



## REVIEW AND SYNTHESIS

# Habitat fragmentation reduces plant progeny quality: a global synthesis

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### Abstract

Most of the world's land surface is currently under human use and natural habitats remain as fragmented samples of the original landscapes. Measuring the quality of plant progeny sired in these pervasive environments represents a fundamental endeavour for predicting the evolutionary potential of plant populations remaining in fragmented habitats and thus their ability to adapt to changing environments. By means of hierarchical and phylogenetically independent meta-analyses we reviewed habitat fragmentation effects on the genetic and biological characteristics of progenies across 179 plant species. Progeny sired in fragmented habitats showed overall genetic erosion in contrast with progeny sired in continuous habitats, with the exception of plants pollinated by vertebrates. Similarly, plant progeny in fragmented habitats showed reduced germination, survival and growth. Habitat fragmentation had stronger negative effects on the progeny vigour of outcrossing- than mixed-mating plant species, except for vertebrate-pollinated species. Finally, we observed that increased inbreeding coefficients due to fragmentation correlated negatively with progeny vigour. Our findings reveal a gloomy future for angiosperms remaining in fragmented habitats as fewer sired progeny of lower quality may decrease recruitment of plant populations, thereby increasing their probability of extinction.

### Keywords

Genetic diversity, germination, growth, inbreeding, mating patterns, offspring performance, plant-pollination interactions, progeny vigour, seedling, sexual plant reproduction, survival.

Ecology Letters (2019)

## INTRODUCTION

Land use changes are predicted to drive the most significant effects on biodiversity throughout this century (Sala *et al.* 2000; Haddad *et al.* 2015). The structural changes imposed by anthropogenic habitat destruction imply the loss and fragmentation of originally continuous habitats, decreasing the area of remnant habitats and increasing their isolation, generating greater edge exposure to human land-use matrices (Lindenmayer & Fischer 2006). These changes affect the structure and function of remaining habitat fragments. For example habitat loss and fragmentation affect plant–animal interactions and the associated ecological processes shaping plant population demography (Aguilar *et al.* 2006, 2008; Gonzalez *et al.* 2011; Brudvig *et al.* 2015; Chavez-Pesqueira *et al.* 2015; Rossetti *et al.* 2017). Habitat fragmentation also affects the global carbon balance, as it increases carbon emissions beyond those caused by deforestation (Brinck *et al.* 2017). However, debate has been raised about the relative effects of habitat loss vs. habitat fragmentation on biodiversity conservation (Fahrig 2003, 2017; Hadley & Betts 2016; Fletcher *et al.* 2018).

Nevertheless, fragmentation has multiple simultaneous effects that are interconnected in complex ways, operating over different spatial and time scales (Haddad *et al.* 2015; Hadley & Betts 2016). In other words, changes in landscape-scale vegetation composition and configuration due to human activity generally occur simultaneously; thus, it is frequently very difficult to disentangle the relative effects of habitat loss and habitat fragmentation *per se* (Didham *et al.* 2012; Hadley & Betts 2016).

Over the past two decades there has been much research to determine habitat fragmentation effects on the mutualistic interactions involved in sexual plant reproduction and seed dispersal, which can affect the reproductive success and genetic diversity of remnant populations, key aspects for long-term plant population persistence (Ghazoul 2005; Aguilar *et al.* 2006, 2008; Sork & Smouse 2006; Eckert *et al.* 2010; Markl *et al.* 2012). The number of progeny produced by plant populations in fragmented habitats represent an important demographic parameter as it defines the maximum potential recruitment of individuals into the next generation (Wilcock & Neiland 2002). However, equally important but less-well

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recognised features of sexual plant reproduction are the genetic and biological quality of the progeny, which represent complementary aspects of reproduction (Cascante *et al.* 2002; Gonzalez-Varo *et al.* 2010; Ashworth & Martí 2011; Aguilar *et al.* 2012). If we are to envision the future of flowering plant populations in the now ubiquitous fragmented landscapes, we need to learn not only about the quantity of progeny produced but also about the genetic quality and fitness of the progeny sired in fragmented habitats.

Previous reviews have shown that adult plant populations in fragmented habitats have lower genetic diversity because of a reduction in population sizes imposed by habitat loss and fragmentation that create genetic bottlenecks (Honnay & Jacquemyn 2007; Aguilar *et al.* 2008; Vranckx *et al.* 2011). Long-term habitat fragmentation coupled with limited gene flow via pollen and seeds, will decrease genetic diversity through random drift over time (Young *et al.* 1996; Aguilar *et al.* 2008). Moreover, outcrossing rates also appear to decrease in fragmented populations compared to conspecific populations in continuous habitats, caused by changes in mating patterns that increase selfing and/or mating among relatives (Aguilar *et al.* 2008; Eckert *et al.* 2010; Breed *et al.* 2015). Such processes will result in the accumulation of deleterious recessive alleles and in the expression of inbreeding depression; lowering fecundity, increasing seedling mortality, and reducing progeny growth rates, all increasing the likelihood of local extinction (Crnokrak & Barrett 2002; Charlesworth & Willis 2009).

The expression of inbreeding depression in fragmented, small and isolated plant populations is expected to differ depending on plant mating systems (Husband & Schemske 1996). For example the progeny of plant populations with a long history of selfing is less likely to express inbreeding depression under new fragmented conditions because continued selfing purges genetic load, eliminating recessive detrimental alleles after some generations of self-pollination (Husband & Schemske 1996; Byers & Waller 1999; Crnokrak & Barrett 2002). When expressed in selfing populations, inbreeding depression occurs at different developmental stages such as seedling growth and reproduction, as it is caused by recessive and mildly deleterious mutations that are difficult to purge (Husband & Schemske 1996; Ouborg *et al.* 2006; Lobo *et al.* 2015). In contrast, if predominantly outcrossing plants shift towards autogamous, geitonogamous or endogamous mating after habitat fragmentation, inbreeding depression will impact early fitness traits such as germination and seedling survival (Husband & Schemske 1996; Aguilar *et al.* 2008; Vranckx *et al.* 2011). As a result, self-compatible plants with either selfing or mixed mating systems may cope better in recently fragmented habitats siring comparatively more fit progeny than outcrossing plants.

Changes in plant mating patterns are tightly linked to the potential effects of habitat loss and fragmentation on pollination vectors (Hadley & Betts 2012; Breed *et al.* 2015). Disruption of pollinator movements due to new landscape configurations and hostile agricultural matrices have been proposed as the main proximate cause of impoverished pollinator assemblages in fragmented habitats. There is evidence that bees, the most important animal pollinators worldwide, show

reductions in species richness and abundance in fragmented habitats (Brosi 2009; Winfree *et al.* 2009). However, response patterns may vary among different pollinator functional groups (Steffan-Dewenter *et al.* 2002; Aguirre-Gutierrez *et al.* 2015; Breed *et al.* 2015). It is expected that vertebrate pollinators with higher flying capability, such as birds and bats, may cope better with landscape changes and may frequently move across anthropogenic matrices, whereas small insect pollinators may not (Aizen & Feinsinger 1994; Quesada *et al.* 2001, 2004; Byrne *et al.* 2007; but see Castilla *et al.* 2017). Moreover, wind-pollinated plants may be more resilient to fragmentation, as their pollen is usually small and light and can travel longer distances (Hamrick 2004; Seltmann *et al.* 2007; Bacles & Ennos 2008). Correlated responses of decreased pollination service and reproductive output due to habitat fragmentation have been detected in many plant species (Aguilar *et al.* 2006). Decreased plant fecundity linked to pollination failure can lead to reduced plant regeneration and long-term population viability (Aguilar *et al.* 2006; Biesmeijer *et al.* 2006; Potts *et al.* 2010). In addition, changes in pollinator behaviour due to habitat fragmentation can modify foraging distances, time spent on flowers or plants, and the number and diversity of pollen sources, all of which influence the size and quality of the pollen pool arriving to floral stigmas in forest patches (Quesada *et al.* 2001; Goverde *et al.* 2002; Hadley & Betts 2009).

Research on genetic diversity and performance of progeny produced in fragmented landscapes has increased over the past decade, showing diverse results. However, there have been no attempts to generalise global response patterns on plant progeny performance to habitat fragmentation; that is the *quality* aspects of reproductive success (Yates *et al.* 2007; Gonzalez-Varo *et al.* 2010; Ashworth & Martí 2011; Aguilar *et al.* 2012). Here we systematically reviewed the scientific literature to determine overall habitat fragmentation effects on progeny performance and on the genetic composition of the progeny. To accomplish this, we used the latest meta-analytical tools to control for potential pseudoreplication due to correlated error structure from multiple effect sizes from a single paper (Rossetti *et al.* 2017) and from the phylogenetic history shared among species (Lajeunesse 2009), by means of hierarchical and phylogenetically independent meta-analyses respectively. In particular, we assessed habitat fragmentation effects on genetic diversity, outcrossing rates, inbreeding coefficients and correlated paternity of the progeny, as well as on early and late progeny performance parameters. Furthermore, we evaluated whether life span, type of pollination vector and/or plant mating system may drive differential responses of habitat fragmentation on progeny quality.

## MATERIALS AND METHODS

### Literature search

We conducted two systematic literature searches in multidisciplinary online databases (ISI Web of Knowledge, SCOPUS and Google Scholar) comprising the period between 1900 and 2018. In order to gather studies that analysed the effects of habitat loss and fragmentation on progeny performance and

on the genetic diversity of progeny we used two different strings of keyword combinations. First, to search for studies assessing fragmentation effects on genetic variables of progeny we used: (progen\* OR seedling\* OR offspring\*) AND ('habitat fragmentation' OR 'forest fragmentation' OR 'habitat loss' OR 'population size') AND (plant\*) AND ('genetic diversity' OR inbreeding OR 'fixation coefficient' OR outcrossing OR 'correlat\*' OR 'paternity OR 'correlated mating' OR 'pollen pool\*' OR 'pollen diversity'). Second, to find studies on progeny vigour we used: (progen\* OR seedling\* OR offspring\*) AND (plant\*) AND ('habitat fragmentation' OR 'forest fragmentation' OR 'habitat loss' OR 'population size') AND (recruitment OR establishment OR surviv\* OR vigour OR growth OR biomass OR performance OR germinat\* OR quality). Each search yielded 323 and 486 papers, respectively, which were subsequently examined for suitability in our synthesis. A study was included if it complied with the following profile: (1) assessed habitat fragmentation effects on genetic variables of plant progeny and/or progeny vigour. The retrieved studies used different approaches that involved one or more factors associated with the structural changes imposed by habitat loss and fragmentation, namely: population size (measured as number or density of individuals), degree of isolation, fragment area, and edge effects; and (2) provided numerical data on progeny vigour (e.g. germination success, biomass, growth rate, survival) and/or genetic variables (namely, genetic diversity, outcrossing rates, inbreeding coefficients and correlated paternity), such as means, standard deviations and sample sizes or correlation coefficients. Therefore, we included studies with both categorical approaches (e.g. comparing fragmented vs. continuous habitats, large vs. small populations) and correlational approaches (e.g. gradients of population size, fragment area, degrees of isolation). We also included five studies (five tree species) evaluating the effects of fragmentation due to selective logging. These studies (2.6% of all studies) compared logged vs. unlogged forest patches, which modify population density of adult trees, a measure of population size (Kunin 1997; Lowe *et al.* 2005). For each plant species included in the meta-analyses we gathered all relevant information on life-history and ecological traits, which was obtained from the source articles or from additional scientific literature. Specifically, we classified each plant species into discrete categories according to their: pollen dispersal vector (vertebrate, invertebrate or wind), mating system (outcrossing, mixed and selfing) and life span, which we classified in two broad categories (woody and non-woody) based on the evidence that woody plant species have on average a projected life span more than four times as long as non-woody plants (Ehrlén & Lehtilä 2002). Thus, woody species such as trees, shrubs and some vine species were considered to be long-lived species, whereas non-woody herbs were considered short-lived species (Ehrlén & Lehtilä 2002) (Appendix S1).

### Data analysis

As the common effect size for all the meta-analyses, we used Hedges'  $d$ , which is an estimate of the unbiased standardised mean difference between the genetic characteristics of the progeny or its performance in fragmented and continuous

habitats. To calculate Hedges'  $d$ , we obtained (either from text or tables) the mean values, sample sizes and standard deviation of a genetic parameter on progeny (e.g. allelic richness, outcrossing rate) or a progeny performance variable (e.g. germination, growth, survival) in each of the two contrasting landscape conditions (e.g. control: continuous, large, non-isolated habitats and treatment: fragmented, small, isolated habitats). When these parameter values were only given in graphs, we took the exact values using the software Data Thief III ([www.datathief.org](http://www.datathief.org)). When some or none of these values were reported, we sought for statistic values of parametric tests (e.g. ANOVAs, Chi-square,  $t$ -tests) assessing fragmentation effects on genetic or progeny performance variables. These statistics were mathematically transformed into Hedges'  $d$  (Borenstein *et al.* 2009; Koricheva *et al.* 2013). When studies assessed fragmentation effects using fragment area size-gradients, degree of isolation distances or gradients of population sizes (i.e. correlational approaches), we took Pearson's correlation coefficients ( $r$ ) or the coefficients of determination ( $R^2$ ) and sample sizes, and used these parameters to obtain Hedges'  $d$  using specific mathematical transformations (see details in Borenstein *et al.* 2009; Koricheva *et al.* 2013). In all cases, negative Hedges'  $d$  values indicate that habitat fragmentation decreases genetic variables or progeny vigour. Accordingly, the sign of Hedges'  $d$  takes a different biological meaning when interpreting fragmentation effects on inbreeding coefficients and correlated paternity: positive Hedges'  $d$  values imply higher inbreeding and correlated paternity in fragmented conditions.

Data were analysed using mixed effects models, which assume that studies within a class (i.e. a moderator variable such as pollen dispersal vectors) share a common effect but that there is also random variation among studies in a class in addition to within-study sampling variation (Borenstein *et al.* 2009; Koricheva *et al.* 2013). Heterogeneity among effect sizes was assessed with  $Q$  statistics, which are weighted sums of squares tested against a Chi-squared test distribution (Hedges & Olkin 1985). Specifically, we examined the  $P$  values of  $Q_M$  statistics that describe the variation in effect sizes that can be attributed to differences among categories of each moderator variable. Effect sizes were considered significantly different from zero if their 95% bias-corrected bootstrap confidence intervals (CI) did not overlap with zero (Borenstein *et al.* 2009; Koricheva *et al.* 2013).

### Hierarchical meta-analysis

Several papers provided more than one progeny performance measurement from the same species (e.g. germination %, biomass, survival, etc.), whereas other papers studied several species simultaneously. Because we were interested in comparing early and late progeny performance parameters and also in including all species even if they were studied within the same paper, we incorporated all these measures into the same analysis. However, having several effect sizes from the same publication violates the assumption of independent effect sizes (Tuck *et al.* 2014). To overcome such potential meta-analytical pseudoreplication we performed a hierarchical meta-analysis, which allows nesting effects within papers/studies. To

accomplish this, we included a publication-level random effect as a nesting factor to incorporate this dependency of multiple outcomes within study observations into the mixed models (Stevens & Taylor 2009). All the analyses were conducted in R using the metafor package (Viechtbauer 2010; R Core Team 2018).

### Phylogenetic meta-analysis

When effect sizes are calculated at the species level in a meta-analysis, the assumption of independent samples may be violated as a result of the inherent evolutionary relationships among species, which incorporates a correlated error structure among them (Lajeunesse 2009; Chamberlain *et al.* 2012). Thus, overall conclusions in a meta-analysis may be biased if we do not test and compare results with phylogenetically independent estimations of overall effects. To run phylogenetic meta-analyses (PMA), we built phylogenetic trees with all the plant species included in each review: genetic variables of progeny and progeny performance. We calculated a single effect size per species, so when several genetic diversity or progeny performance measures were estimated for a single species, we pooled these multiple effect sizes per species using a traditional meta-analysis with a fixed effects model (Koricheva *et al.* 2013). We used the Slik *et al.* (2018) classification as the genus-level reference configuration of our phylogenetic tree. This tree was further resolved to species level using matK and rbcL sequences for each species retrieved from the NCBI GenBank database and aligned using the MUSCLE algorithm in the software PHYDE 0.9 (Müller *et al.* 2006). Phylogenetic relationships between species were obtained using Bayesian inference (BI) in MRBAYES v 3.1.2 (Ronquist *et al.* 2012). All phylogenetic trees are given in the supplementary online material (Fig. S1 and S2a–d). To run PMAs we used PHYLOMET v1.3 (Lajeunesse 2011) that uses a weighted Generalised Least Squares approach to account for the phylogenetic correlations among species. When analysing each predictor or moderator variable, we constructed a subset phylogenetic tree for each moderator (e.g. plant mating system), which contained only the species present in that particular comparison, retaining all branch length information from the original phylogenetic tree.

### Publication bias

A common problem of any quantitative review is that it may include only the studies showing significant results, as they may have a greater possibility of being published than those showing non-significant results. To detect the existence of publication bias in our dataset and to estimate how such bias, if it exists, may affect the overall results, we used statistical (rank correlation tests and ‘trim and fill’ procedures), and numerical (Rosenthal’s fail-safe number) methods (Jennions *et al.* 2013). Kendall’s rank correlation tests examine the relationship between effect sizes and sample sizes across studies. If publication bias exists then studies with small or null effect sizes are missing and the correlation tests are significant. The ‘trim and fill’ method recalculates the estimated mean effect size by trimming the smaller studies from one side of the funnel plot and refilling it on the other side of funnel plot until the funnel is

fully symmetric. Thus, it provides an estimate of how the overall effect size would change if we were able to incorporate all potential missing studies (Jennions & Moller 2002). On the other hand, the weighted fail-safe number value indicates the number of non-significant, unpublished or missing studies that would need to be added to a meta-analysis in order to nullify the overall effect sizes (Rosenthal 1979). If the calculated fail-safe number is  $> 5n+10$ , where  $n$  is the number of studies, then publication bias may be safely ignored (Rosenberg 2005).

## RESULTS

### Articles and species included in the review

In our first literature search we were able to extract data from 101 publications assessing fragmentation effects on at least one genetic parameter from plant progeny allowing the estimation of 240 effect sizes from 107 plant species. In the second literature search we included a total of 90 publications that analysed fragmentation effects on progeny performance. These publications allowed us to estimate 196 effect sizes from 108 plant species. There were 36 species from which either, within the same paper or in different publications, fragmentation effects were assessed on both genetic variables of progeny and progeny vigour. Considering both literature searches we gathered a total of 179 unique plant species from several biomes of the world (Appendix S1). Most of these species were trees (58%) and perennial herbs (26%), followed by shrubs (11%), epiphytes (4%) and vines (1%) (Appendix S1). Species were predominantly hermaphrodite (73%) with mostly outcrossing (58%) and mixed (35%) mating systems (Appendix S1). There were only three mostly selfing species. Most plant species were insect-pollinated (67%), with a lower representation of vertebrate (18%) and wind (15%) pollination (Appendix S1). Nearly 90% of all studies measured genetic variables from seed tissue germinated under controlled conditions, whereas only 10% took samples from seedlings in the field (Appendix S1). Studies that collected seeds from parental plants from different conditions and then measured progeny performance in controlled greenhouses, common gardens or laboratories comprised nearly 70% of the studies, whereas the remaining minority of studies assessed emergence, survival and growth in field plots. Most studies assessed fragmentation effects on genetic variables and progeny performance at the patch level, evaluating plant population sizes (48%), fragment area (35%) and edge effects (7%) on plant progeny. Only 10% of the studies assessed degree of isolation of habitat remnants on plant progeny. These four different fragmentation factors had similar effects on the genetic variables of the progeny ( $Q_{M(df=3)} < 6.51$ ,  $P > 0.158$ ) and on progeny performance ( $Q_{M(df=3)} = 4.51$ ,  $P = 0.211$ ). Only 40% of the studies provided information on the time elapsed in fragmented conditions and most of these studies (71%) reported times that were  $\leq 100$  years (Appendix S1).

### Habitat fragmentation effects on genetic variables of progeny

The hierarchical meta-analyses conducted on each of the genetic variables assessed indicates that progeny sired in

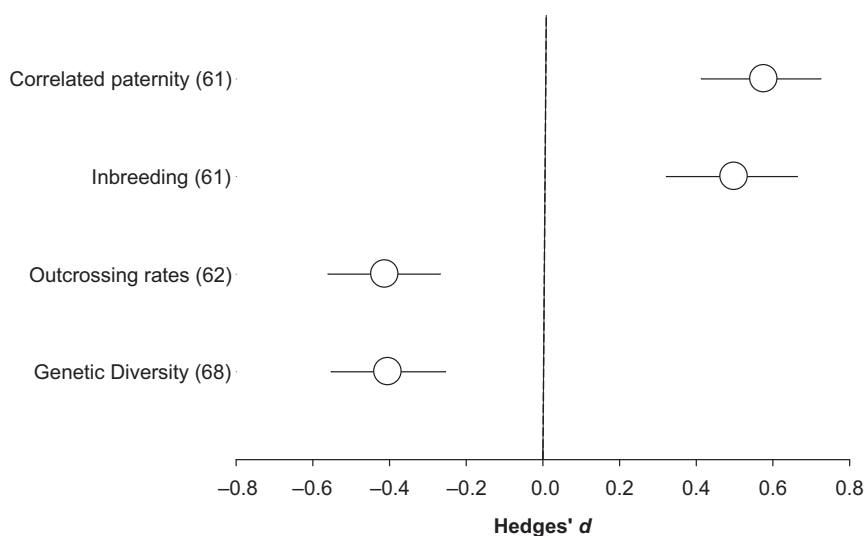
fragmented habitats shows overall genetic erosion, with decreased genetic diversity (either measured as heterozygosity or allelic richness) and outcrossing rates as well as increased inbreeding coefficients and correlated paternity (Fig. 1). Woody and non-woody species experienced similar negative fragmentation effects on the four genetic variables assessed on the progeny, despite the unbalanced comparisons that included mostly woody species (Table S1). Habitat fragmentation had no significant effect on any of the genetic variables in the progeny of plants pollinated by vertebrates (Fig. S1a–d). In contrast, progeny of either wind- or insect-pollinated plants, showed strong genetic erosion (Fig. S1a–d), with the exception of wind-pollinated plants, which showed no fragmentation effects on correlated paternity. Plants with different mating systems showed similar genetic erosion in all genetic variables (Fig. S1a–d). When overall fragmentation effects were calculated through PMAs on each genetic variable (phylogenetic trees shown in Fig. S2a–d) as well as with the categorical moderators (e.g. pollinator vectors, etc.; not shown), we found similar response patterns as those obtained by the traditional meta-analyses; thus, we only show results for the latter.

#### Habitat fragmentation effects on progeny vigour

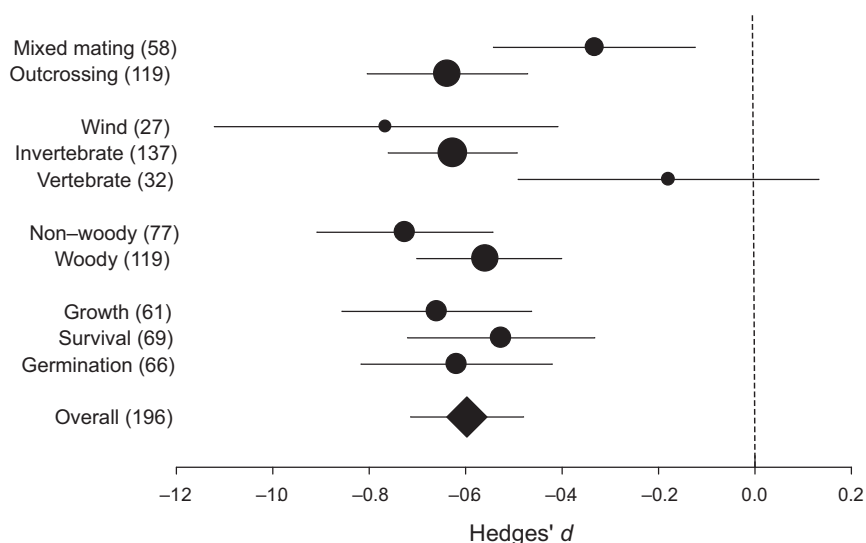
The hierarchical meta-analysis showed a significantly negative overall habitat fragmentation effect on progeny vigour, implying that progeny generated in fragmented conditions has on average lower vigour than progeny sired in continuous habitats (Fig. 2). Woody and non-woody plant species showed similar negative effects on progeny vigour ( $Q_{M(df=1)} = 0.98$ ,  $P = 0.32$ ; Fig. 2), and there was no difference in fragmentation effects on germination, survival and progeny growth ( $Q_{M(df=2)} = 1.88$ ,  $P = 0.389$ ; Fig. 2). There was a differential fragmentation effect on progeny vigour of plant species with different pollination vectors ( $Q_{M(df=2)} = 11.09$ ;  $P = 0.004$ ): entomophilous and anemophilous plants showed negative

effects, whereas plants pollinated by vertebrates (birds and mammals) showed no significant effects (Fig. 2). Similarly, fragmentation effects on progeny vigour were different depending on the mating system. Outcrossing species showed higher negative effects on progeny vigour than mixed mating ones ( $Q_{M(df=1)} = 9.53$ ,  $P = 0.008$ ; Fig. 2). Selfing species were not included in this analysis because of their low representation. When analysing species responses by the combination of mating system and early-late progeny vigour parameters, mean effect sizes differed by mating system ( $Q_{M(df=5)} = 12.32$ ,  $P = 0.031$ ; Fig. S3), but not by the stage of progeny vigour, as observed by the overlapping CI's within each group of outcrossing and mixed-mating plant species (Fig. S3).

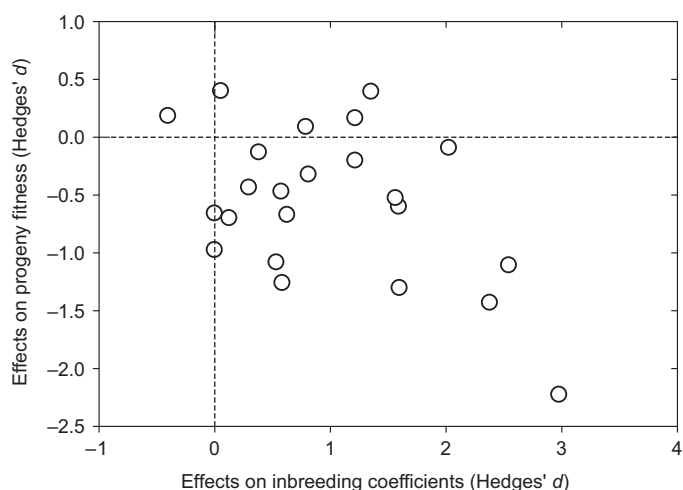
When incorporating the phylogenetic structure of plant species included in this review (Fig. S4), we observed similar qualitative results as those found in the hierarchical meta-analyses. The overall phylogenetically independent meta-analysis (PMA) showed a similar negative effect on progeny vigour but of slightly lower magnitude (Hedges'  $d = -0.375$ , CI:  $-0.511$  to  $-0.235$ ,  $N = 108$ ; Fig. S5). Because running PMA implies calculating one effect size per species, we had to pool several effect sizes in cases where more than one vigour parameter was measured in the same species. As a result, we were not able to compare early vs. late progeny vigour parameters in a phylogenetic context. When comparing fragmentation effects on progeny vigour in plants with different pollination vectors and plant mating systems under PMA we observed similar qualitative response patterns as in previous hierarchical meta-analyses (Fig. S5). However, because of lower sample sizes, all categorical moderator variables had larger confidence intervals. As a result, while they showed similar negative effects as the hierarchical meta-analyses, plants with mixed mating systems showed no significant fragmentation effects on progeny performance (Fig. S5). Finally, in 23 plant species we were able to run a correlation analysis between fragmentation effects on vigour and inbreeding



**Figure 1** Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on four genetic variables estimated from progeny tissue. Sample sizes of each category are given in parentheses. Dotted line shows Hedges'  $d = 0$ .



**Figure 2** Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on early and late progeny vigour parameters and for plant species with different lifespan, pollination vectors and mating systems. Sample sizes of each category are given in parentheses. Dotted line shows Hedge's  $d = 0$ .



**Figure 3** Relationship between habitat fragmentation effects on inbreeding coefficients and progeny performance. Each point represents a unique plant species where fragmentation effects were assessed simultaneously on both inbreeding coefficients and a measure of progeny vigour. Dotted lines indicate values of zero for the effect sizes. Relationship is negative and significant (Pearson's  $r = -0.471$ ;  $P = 0.023$ ).

coefficient of the same progeny. The correlation was negative and significant (Pearson's  $r = -0.471$ ;  $P = 0.023$ ; Fig. 3), indicating that increased inbreeding coefficients due to habitat fragmentation are associated with decreased progeny vigour.

#### Publication bias

Each meta-analysis on genetic diversity, outcrossing rates, inbreeding and correlated paternity showed no evidence of publication bias (Table S2). That is there were no significant correlations between effect sizes and sample sizes and no changes in overall effect sizes after 'trim and fill' procedures

(Table S2). Finally, in these meta-analyses, the calculated weighted fail-safe numbers were also always larger than  $5n+10$  (Table S2). In contrast, the Kendall's rank correlation between effect sizes and sample sizes across studies assessing progeny vigour parameters was statistically significant ( $z = -0.152$ ,  $P = 0.015$ ,  $N = 196$ ), which suggests the potential presence of publication bias whereby studies with small or nil effects might be missing from our sample. However, the 'trim and fill' procedure indicated that after correcting such initial asymmetry in the funnel plot (which resulted in a significant rank correlation test), the overall effect size only slightly decreased but remained negative and significantly different from zero (Fig. S6, Table S3). In other words, if we were to incorporate the potentially missing studies from our review the overall results observed would not change. On the other hand, the calculated weighted fail-safe number was 17 680, which is larger than  $5n+10 = 990$ , implying that publication bias may be safely ignored in our database.

#### DISCUSSION

The results of our synthesis support theoretical expectations regarding the ecological and genetic consequences of reduced population sizes and increased isolation among populations imposed by anthropogenic habitat loss and fragmentation (Young *et al.* 1996; Sork *et al.* 1999; Frankham *et al.* 2010). These findings suggest that habitat fragmentation often disrupts gene flow and increases random genetic drift and inbreeding, which erodes genetic diversity of plant progeny reducing its viability and vigour, regardless of plant species characteristics. Moreover, we found reduced outcrossing rates and increased inbreeding and correlated paternity in progeny sired in fragmented habitats, indicating changes in plant mating patterns. Thus, habitat fragmentation not only reduce the reproductive output and genetic diversity of adult plant populations (Aguilar *et al.* 2006, 2008; Leimu *et al.* 2006; Honnay

& Jacquemyn 2007; Vranckx *et al.* 2011), but it also strongly affects the performance of the progeny (Aguilar *et al.* 2008; Vranckx *et al.* 2011). In demographic terms, such effects are likely to increase seedling mortality, affecting the recruitment of plant populations in fragmented conditions, thereby increasing the probability of extinction (Quesada *et al.* 2001; Charlesworth & Willis 2009; Gonzalez-Varo *et al.* 2010; Ashworth & Martí 2011; Aguilar *et al.* 2012).

In a recent review, Fahrig (2017) points out that habitat fragmentation is a landscape-scale phenomenon that, when properly measured at such scale, has nil or even positive effects on biodiversity. Moreover, Fahrig (2017) argues that extrapolation of patch-scale patterns to landscape-scale inferences is inappropriate. Most of the studies included in our review analysed fragmentation effects on plant progeny fitness at the patch-scale, involving reduced population sizes and fragment areas, edge effects and increased degree of isolation, all of which were a consequence of human land use changes, as explicitly stated by the authors (see Appendix S1). Our review represents a synthetic view of the ways research on fragmentation effects have been conducted across the last few decades. More recently, Fletcher *et al.* (2018) argued that while habitat fragmentation may often (but not always) occur at a landscape-scale, there are mechanisms of biodiversity responses that occur at the patch-scale level. Adding to the arguments provided by Fletcher *et al.* (2018) on the missing or biased evidence on biodiversity effects included in Fahrig's review (2017), several quantitative reviews have shown that habitat fragmentation at the patch scale has overall strong negative effects on the genetic composition and fitness of adult plant populations as well as in their progeny (Aguilar *et al.* 2006; Honnay & Jacquemyn 2007; Aguilar *et al.* 2008; Vranckx *et al.* 2011; this study), none of which were considered by Fahrig (2017) or Fahrig *et al.* (2019). Our results on the pervasive effects of fragmentation on genetic diversity and population fitness indicate that the long-term conservation of plant populations in fragments are globally at risk, regardless of the debate that evaluates the effects of habitat fragmentation on static measures of species diversity at any given spatial scale derived from sampling efforts restricted in time.

#### Pollination vectors affect progeny quality in fragmented habitats

Changes in pollination patterns, which make the largest contribution to gene flow, should be readily detected in the progeny. Here we observed that, on average, plants pollinated by vertebrates (bats and birds) sired progeny of similar quality in both fragmented and continuous habitats. Thus, these animal vectors are currently able to counteract habitat fragmentation effects by connecting isolated remnant plant populations, preventing genetic drift and inbreeding. The progeny of vertebrate-pollinated plants was not affected on any of the genetic variables assessed because vertebrates are able to fly long distances and maintain gene flow via pollen among fragmented populations (e.g. Hadley & Betts 2009). These results concur with the review of Vranckx *et al.* (2011) for trees and shrubs, highlighting the importance of vertebrate pollinators for buffering fragmentation effects on angiosperm progeny quality.

In contrast, the progeny of insect- and wind-pollinated plants were strongly negatively affected by habitat fragmentation, showing both increased overall genetic erosion and reduced performance. Our findings support prior reports of drastic declines in insect pollinator richness and abundance and decreased pollination services in plants growing in fragmented habitats (Aizen & Feinsinger 1994; Quesada *et al.* 2004; Aguilar *et al.* 2006; Winfree *et al.* 2009; Alves Ferreira *et al.* 2013; Janzen & Hallwachs 2019; Sánchez-Bayo & Wyckhuys 2019). Particularly, Hymenoptera and Lepidoptera appear to be the most affected insect orders by extinctions across the globe (reviewed by Sánchez-Bayo & Wyckhuys 2019). Because bees, wasps, butterflies, moths and hawkmoths are key pollinators of most of plant species in tropical and subtropical habitats (Ollerton *et al.* 2011), it is likely that our results reveal the impact of these declines on the quality of plant progeny. Thus, we highlight the importance of increasing conservation efforts of invertebrate pollinator species.

Our results did not support the initial expectation that fragmentation would have little or no effects on the mating patterns of wind-pollinated species (Hamrick 2004). This expectation was supported by case studies showing extensive gene flow in fragmented populations of wind-pollinated species, which may result from the reduced intervening vegetative structure imposed by habitat loss (e.g. Hamrick 2004; Sork & Smouse 2006; but see Broadhurst 2015). Likewise, there are case studies of insect-pollinated tree species that show increased gene flow in fragmented conditions, possibly associated with a lowered tree density that forces specialist pollinators to expand their foraging areas for the same resource (Nason & Hamrick 1997; White *et al.* 2002; Fuchs & Hamrick 2011; Rosas *et al.* 2011). However, after synthesising evidence across many species with different life-history and ecological traits from several regions across the world, we argue that these contrasting examples represent the exception rather than the rule. Our review strengthens the conclusions from earlier reviews of fragmentation effects on genetic variables of mostly adult plant population species with different pollination systems (Aguilar *et al.* 2008; Vranckx *et al.* 2011), and provides further evidence that these effects are translated into decreased progeny performance in fragmented habitats. Moreover, while large pollen dispersal distances are important for connecting fragmented populations, they do not necessarily guarantee an increase in outcrossing rates and genetic diversity (Quesada *et al.* 2001; Sork & Smouse 2006; Vranckx *et al.* 2011; Breed *et al.* 2015). In fact, here we provide additional evidence for decreased outcrossing rates in fragmented habitats, in agreement with previous reviews (Aguilar *et al.* 2008; Eckert *et al.* 2010; Breed *et al.* 2015), but we also show for the first time the overall erosion of genetic diversity in plant progeny.

#### Habitat fragmentation effects on correlated paternity

In addition to pollen dispersal distances, if immigrant pollen pools originate from just a few parental sources there will be high paternity correlation in progeny sired within fragments. While we did not assess fragmentation effects on pollen flow distances due to the scarcity of metadata, we did find overall

increased correlated paternity in progeny generated in fragmented conditions, which agrees with a recent meta-analysis on 29 woody plant species (Breed *et al.* 2015). Tree species in isolated or fragmented conditions produce larger floral displays than those in continuous forests, as a result of increased space and light availability (Quesada *et al.* 2001; Fuchs *et al.* 2003; Herrerías-Diego *et al.* 2006; Aguilar *et al.* 2012). Larger floral displays can increase correlated paternity of progeny by reducing pollen donor diversity through increased geitonogamy in self-compatible species or reduced density of conspecifics in self-incompatible species. Higher correlated paternity, in turn, may affect progeny fitness by reducing competition among male gametophytes within (i.e. pollen tubes) and among flowers (selective abortion), which lowers the potential for gametophytic selection (Quesada *et al.* 2001; Cascante *et al.* 2002; Breed *et al.* 2012). Male and female gametophytic performance may also be subject to inbreeding depression (Carr & Dudash 1995; Gargano *et al.* 2011). Although little is known about the mechanisms of inbreeding depression at the male gametophytic level, a review by Losdat *et al.* (2014) showed that inbreeding depression negatively impacts pollen production, pollen size, pollen performance and siring success (Jóhannsson *et al.* 1998; Stephenson *et al.* 2003). Therefore, inbreeding depression is likely to negatively affect the competitive ability of male gametophytes in fragmented populations, reducing the number and quality of the progeny produced.

#### Habitat fragmentation and inbreeding depression

The expression and magnitude of inbreeding depression depends on both the population's mating pattern history and the time elapsed in small areas and isolated conditions (e.g. Young *et al.* 1996; Hamrick 2004; Aguilar *et al.* 2008). Our quantitative synthesis of scientific research conducted across the past three decades indicates that we are observing short-term effects of habitat loss and fragmentation (Ouborg *et al.* 2006; Aguilar *et al.* 2008). We should highlight that the majority of fragmentation events in the studies conducted so far have occurred relatively recently (*c.a.* 100 years) and most of the species studied involved woody species with long lifespans (Appendix S1). Altogether, these characteristics imply that most researchers have measured only recent consequences of habitat loss on plant populations with a relatively short history of inbreeding. Thus, our synthesis provides indirect evidence of an extinction debt for most woody plant species remaining in fragmented habitats, which will eventually be paid off in subsequent generations (Vranckx *et al.* 2011; Aguilar *et al.* 2018; Auffret *et al.* 2018). In other words, if these environments fail to increase natural habitat and connectivity, these plant populations will steadily decline and remain as ghost populations on their way to extinction (Jackson & Sax 2010; Aguilar *et al.* 2018; Auffret *et al.* 2018).

#### Relationship between inbreeding coefficient and progeny vigour

Here we also corroborated previous general response patterns of increased inbreeding in progeny sired in fragmented habitats (Aguilar *et al.* 2008; Eckert *et al.* 2010; Breed *et al.* 2015).

More interestingly, we were able to quantitatively summarise for the first time a negative correlation response across 23 species between habitat fragmentation effects on inbreeding coefficients and progeny fitness. Such negative correlation implies that the most proximate cause of decreased progeny performance in fragmented habitats is increased inbreeding, and concomitant inbreeding depression. These results suggest inbreeding depression may threaten the viability of plant populations in fragmented habitats, regardless of the plant mating system (Spielman *et al.* 2004).

#### Methodological bias in assessing progeny quality

In our literature review, 90% of the studies assessed the genetic composition of seeds directly collected from maternal plants, which may differ markedly from recruited seedlings in fragmented conditions, as they are likely to be subject to natural selection from biotic interactions (e.g. seed predators, herbivores) or environmental stochasticity (e.g. Cascante *et al.* 2002; Honnay *et al.* 2008; Rossetti *et al.* 2017). Furthermore, two-thirds of the studies assessed progeny performance in controlled greenhouse or common garden conditions. Thus, there is little representation of studies on established progeny in the field, which suggests that we may be underestimating the *in situ* environmental effects of habitat fragmentation on progeny quality (e.g. Gonzalez-Varo *et al.* 2012). Moreover, there is a gap of studies assessing fragmentation effects on selfing plant species, which are reproductively less dependent on pollinators and conspecific mates and therefore, more likely to establish outside their original range and become naturalised (Baker 1955; Razanajatovo *et al.* 2016). The progeny of these species is less likely to experience negative fragmentation effects. Therefore, we stress the need to increase the number of studies on established progeny and on selfing, early successional plant species in fragmented habitats.

#### CONCLUDING REMARKS

Today, more than 75% of the earth's land surface is under human use (Foley *et al.* 2005; Ellis & Ramankutty 2008). Our findings, together with previous important generalisations, reveal a gloomy future for plant populations remaining in fragmented habitats, the pervasive condition of current landscapes. In natural conditions, habitat loss and fragmentation occur simultaneously and it is difficult or infeasible to disentangle their effects in observational studies (Didham *et al.* 2012). Should landscapes remain as they are now, without any proactive restoration efforts for increasing the area and connectivity of natural habitats, we may expect lower population recruitment and establishment of genetically depauperate plant progeny generated in fragmented conditions. Based mostly in patch-scale studies we conclude that angiosperms surviving in fragmented habitats yield a lower quantity of progeny (Aguilar *et al.* 2006) of lower quality, and these results cannot be overlooked while we attempt to disentangle the consequences of landscape vs. patch-scale effects (Fletcher *et al.* 2018). In this regard, we call for a serious examination of the current paradigm of human land use and recent views that habitat fragmentation is positive for biodiversity (e.g.



Fahrig 2017). Because almost all life on earth relies directly or indirectly on primary producers, we need to preserve plant diversity by maintaining the genetic diversity and the long-term population viability of angiosperms, the most important terrestrial plants in currently anthropogenic-dominated landscapes.

## ACKNOWLEDGEMENTS

We are truly grateful for the positive and detailed feedbacks from three anonymous reviewers and the editor Dr. José María Gómez. Their critical, thoughtful, and constructive observations greatly improved the original version of this MS. This project was partially funded by Agencia de Promoción Científica y Técnica (FONCyT 2016-0764), CONICET (PIP 2015-0371) and grants from DGAPA UNAM (PAPIIT # 212714 and IV200418 to MQ, IA207318 to SMR), CONACyT (CB-2009-131008, SAGARPA-CONACYT 291333 to MQ, Proyecto Laboratorio Nacional de Análisis y Síntesis Ecológica 2015-250996, 2016-271449, 2017-280505, and 2018-293701 to MQ and SMR), and Programa Iberoamericana de Ciencia y Tecnología para el Desarrollo RED CYTED-SEPODI (417RT0527). RA, LA, and GB are researches from CONICET.

## CONFLICT OF INTEREST

The authors declare no competing financial interests.

## AUTHORSHIP

R.A., M.Q., L.A., J.L.S., S.M.R., G.B. and E.J.F. conceived the review; E.J.C.P., F.J.B.O., M.J.A.A., N.A.A. G.S.M. and R.A. conducted the literature search, retrieved the information and processed the meta-data. R.A. led data analysis and drafted the first version of the manuscript. M.Q., L.A., J.L.S., S.M.R., G.B. and E.J.F. participated in data analyses and helped draft the manuscript. All authors commented on manuscript drafts and gave final approval for publication.

## DATA ACCESSIBILITY STATEMENT

All data used are already published data available in scientific journals.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, José María Gomez

Manuscript received 21 January 2019

First decision made 1 March 2019

Manuscript accepted 10 April 2019