# Do plant traits influence a species' response to habitat disturbance? A meta-analysis

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## ABSTRACT

The vast majority of plant species, including one-third of crops, require a pollinator in order to set seed. While habitat disturbance has been shown to reduce the abundance and species richness of native bee species, a comprehensive study of the impacts of disturbance on plant reproductive success is lacking. In a meta-analysis of 41 studies we show that, overall, habitat disturbance is associated with a decrease in fruit set. Moreover, the magnitude of this effect depends on disturbance type. The presence of livestock or fire in a plant's habitat was associated with a reduction in fruit set, whereas the presence of human use, deforestation, or agricultural use was associated with a non-significant trend in the same direction. We also examined the potential for plant traits to influence a species' response to disturbance. We found that tropical plants suffered a greater impact of habitat disturbance than temperate plants, as did plants with dry relative to fleshy fruit types. No differences were found between woody and herbaceous plants, or between crops and non-crop species. Self-incompatible species in disturbed temperate habitats suffered a greater reduction in fruit set than self-compatible species, suggesting a role of pollination on the effect of the disturbance. Our results indicate that while species' responses to habitat disturbance are highly variable, certain plant traits could serve to predict the impact of a disturbance on a species' reproductive success. This information will be useful in focusing conservation efforts on the plant species most vulnerable to disturbance.

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## 1. Introduction

Pollination is vital to the health of managed and natural ecosystems. Animal-mediated pollination is a necessary component of reproduction for an estimated 35% of our food crop species (Klein et al., 2007) and the pollination of these crops by native pollinators alone is estimated to be worth over three billion dollars in the United States (Losey and Vaughan, 2006). The proportion of flowering plants requiring animal pollination in natural ecosystems has been estimated at 78% for temperate regions and 94% for tropical regions (Ollerton et al., 2011). Alarmingly, both native and managed pollinator populations are declining in number (Biesmeijer et al., 2006; Potts et al., 2010; Levy, 2011). This decline could negatively impact global food production and the reproductive success of both managed and native plant species, with potential implications ranging from economic losses to impaired ecosystem function and an increase in the extinction of vulnerable plant species. Crucially, much of the decline in pollinator populations has been attributed to the deterioration of habitat availability and quality (Winfree et al.,

2009). With an increase in the prevalence of habitat fragmentation and the magnitude and frequency of habitat disturbance (Opdam and Wascher, 2003) – broadly defined here as a degradation of a plant's environment, generally, but not necessarily, inflicted by human use – it is paramount to evaluate the impacts on plant reproduction.

Plant reproductive success is influenced by a wide variety of factors, including resource limitation (Burd, 1994), herbivory (Maschinski and Whitham, 1989), and pollen limitation (Ashman et al., 2004; Davila et al., 2012). Pollen limitation, where seed or fruit production is limited by pollen quantity or quality (Burd, 1994), is positively correlated with the presence and diversity of pollinator communities (Klein et al., 2003a; Ashman et al., 2004). Habitat disturbance has been shown to negatively impact the overall abundance and richness of unmanaged bee species, according to a meta-analysis (Winfree et al., 2009), with the negative impact most evident in areas that experienced habitat loss. Williams et al. (2010) also found a negative impact of environmental disturbance on the relative abundance of bee species across 19 studies. In another meta-analysis (23 studies), pollinator richness and visitation were shown to decline steeply with increasing distance from natural habitat (Ricketts et al., 2008). A more recent meta-analysis also demonstrated significant negative impacts of landscape alteration on pollinator abundance (22 studies) and visitation rates (50

studies) (Montero-Castano and Vila, 2012). The evidence thus overwhelmingly supports the hypothesis that habitat disturbance has a detrimental effect on native pollinator populations and communities.

If habitat disturbance has a negative impact on pollinator abundance and diversity, it may also lead to higher pollen limitation, which could limit reproductive success through female function. Indeed, Garibaldi et al. (2011) found that fruit set, pollinator visitation, and pollinator richness in agricultural crop fields all declined with increasing distance from natural areas. The same study showed no relationship among visitation of managed honey bees and distance from natural areas. Ricketts et al. (2008) found steep declines in native pollinator richness and visitation rates to 16 different bee-pollinated crops with increasing distance from natural habitats, but only minimal declines in seed and fruit set of the same crops with increasing distance from natural habitats, at least given the limited statistical power of the dataset ($n = 12$). However, it is not uncommon for pollinator services and plant reproductive success to show different responses to similar environmental conditions (Thomann et al., 2013). For example, in a meta-analysis, Morales and Traveset (2009) reported that significant differences in pollinator visitation in invasive and native plants did not lead to any differences in reproductive success ($n = 58$ and $n = 37$ for pollinator visitation and plant reproductive success, respectively). Similarly, Aguilar et al. (2006) demonstrated a negative impact of habitat fragmentation on both pollen receipt and fruit or seed set in animal-pollinated plants; however, the effect of fragmentation on plant reproductive success was smaller than the effect on pollen receipt. Regardless of the response of plant reproduction to pollinator richness and visitation, pollen limitation is very common, and is estimated to occur in between 53% and 73% of natural plant populations (Burd, 1994).

Despite the demonstrated negative impacts of distance from natural habitat (Garibaldi et al., 2011) and habitat fragmentation (Aguilar et al., 2006) on plant reproductive success, and the demonstrated negative impacts of landscape alteration to pollinator abundance and visitation (Montero-Castano and Vila, 2012), a comprehensive exploration of different types of habitat disturbance on plant reproductive success is lacking. An examination of the impacts of different disturbance types on plant fruit set within or in the proximity of the plant habitat, analogous to those tested by Winfree et al. (2009) for bee abundance and diversity, is also lacking. In this paper we synthesize the current literature on this topic using a meta-analysis to address the following questions: (i) what is the overall impact of habitat disturbance on plant female reproductive success, measured as fruit set? and (ii) can we identify either plant traits or disturbance types that are associated with an increase in the susceptibility of a plant species' reproductive success to habitat disturbance? Given the demonstrated negative impacts of habitat disturbance on pollinator abundance and diversity, we predict that similar disturbances will negatively influence fruit set of animal-pollinated plants. However, these effects may vary depending on the type of disturbance, and on characteristics of the plant species and habitat, such as plant mating system, biome, fruit type, growth form, and crop potential. We discuss our findings in the context of potential predictor variables that could be used to focus conservation efforts on the plant species that are most susceptible to habitat disturbance.

## 2. Materials and methods

### 2.1. Literature survey

To identify published studies that provide data on plant reproductive success in the face of habitat disturbance, we searched ISI Web of Science using combinations of the following search terms: (crop success), (reproductive success), (pollination), or (pollen limitation) AND (disturbance), (deforestation), (agriculture), (fire), or (livestock) covering all years of the database at the time of the search (1898–2011). Where necessary, individual authors were contacted for their raw data ($n = 8$). In order to be included in the meta-analysis, a study had to report fruit set as a proportion of flowers set for an animal pollinated plant species, across varying levels of habitat disturbance. The final data set comprised 72 data points from 41 published studies. Data points from the same studies were considered independent if they represented different plant species (following Aguilar et al., 2006). For consistency, if data from multiple years were available for a single species/study, the final year of the study was chosen for the analysis (as described by Aguilar et al. (2006) and Winfree et al. (2009)).

### 2.2. Data categorization

All data points were categorized by disturbance type, based on the description in the original study (Table 1), as one of the following: (a) agricultural, (b) fire, (c) deforestation, (d) livestock, or (e) general human use. In all cases, the disturbance had occurred either directly in the studied habitat, or in direct proximity of the habitat. Agricultural disturbance refers to disturbance due to agricultural activities. This category included studies looking at the effects of proximity to natural habitat on the reproductive success of a crop species (e.g. Chacoff et al., 2008), as well as studies looking at the effects of proximity to agricultural operations on the reproductive success of native species (e.g., Parra-Tabla et al., 2000). Fire disturbance included studies comparing reproductive success of plants inhabiting areas which had been burned in the past 3–15 years to those in unburned adjacent areas (e.g., Ne'eman et al., 2000). Deforestation disturbance included studies examining the effects of tree removal on the reproductive success of forest understory species (e.g., Totland et al., 2006), as well as studies examining the effects of the distance to the nearest intact forest patch on the reproductive success of forest-dwelling species (e.g. Broadhurst and Young, 2006). Livestock disturbance included studies comparing the fruit set of plants inhabiting areas excluded from livestock trampling and grazing with that of the same species inhabiting areas open to livestock (e.g., Aschero and Vazquez, 2009), as well as studies comparing fruit set across areas of varying levels of livestock trampling and grazing (e.g., Riginos and Hoffman, 2003). Disturbance involving human use included studies looking at the impact of proximity to foot paths and the proximity of urban neighborhoods (e.g., Van Rossum et al., 2002) on a species' fruit set (e.g., Huang et al., 2009). When a study could potentially be classified into more than one category, for example deforestation for the purpose of agricultural development, the description given by the original study authors was used to determine the primary categorization.

### 2.3. Species

Plant species from 40 different angiosperm families were included in the meta-analysis. The species and studies were distributed world-wide, and include data from 23 countries with representatives from all continents except Antarctica (Table 1).

### 2.4. Analyses of effect size and heterogeneity

Effect sizes were calculated as Hedges' unbiased standardized mean difference (Hedges' $d$) using reported mean values, sample sizes, and standard deviation (Hedges and Olkin, 1985). In cases where these measures were not directly reported ($n = 62$), Hedges' $d$ was calculated from reported $r$, $t$, $F$, $\chi^2$, or $z$ values (following

**Table 1**
Plant species from studies included in the meta-analysis, categorized by disturbance type, mating system, biome, fruit type, growth form, and crop potential.

| Name-latin | Name-common | Family | Location | Authors | Disturbance type | Mating system | Biome | Fruit type | Growth form | Crop potential |
|---|---|---|---|---|---|---|---|---|---|---|
| *Citrus × paradisi* | Grapefruit | Rutaceae | Argentina | Chacoff et al. (2008) | Agriculture | Self-compatible | Temperate | Fleshy | Woody | Crop |
| *Macadamia integrifolia* | Macadamia | Protaceae | Australia | Blanche et al. (2006) | Agriculture | Self-compatible | Tropical | Dry | Woody | Crop |
| *Dimocarpus longan* | Longan | Sapindaceae | Australia | Blanche et al. (2006) | Agriculture | Self-compatible | Tropical | Fleshy | Woody | Crop |
| *Ooncidium ascendens* | | Orchidaceae | Mexico | Parra-Tabla et al. (2000) | Agriculture | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Coffea canephora* | Lowland coffee | Rubiaceae | Indonesia | Klein et al. (2003) | Agriculture | Self-incompatible | Tropical | Fleshy | Woody | Crop |
| *Primula vulgaris* | | Primulaceae | Belgium | Brys et al. (2004) | Agriculture | Self-incompatible | Temperate | Dry | Herbaceous | Non-crop |
| *Babiana ambigua* | | Iridaceae | South Africa | Donaldson et al. (2002) | Agriculture | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Berkheya armata* | | Asteraceae | South Africa | Donaldson et al. (2002) | Agriculture | Unknown | Tropical | Dry | Herbaceous | Non-crop |
| *Cyanella lutea* | | Tecophilaeaceae | South Africa | Donaldson et al. (2002) | Agriculture | Unknown | Tropical | Dry | Herbaceous | Non-crop |
| *Gladiolus liliaceus* | | Iridaceae | South Africa | Donaldson et al. (2002) | Agriculture | Unknown | Tropical | Dry | Herbaceous | Non-crop |
| *Ornithogalum thyrsoides* | | Hyacinthaceae | South Africa | Donaldson et al. (2002) | Agriculture | Self-compatible | Tropical | Dry | Herbaceous | Non-crop |
| *Pterygodium catholicum* | | Orchidaceae | South Africa | Donaldson et al. (2002) | Agriculture | Unknown | Tropical | Dry | Herbaceous | Non-crop |
| *Trachyandra hirsuta* | | Asphodelaceae | South Africa | Donaldson et al. (2002) | Agriculture | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Coffea arabica* | Highland coffee | Rubiaceae | Brazil | De Marco and Coelho (2004) | Agriculture | Self-compatible | Tropical | Fleshy | Woody | Crop |
| *Petunia × hybrida* | Surfinia® Hot Pink | Solanaceae | Italy | Brittain et al. (2010) | Agriculture | Self-compatible | Temperate | Dry | Herbaceous | Non-crop |
| *Eulophia alta* | | Orchidaceae | Brazil | Jurgens et al. (2009) | Burn | Self-compatible | Tropical | Dry | Herbaceous | Non-crop |
| *Satureja thymbra* | | Lamiaceae | Israel | Potts et al. (2001) | Burn | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Asphodelus ramosus* | | Liliaceae | Israel | Ne'eman et al. (2000) | Burn | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Salvia fruticosa* | | Lamiaceae | Israel | Ne'eman et al. (2000) | Burn | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Satureja thymbra* | | Lamiaceae | Israel | Ne'eman et al. (2000) | Burn | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Phlomis viscosa* | | Lamiaceae | Israel | Ne'eman et al. (2000) | Burn | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Melampyrum pratense* | | Scrophulariaceae | Norway | Totland et al. (2006) | Deforestation | Self-compatible | Temperate | Dry | Herbaceous | Non-crop |
| *Elaeocarpus ganitrus* | Rudraksh | Elaeocarpaceae | India | Khan et al. (2005) | Deforestation | Self-compatible | Tropical | Fleshy | Woody | Non-crop |
| *Shorea siamensis* | | Dipterocarpaceae | Thailand | Ghazoul et al. (1998) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Acacia dealbata* | | Mimosaceae | Australia | Broadhurst and Young (2006) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Anacardium excelsum* | | Dipterocarpaceae | Costa Rica | Ghazoul and McLeish (2001) | Deforestation | Self-compatible | Tropical | Fleshy | Woody | Non-crop |
| *Lantana camara* | | Verbanaceae | Uganda | Totland et al. (2005) | Deforestation | Self-incompatible | Tropical | Fleshy | Woody | Non-crop |
| *Lonicera maackii* | Amur honeysuckle | Caprifoliaceae | USA | Goodell et al. (2010) | Deforestation | Self-compatible | Temperate | Fleshy | Woody | Non-crop |
| *Curculigo orchioides* | Kalo musali | Hypoxidaceae | Nepal | Shrestha et al. (2011) | Deforestation | Unknown | Tropical | Fleshy | Herbaceous | Non-crop |
| *Coffea arabica* | Highland coffee | Rubiaceae | Costa Rica | Ricketts et al. (2004) | Deforestation | Self-compatible | Tropical | Fleshy | Woody | Crop |
| *Lapageria rosea* | | Philesiaceae | Chile | Valdivia et al. (2006) | Deforestation | Self-compatible | Temperate | Fleshy | Woody | Non-crop |
| *Ilex verticillata* | | Aquifoliaceae | USA | Tewksbury et al. (2002) | Deforestation | Self-incompatible | Temperate | Fleshy | Woody | Non-crop |
| *Diospyros montana* | | Ebenaceae | India | Somanathan and Borges (2000) | Deforestation | Self-incompatible | Tropical | Fleshy | Woody | Non-crop |
| *Ceiba aesculifolia* | | Bombaceae | Mexico | Quesada et al. (2004) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Ceiba grandiflora* | | Bombaceae | Mexico | Quesada et al. (2004) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Ceiba grandiflora* | | Bombaceae | Mexico | Quesada et al. (2003) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Senna artemisioides* | | Caesalpiniaceae | Australia | Cunningham (2000) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Acacia brachybotrya* | | Mimosaceae | Australia | Cunningham (2000) | Deforestation | Self-compatible | Tropical | Fleshy | Woody | Non-crop |
| *Eremophila glabra* | | Myoporaceae | Australia | Cunningham (2000) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Dianella revoluta* | | Phormiaceae | Australia | Cunningham (2000) | Deforestation | Self-compatible | Tropical | Fleshy | Herbaceous | Non-crop |

**Table 1** (*continued*)

72

| Name-latin | Name-common | Family | Location | Authors | Disturbance type | Mating system | Biome | Fruit type | Growth form | Crop potential |
|---|---|---|---|---|---|---|---|---|---|---|
| *Heliconia acuminata* | | Heliconiaceae | Brazil | Bruna and Kress (2002) | Deforestation | Self-incompatible | Tropical | Fleshy | Herbaceous | Non-crop |
| *Cestrum parqui* | | Solanaceae | Argentina | Aguilar and Galetto (2004) | Deforestation | Self-incompatible | Temperate | Fleshy | Woody | Non-crop |
| *Cassia aphylla* | | Fabaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Cercidium australe* | | Fabaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Tillandsia ixioides* | | Bromeliaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Acacia aroma* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Acacia atramentaria* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Fleshy | Woody | Non-crop |
| *Acacia furcatispina* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Acacia praecox* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Atamisquea emarginata* | | Capparaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Caesalpinia gilliesi* | | Fabaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-compatible | Tropical | Dry | Herbaceous | Non-crop |
| *Justicia squarrosa* | | Acanthaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-compatible | Tropical | Fleshy | Herbaceous | Non-crop |
| *Ligaria cuneifolia* | | Loranthaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Mimosa detinens* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Fleshy | Woody | Non-crop |
| *Opuntia quimilo* | | Cactaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Prosopis nigra* | | Mimosaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Fleshy | Herbaceous | Non-crop |
| *Rhipsalis lumbricoides* | | Cactaceae | Argentina | Aizen and Feinsinger (1994) | Deforestation | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Peraxilla tetrapetala* | New Zealand mistletoe | Loranthaceae | New Zealand | Kelly et al. (2000) | Deforestation | Self-compatible | Temperate | Fleshy | Herbaceous | Non-crop |
| *Phaius delavayi* | | Orchidaceae | China | Huang et al. (2009) | Human use | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Ponerorchis chusua* | | Orchidaceae | China | Huang et al. (2009) | Human use | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Sabatia kennedyana* | Plymouth gentian | Gentianaceae | Canada | Trant et al. (2010) | Human use | Self-compatible | Temperate | Dry | Herbaceous | Non-crop |
| *Primula elatior* | | Primulaceae | Belgium | Van Rossum et al. (2002) | Human use | Self-incompatible | Temperate | Dry | Herbaceous | Non-crop |
| *Lupinus sulphureus* ssp. *kincaidii* | Kincaid's lupine | Fabaceae | USA | Severns (2003) | Human use | Self-incompatible | Temperate | Dry | Herbaceous | Non-crop |
| *Vincetoxicum hirundinaria* | | Asclepiadaceae | Finland | Leimu and Syrjanen (2002) | Human use | Self-incompatible | Temperate | Dry | Herbaceous | Non-crop |
| *Prosopis flexuosa* | | Fabaceae | Argentina | Aschero and Vazquez (2009) | Livestock | Self-incompatible | Temperate | Dry | Woody | Non-crop |
| *Pedicularis palustris* ssp. *palustris* | | Scrophulariaceae | Germany | Schmidt and Jensen (2000) | Livestock | Self-compatible | Temperate | Dry | Herbaceous | Non-crop |
| *Enterolobium cyclocarpum* | Guanacaste | Fabaceae | Costa Rica | Rocha and Aguilar (2001) | Livestock | Self-compatible | Tropical | Dry | Woody | Non-crop |
| *Pachira quinata* | | Bombaceae | Costa Rica | Fuchs et al. (2003) | Livestock | Self-incompatible | Tropical | Dry | Woody | Non-crop |
| *Anemone coronaria* | | Ranunculaceae | Israel | Perevolotsky et al. (2011) | Livestock | Self-incompatible | Tropical | Dry | Herbaceous | Non-crop |
| *Ruschia robusta* | | Mesembryanthemaceae | South Africa | Riginos and Hoffman (2003) | Livestock | Unknown | Tropical | Dry | Woody | Non-crop |
| *Cheiridopsis denticulata* | | Mesembryanthemaceae | South Africa | Riginos and Hoffman (2003) | Livestock | Self-incompatible | Tropical | Dry | Woody | Non-crop |

Rosenthal (1994), and Borenstein (2009)). If none of these measures were obtainable from the text, study authors were contacted for the missing data, with eight out of 11 authors replying.

All data points were categorized by disturbance type, as described above, and analyzed using a random effects meta-analysis model in R (R Development Core Team, 2012), employing the *metagen* function within the meta package (Schwarzer, 2012). Unlike a fixed effects meta-analysis, a random effects meta-analysis does not assume that all studies have equal variances, and is therefore a more appropriate model for data that includes ecological studies (Borenstein et al., 2009). The effects of disturbance were considered significant if the 95% confidence intervals of the effect size (Hedges' *d*) did not overlap with zero. Q-statistics were used to examine the heterogeneity of effect sizes, in order to determine whether there was more variance present than would be expected by chance. Heterogeneity was examined both among the disturbance categories and over all of the data points.

In subsequent analyses performed in order to determine plant life history traits that might be indicative of a particular susceptibility to habitat disturbance, the data points were categorized by plant mating system (self-compatible or self-incompatible), biome (tropical or temperate), fruit type (fleshy or dry), growth form (woody or herbaceous), and crop species or not (shown in Table 1). When possible, these life history traits were taken from the species descriptions given in the original studies. If the information was not available in the original study, the life history traits were obtained through a literature search. We were unable to locate mating system information for six plant species, resulting in a data set of 66 independent data points for this analysis. All data was analyzed using random effects meta-analysis models as described above.

## 2.5. Publication bias testing

Before making inferences from a meta-analysis it is important to consider publication bias: if studies showing significant effects are accepted for publication more often than studies showing non-significant results, a meta-analysis of published studies will reflect only part of the actual pattern (Dickerson, 1990). We tested for publication bias using visual inspection of funnel plots, Spearman's rank correlation testing between effect size and sample size (Begg, 1994), and Rosenberg's fail-safe number estimates. The fail-safe number, calculated using Rosenberg's (2005) calculator, estimates the number of non-significant unpublished studies that would be necessary to nullify the overall results of the analysis (Rosenthal, 1979).

## 3. Results

### 3.1. Overall habitat disturbance and disturbance type

Overall, habitat disturbance had a significant, negative impact on plant reproductive success ($z = -4.0224$, $p = <0.0001$; Fig. 1a). All disturbance types were associated with a reduction in fruit set; however, only disturbances categorized as fire or livestock were associated with statistically significant lower fruit set than the control (group means and 95% confidence intervals not overlapping zero; Fig. 1a). The data exhibited significant total heterogeneity in their response ($Q_{total} = 722.71$, $p = <0.0001$), indicating the presence of further explanatory variables in the dataset (Hedges and Olkin, 1985). We also found significant heterogeneity among the disturbance types ($Q_{between} = 24.01$, $p = <0.0001$), confirming that significant differences exist among some of the categories.

### 3.2. Mating systems

A smaller data set, used to assess species for which we found information on mating system ($n = 66$), also revealed an overall negative impact of habitat disturbance on plant reproductive success ($z = -3.7308$, $p = 0.0002$; Fig. 1b). Self-incompatible plants exhibited significantly reduced fruit set in disturbed habitats, whereas self-compatible plants exhibited a negative, but non-significant, effect of disturbance on fruit set (Fig. 1b). Again, the data exhibited significant heterogeneity ($Q_{total} = 714.38$, $p = <0.0001$); however, there was no significant difference in the response of self-compatible and self-incompatible species to disturbance ($Q_{between} = 1.30$, $p = 0.255$).

### 3.3. Biome

A tropical habitat was associated with a significant, negative impact of disturbance on fruit set; plant species in temperate habitats experienced a negative, but non-significant response to disturbance (Fig. 1c). Indeed, significant heterogeneity was seen between the temperate and tropical biome groups ($Q_{between} = 3.75$, $p = 0.05$). Plants with different mating systems were evenly represented, but the observed effect of plant mating system on fruit set varied between the two biomes. Both self-incompatible and self-compatible species within the tropical biome showed significant effects of disturbance on fruit set, however there was no significant difference between these two groups ($Q_{between} = 1.31$, $p = 0.252$; Fig. 1d). In the temperate biome, self-incompatible species exhibited a significant, negative effect of disturbance on fruit set whereas, intriguingly, self-compatible species exhibited a significant, positive effect of disturbance on fruit set ($Q_{between} = 9.06$, $p = 0.003$, Fig. 1d).

### 3.4. Fruit type

Plants with dry fruits exhibited a significant decline in fruit set in response to disturbance, whereas the impact of disturbance on plants with fleshy fruits did not significantly differ from zero (Fig. 1e). In accordance with this, we detected significant heterogeneity between the two fruit types ($Q_{between} = 7.35$, $p = 0.007$).

### 3.5. Growth form and crop potential

Plant species with a woody growth form and plant species with a herbaceous growth form both experienced a decrease in fruit set in response to disturbance, and no significant differences were detected in terms of the magnitude of response ($Q_{between} = 0.1$, $p = 0.748$). Conversely, non-crop plant species exhibited a significant decline in fruit set in response to disturbance, whereas plants being grown as crops did not. There were, however, no significant differences between these two groups ($Q_{between} = 0.8$, $p = 0.371$).

### 3.6. Publication bias

A visual inspection of a funnel plot of the data suggests no publication bias, as evidenced by the presence of data points around the effect size of zero, indicating that studies with small effect sizes have been included in the analysis (Fig. 2). A Spearman's rank correlation demonstrated that there was no statistically significant correlation between sample size and effect size of the studies included in the meta-analysis ($\rho = 0.203$, $p = 0.087$). Rosenberg's fail-safe number indicated that 28 unpublished non-significant studies would be needed to nullify the overall results of this meta-analysis. The dataset includes 32 studies reporting non-significant results, suggesting that a lack of significant results has not seriously impeded publication on this topic.
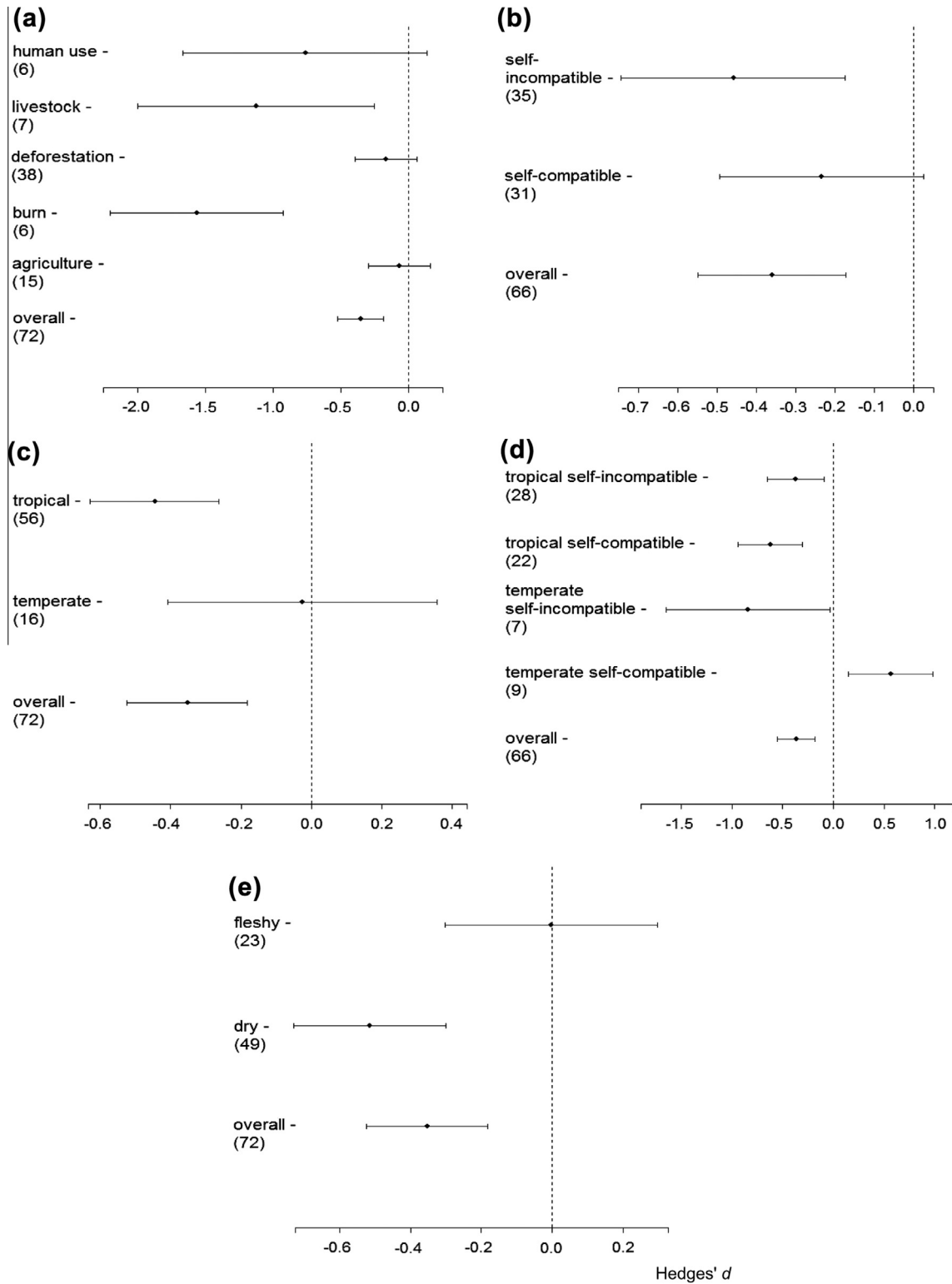
**Fig. 1.** Effect sizes of habitat disturbance on fruit set in animal pollinated plants grouped by: (a) disturbance category, (b) plant mating system, (c) biome, (d) plant mating system with biome, and (e) fruit type. Horizontal bars represent 95% confidence intervals. Numbers in parentheses indicate the number of data points in each grouping.

## 4. Discussion

Our study demonstrates that a wide diversity of familiar forms of habitat disturbance are associated with a significant loss of fruit set in animal-pollinated plants (Fig. 1a). This finding, which, to our knowledge, represents the first quantitative synthesis of the topic,

is consistent with previous studies that have documented negative impacts of disturbance on the abundance and diversity of pollinator species (Ricketts et al., 2008; Williams et al., 2010; Winfree et al., 2009) and plant reproductive success (Aguilar et al., 2006). Combined with evidence of a worldwide decline in native pollinator populations (Biesmeijer et al., 2006; Potts et al., 2010; Levy,
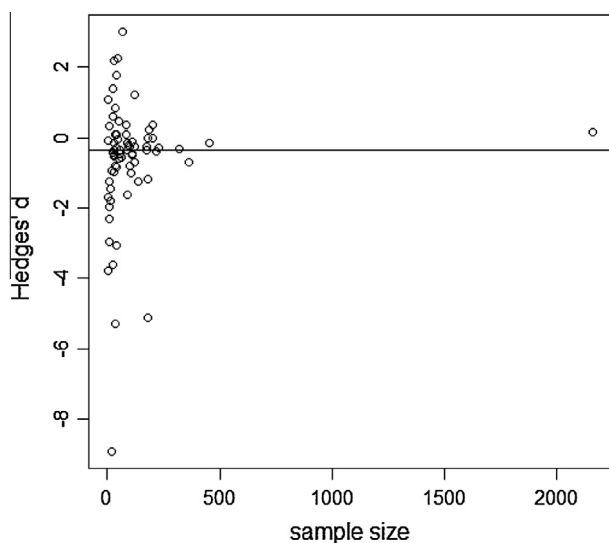
**Fig. 2.** Funnel plot of effect size (Hedges' $d$) and sample size. The solid horizontal line represents the mean effect size of all data points.

2011), our results suggest that animal-pollinated plants, many of which are human food crops, are facing some danger from habitat disturbance. This is especially important because habitat disturbance, whether natural or anthropogenic, is likely to increase in magnitude and frequency, due to increasing extreme weather events linked to climate change (Opdam and Wascher, 2003) as well as increasing human population size (Vitousek et al., 1997).

The overall effect of habitat disturbance on fruit set (weighted-mean effect size = −0.3521) is small to medium, using a scale where small effect sizes are ⩽0.20 and medium effect sizes are ⩽0.50 (Cohen, 1977). Smaller effect sizes are not uncommon in studies carried out using natural systems, such as those included in our analysis, because of the difficulty in controlling for extraneous variables in natural environments (Cohen, 1977). Aguilar et al. (2006) found a greater effect size in their study of the impacts of habitat fragmentation on plant reproductive success (overall Hedges' $d$ = −0.608). However, their response variable combined both fruit set and seed set; seed set being a more fine-scale measurement of reproductive success than fruit set (Fenner and Thompson, 2005). In a supplementary meta-analysis using the data set from Aguilar et al. (2006), we tested for differences in effect sizes detected between fruit set and seed set measures, and confirmed that fruit set exhibits greater variation in effect size than seed set. Fruit set could be regarded as a more conservative measure of the impact of disturbance on reproductive success.

While the overall effect of habitat disturbance on fruit set in our study was negative, the magnitude of the effect size varied considerably with disturbance type. Specifically, disturbance due to livestock and fire were associated with a significant decline in fruit set, in spite of their relatively low sample size, suggesting that the negative effects were consistent across the variety of studies. In contrast, the effects of disturbance due to human use, agriculture, and deforestation categories were only weakly negative (Fig. 1a). Winfree et al. (2009) subdivided their habitat loss category into extreme and moderate habitat loss cases. In their study, the negative impact of habitat loss on pollinator abundance and diversity was amplified in cases of extreme habitat loss. If the pattern of greater effects under extreme disturbance is applicable to fruit set in animal-pollinated plants, it is possible that studies of disturbance via fire and livestock detected a greater effect of disturbance because they were carried out in more extreme disturbance environments. We note that although the results for the human use, agriculture, and deforestation categories were not significantly different from

zero, the mean weighted effect size for each category did fall below zero. It should also be noted that studies considering both fire and livestock usually measure fruit set directly within the disturbance area, whereas studies looking at deforestation or agriculture often measure fruit set in habitats adjacent to the disturbance area. In our dataset, all studies in the fire and livestock data categories ($n$ = 13) recorded the fruit set of plants within the disturbance area, while 48 out of 59 of the studies in other categories recorded fruit set of plants in areas adjacent to the disturbed area. A supplemental analysis confirmed that studies that recorded fruit set of plants found within the disturbed area exhibited a significantly more negative effect of disturbance on fruit set compared to studies of plants adjacent to the disturbance area ($Q_{between}$ = 7.6, $p$ = 0.006). A direct disturbance to the study plants would be expected to have a greater impact than a disturbance in a nearby area, and this difference may help explain the variation among the disturbance categories. In that case, preservation of remnant habitat patches in the vicinity of areas slated for disturbance activities may be an important conservation strategy because the negative effects of the disturbance on fruit set could be mitigated by distance from the actual site of disturbance.

The overall effect of habitat disturbance on fruit set (mean Hedges' $d$ = −0.3521; Fig. 1a) in the present study is similar in size to the effect of habitat disturbance on wild bee abundance (mean Hedges' $d$ = -0.32) and bee species richness (mean Hedges' $d$ = −0.37) reported by Winfree et al. (2009). The similarity of our effect size suggests that declines in pollinator abundance and richness may be a factor in the lower fruit set found in certain disturbed habitats. We indirectly examined the association between pollination services and the response to habitat disturbance by examining the impact of disturbance on fruit set in the context of a species' mating system. We found that habitat disturbance is associated with a decline in fruit set in self-incompatible plants, but not in self-compatible plants (Fig. 1b). One interpretation of this result is that fruit set in self-incompatible plants is more sensitive to habitat disturbance because these species require a pollinator for fruit set. In contrast, self-compatible plants are able to set fruit without a pollinator, and may therefore be less sensitive to a decline in pollinator services that may be associated with habitat disturbance. However, we note that both categories exhibited large confidence intervals and that the mean effect sizes for the two groups were not significantly different from one another (Fig. 1b). This finding is similar to those reported by two previous studies of the effects of disturbance with respect to plant mating systems (Aizen et al., 2002; Ghazoul, 2005). On the other hand, Aguilar et al. (2006) found that habitat fragmentation was associated with a greater decline in plant reproductive success in studies of self-incompatible species when compared to studies of self-compatible species. As discussed earlier, this may reflect the fact that subtle differences attributable to mating system may be more readily detected in seed set than fruit set (Fenner and Thompson, 2005).

Plant species in tropical biomes exhibited a significant, negative effect of disturbance on fruit set, whereas plant species in temperate biomes did not (Fig. 1c). When analyzed separately, plant mating system was a significant factor in the response of fruit set to disturbance in temperate biomes, but not in tropical biomes (Fig. 1d). Tropical ecosystems have higher species richness than temperate areas, which has been linked to higher pollen limitation for species with biotic pollination (Vamosi et al., 2006). Plants already experiencing high levels of pollen limitation could be more susceptible to disturbance than those with lower levels of pollen limitation, potentially explaining the difference in the effect of disturbance on fruit set in these two biomes. Intriguingly, we found a statistically significant positive impact of disturbance on the fruit set of self-compatible species in temperate regions. Temperate

areas of the globe have historically been more subject to human-caused disturbances than tropical areas (Hannah et al., 1995). As such, the plants in these regions, especially self-compatible plants with their reduced reliance on outside pollinators, may be adapted to live in disturbed areas. It is also possible that the effect seen is an artifact of the relatively small sample of studies from the temperate biome ($n = 16$).

Plant species with dry fruits exhibited a significantly greater reduction in fruit set in response to habitat disturbance than plants with fleshy fruits (Fig. 1e). It is difficult to interpret this result in terms of pollination; this trait may in fact be responding due to its correlation with other plant traits. No significant differences in fruit set were seen among species exhibiting different growth forms or between crop and non-crop plant species. Crop species in our dataset exhibited considerably more variation in effect sizes than non-crop species, which is most likely attributable to the much smaller sample size (6 crop species vs. 66 non-crop species). It is interesting to note that the plant species that humans grow for food are not immune to the negative impacts of disturbance, and in fact exhibit a greater mean negative impact of disturbance than do non-crop species.

## 5. Conclusions

We have demonstrated that habitat disturbance, which has been demonstrated to have a detrimental impact on pollinator abundance and diversity, also has important implications for plant reproductive success. Our results indicate not only that habitat disturbance generally has a negative impact on plant reproductive success, but also that most of the categories of disturbance studied exact a toll on fruit set, although there is a high degree of variation in the size of the effect. Two disturbance types, those related to fire and those related to the presence of livestock, were especially likely to be associated with a reduction in plant fruit set.

We also explored the role of plant mating system, biome, fruit type, growth form, and whether the species is a crop on the response of fruit set to habitat disturbance. Using these commonly reported plant traits, we can now better predict the possible severity of disturbance on fruit set on native and commercial species. Plants growing in disturbed habitat in tropical biomes experienced a greater reduction in fruit set than those in disturbed habitat in temperate biomes. Within the temperate biome, self-incompatible plants experienced a greater reduction in fruit set than self-compatible plants. Plants with dry fruit types experienced a greater reduction in fruit set than those with fleshy fruit types. Conversely, growth form (woody vs. herbaceous), and crop potential (crops vs. non-crop species) were not a reliable predictor of the magnitude of the impacts of habitat disturbance on fruit set.

While the overall negative impact of habitat disturbance on fruit set indicates that minimizing habitat disturbance would likely benefit all plant species, future conservation efforts would be best focused on disturbance types that directly impact the focal plant species, such as fire or the presence of livestock. Moreover, species native to tropical biomes, self-incompatible species that are native to temperate biomes, and species possessing dry fruit types were particularly likely to suffer a reduction in fruit set in the face of disturbance. Any combination of these traits in one species might merit more concern than a single factor because of the potential for compounding effects. By focusing our conservation efforts, we can better manage the effects of disturbance on the most vulnerable plant populations.

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