (Bond 1994; Waser *et al.* 1996; Renner 1999; Johnson & Steiner 2000). A possible explanation for this unexpected response pattern has been recently proposed by Ashworth *et al.* (2004). These authors suggest that this trend could be explained by jointly considering two aspects: (i) the asymmetric nature of plant–pollinator interaction webs, which imply that S plants are mainly pollinated by generalist pollinators whereas G plants are pollinated by both specialist and generalist pollinators (Vázquez & Simberloff 2002; Bascompte *et al.* 2003; Vázquez & Aizen 2004); and (ii) the fact that generalist pollinators, which are able to feed on a wide array of flower species, are less affected by habitat fragmentation than specialist pollinators (Bronstein 1995; Murcia 1996; Aizen & Feinsinger 2003). If specialist plants interact mainly with generalist pollinators, they would have greater likelihood of keeping their few pollinators in fragmented habitats, and thus their reproduction would not be so drastically affected as previously thought. Generalist plants, which interact with both generalist and specialist pollinators, would tend to lose their specialist pollinator fraction from their assemblages and retain their generalist pollinators. Thus, decreases in abundance of the remaining generalist pollinators would therefore, potentially, have equal effects on the two groups of plants (Ashworth *et al.* 2004).

### Fragmentation effects on pollination process

The widespread expectation of decreased levels of pollination in fragmented habitats (e.g. Rathcke & Jules 1993; Kearns *et al.* 1998; Aizen & Feinsinger 2003) was confirmed through the separate meta-analysis on 50 plant species, showing a strong negative mean effect size. Failure or restrictions at the pollination stage, either as a result of decreases in the abundance or changes in the composition or behaviour of pollinators, will lead to a limited quantity or quality of pollen available on stigmas (Wilcock & Neiland 2002). Although pollen limitation is a common phenomenon among flowering plants (Burd 1994), it is likely to increase substantially with environmental perturbations,

such as anthropogenic habitat fragmentation (Wilcock & Neiland 2002; Ashman *et al.* 2004). Moreover, the highly significant correlation between the effect sizes of pollination and reproductive success shows that, for most species, positive or negative effects of fragmentation on pollination were translated into effects in the same direction (and sometimes magnitude) as the reproductive success of plants. There were only very few species whose directions of fragmentation effects on pollination and reproduction differed (cf. Fig. 4). These results suggest that, in effect, pollen limitation (either in quality or quantity) may be the main or most proximate cause of reduced reproductive success in plant populations in fragmented habitats. Finally, pollen limitation will have particularly strong effects on those species whose population dynamics are sensitive to changes in seed production, such as those incapable of clonal growth, with few reproductive episodes, and/or lack of a seed bank (Bond 1994; Larson & Barrett 2000; Ashman *et al.* 2004).

### Conservation implications and future research prospect

The results of this review have important implications for plant conservation. By determining the compatibility systems of plants, a feasible and readily undertaken task, we should be able to obtain first-hand information on their potential reproductive susceptibility to habitat fragmentation. Once SI plants have been identified in fragmented habitats, conservation efforts should be focused on identifying their effective pollinators and on assuring pollination service and an adequate number of reproductive conspecific individuals. One way to accomplish this would be to make the surrounding anthropogenic matrices less hostile and more permeable to pollinators and seed dispersers. This would increase the probability of arrival of both outcross pollen from other populations to ensure sexual reproduction, and of seeds that may eventually germinate and establish in the fragment, thus increasing the population size in the long term.

The possibility of predicting the impacts of habitat fragmentation on plant demography depends on our ability to understand how species with contrasting characteristics respond to the same factor (Hobbs & Yates 2003). As a first approach towards this objective, here we reviewed the literature and tested hypotheses considering exclusively the reproductive stage of plants. Sexual reproduction is crucial for long-term persistence of plant populations. Through sexual seed production, plants benefit from an independent dispersal phase, the opportunity to increase or maintain genetic diversity, and the potential to adapt to new environments (Wilcock & Neiland 2002). However, reproduction is not the only ecological process that determines the growth and persistence of plant populations

(e.g. Jules & Rathcke 1999; Lennartsson 2002). Other stages in the life cycle of plants such as seed dispersal and germination or seedling survival and establishment are also important in affecting the demographic dynamics of plant populations (e.g. Santos & Telleria 1997; Benitez-Malvido 1998; Bruna 2003). In spite of their importance, much less attention has been given to the effects of habitat fragmentation on these ecological processes. It seems critical, therefore, to increase the study of these processes and their biological interactions with dispersers, predators, herbivores and competitors in fragmented systems, and eventually be able to make generalizations on these demographic processes as well (Midgley & Bond 2001; Hobbs & Yates 2003). Finding general response patterns of plants to habitat fragmentation on different demographic processes from relatively easily determinable plant traits will allow us to detect not only the species but also the processes most susceptible to habitat fragmentation. This kind of information will be of major importance for the management and conservation of biodiversity and ecosystem functioning in the near future.

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**SUPPLEMENTARY MATERIAL**

This material is available online at <http://www.Blackwell-Synergy.com>:

**Table S1** List of 89 plant species selected for the meta-analysis. For each species we give the value of effect size and its variance, each of the ecological characteristics evaluated and the source publication where information was obtained.

**Figure S1** Weighted-mean effect sizes and confidence intervals of habitat fragmentation on plant reproduction for the Chaco Serrano subsample of species.

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