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Cover image: A generalist native pollinator *Bombus terrestris* visiting an introduced plant species *Hedysarum coronarium* in the Balearic Islands, Spain. See Montero-Castaño & Vilà, pp. 884–893. Photo: Ana Montero-Castaño.

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- Analysis of a negative plant–soil feedback in a subtropical monsoon forest
- Home site advantage in two long-lived arctic plant species
- Impact of landscape alteration and invasions on pollinators
- Gender and abiotic stress affect facilitation and its costs
- Genetic variation in anti-herbivore chemical defenses in invasive plants

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Impact of landscape alteration and invasions on pollinators: a meta-analysis

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Summary

1. Alterations in land use and biological invasions are two major components of global change that threaten biodiversity. There is high concern about their impact on pollinators and the pollination services they provide. However, the growing literature shows different, even contradictory results.

2. We present a global meta-analysis of 58 publications reporting 143 studies (37 on landscape alteration and 21 on biological invasions) to assess the extent to which these components affect pollinators, and whether taxonomic and ecosystem-type differences in pollinator responses occur. We also quantified which component of landscape alteration had the largest effect on pollinators and assessed whether animal invasions differ from plant invasions in their effect on native pollinators.

3. Habitat alteration and invasions affected pollinators to the same magnitude by decreasing visitation rates. Vertebrates in altered landscapes and insects (excluding bees) in invaded areas were the most affected pollinator taxa.

4. Pollinator abundance was more reduced in altered forest ecosystems than in altered grasslands; while the reverse pattern was found for pollinator richness. However, the response of pollinators to invasions was independent of ecosystem type.

5. Disturbance of the surrounding matrix was more important in decreasing pollinator visitation rates than fragment size.

6. Invasive animals seemed to have a more consistent negative effect on visitation rates than invasive plants.

7. *Synthesis*. Our study highlights that different components of global change have similar negative outcomes on pollination patterns, but that responses of pollinators vary among taxa and ecosystem types, as well as the attributes of landscape alteration considered and whether the invader is an animal or a plant.

Key-words: alien species, global change, habitat fragmentation, invasion ecology, land use change, plant–animal interactions, pollination

Introduction

Among the different components of global change, landscape alteration and biological invasions are, in certain regions, the major causes of the biodiversity crisis (Wilcove *et al.* 1998; Sala *et al.* 2000; Secretariat of the Convention on Biological Diversity 2010). These components of global change decrease species diversity and disrupt biotic interactions (Tylianakis *et al.* 2008). For example, there is high concern regarding the impact these factors pose on pollinators and on the ecosystem service they provide (Buchmann & Nabhan 1996; Biesmeijer *et al.* 2006; Goulson, Lye & Darvill 2008; Carvalheiro *et al.* 2010; Potts *et al.* 2010). Changes in pollinator abundance, richness

and behaviour might also have important consequences for the persistence of many flowering plants. Approximately, 300 000 plant species around the world rely on pollinators for their sexual reproduction (Kearns, Inouye & Waser 1998; Ollerton, Winfree & Tarrant 2011), including different crops that as a whole constitute 35% of global food production (Klein *et al.* 2007).

Landscape alteration implies habitat fragmentation, habitat loss (i.e. reduction in the total amount of the habitat), habitat isolation and modification of the structure of the landscape. Landscape alteration can affect pollinators in several different ways. First, it can change the availability of food resources. The response of pollinators to the reduction and isolation of their food resources depends on their diet breadth, foraging range, longevity and migration capability (Rathcke & Jules

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1993; Winfree, Bartomeus & Cariveau 2011). Second, the availability of nesting sites and larval host plants (Cane 2001; Winfree, Bartomeus & Cariveau 2011) can be modified. Finally, the response of pollinators to landscape alteration might be influenced indirectly by changes in the presence, abundance or behaviour of parasites and predators (Rathcke & Jules 1993).

Alien species can become invasive and cause impacts on native species, communities and ecosystem processes (Levine *et al.* 2003). Their presence can affect pollinators in different ways depending on the type of alien organism, which can be another pollinator, an herbivore, a pollinator's predator or parasite, or an animal-pollinated plant (Traveset & Richardson 2006). For example, an invasive plant species can increase the floral resources offered and be included in the diet of generalist pollinators (Memmott & Waser 2002; Vilà *et al.* 2009). In contrast, an alien pollinator can compete for the same resources as the native pollinators to the detriment of the latter (Bjerknes *et al.* 2007).

Therefore, studies that address the effects of landscape alteration and invasions on pollinators show mixed and even contradictory results. Moreover, these global change components are not independent and their effects can be additive, synergic or even antagonist (Sala *et al.* 2000; Didham *et al.* 2005, 2007). The growing literature addressing their effect on pollination suggests that it is an opportune time to synthesize the available information to establish whether there is a clear pattern of global pollination decline. Meta-analysis techniques provide a quantitative tool for conducting such a synthesis (Rosenberg, Adams & Gurevitch 2000). Some recent reviews have already relied on meta-analysis to evaluate whether the effect of fragmentation on the pollination and reproduction of plants differs depending on plant reproductive traits (Aguilar *et al.* 2006); the effect of alien plants on pollination and seed set of neighbouring native plants (Morales & Traveset 2009); and the influence of landscape disturbances on bees (Winfree *et al.* 2009). Apart from the latter, most effort has focused on the impact on plants and not on pollinators. Moreover, Winfree *et al.* (2009) explored only bees, and while they are the most studied pollinators, they are not the only ones. Other insect taxa and vertebrates, such as birds, bats, small mammals and even lizards, are reported to be efficient pollinators as well (Olesen & Valido 2003; Quesada *et al.* 2003; Rodríguez-Rodríguez & Valido 2008).

A review of the overall effect of the different components of landscape alteration and biological invasions from the pollinators' perspective is lacking. In this study, we address the following questions: (i) Do landscape alteration and biological invasions affect pollinators? (ii) Are there taxonomic differences in pollinator responses to these global change components? (iii) Do the effects differ among ecosystem types? (iv) Do results differ between observational and experimental studies? (v) Which component of landscape alteration affects pollinators the most? (vi) Do animal invasions differ from plant invasions in their effect on native pollinators?

Materials and methods

LITERATURE SEARCH AND DATA EXTRACTION

To survey the published literature on the effect of landscape alteration and alien species on pollinators, we conducted a search using the ISI Web of Science data base up to August 2010 using the keyword combinations (pollinat* AND invas*), (pollinat* AND alien), (pollinat* AND fragm*) and (pollinat* AND habitat loss). In the literature, it is common to find the term 'habitat fragmentation' referring to the wider concept of landscape alteration instead of exclusively the breaking apart of the habitat (Fahrig 2003; Holzschuh, Steffan-Dewenter & Tscharntke 2010). Therefore, many of the matches for the keyword combination (pollinat* AND fragm*) referred to other landscape alteration components and not habitat fragmentation *per se*. We also screened the reference lists from all retrieved papers for other relevant publications. Only field observational or experimental studies were considered, excluding predictive modelling and anecdotal observations. As response variables we considered pollinator abundance, pollinator species richness and visitation rates to flowers, regardless of whether they referred to the whole pollinator community or to specific pollinator taxa.

For studies on landscape alteration, we classified them depending on the landscape characteristic explored: fragment and/or plant population size (small versus large) and nature of the surrounding matrix (disturbed versus nondisturbed or continuous). In studies on biological invasions, we distinguished whether the invader was a plant or an animal. Only the presence/absence of the invasive species was considered. Therefore, the independent variables were categorical with two levels: control and treatment groups. For studies on landscape alteration, control groups were those with the largest fragments, largest population sizes, closest to other fragments of the same cover type or to continuous habitats and fragments with the least disturbed surrounding matrices. For studies on invasions, control groups were those with the absence of the invasive species.

In total, we retrieved 207 publications for which the following criteria for data inclusion were adopted:

1 When the effect of invasion or landscape alteration was measured on the same pollinator taxa or community, but in different and independent sites, we included all of them as independent records. When multiple taxa were simultaneously studied, we included all in the data set. An exception to the latter was when the same response variable was measured simultaneously for both the whole pollinator community and specific taxa, in which case the values of the whole community were discarded as they were not independent of those of the specific taxa. A possible criticism of this criterion is the inclusion of pseudo-replicated entries in the data set. This is a problem that meta-analysts continuously face and in this work we aimed at reaching a compromise between avoiding pseudo-replication and not sacrificing too much information, as has been done in previous meta-analyses (Liao *et al.* 2007; Rey-Benayas, Galvan & Carrascal 2010; Vilà *et al.* 2011). We considered that different taxonomic pollinator groups might not necessarily respond similarly to landscape alteration (Klein *et al.* 2002; Brosi *et al.* 2008; Tscheulin *et al.* 2011), or to invasion (Bartomeus, Vilà & Santamaria 2008), and that the response of one single taxonomic group to these components (Jennersten & Nilsson 1993), or the impact of a single invasive species (see Lopezaraiza-Mikel *et al.* 2007; Nienhuis, Dietzsch & Stout 2009) might be context-dependent and therefore not necessarily the same in different sites. Moreover, two of the questions that we address in this work are whether there are taxonomic differences

in the response to these global change components, and whether the responses differ depending on the type of ecosystem altered or invaded, which justifies the inclusion of this kind of entry.

2   In studies on invasions, we only included those in which the response variables were measured on native pollinator communities (i.e. excluding pollinators visiting the alien plant species).

3   When a study was repeated over several years, we took the mean value of the response variable for the whole study period. However, if results were given for each year separately, we only included the data for 1 year to avoid pseudo-replication, despite the high temporal variability described for pollinator communities (Alarcón, Waser & Ollerton 2008; Olesen *et al.* 2008; Petanidou *et al.* 2008). We considered that data gathering would improve and be more accurate with increasing sampling experience. Therefore, unless authors explicitly indicated otherwise, we chose the last year for analysis. If the study was repeated at different time periods separately, we included only the results for the time range with the highest value of the response variable in the control group. Such a time range would be the closest to pollinators' activity optimum and potential differences with treatment groups would be easier to detect.

4   When a study considered the independent variable as a gradient instead of a two-level factor, and replicates of each level existed, only the lowest and highest extreme levels of the gradient were considered. On the other hand, for gradients with numerous and un-replicated levels, we averaged the response variable values for the lowest and highest levels of the gradient.

5   In some studies of landscape alteration, the two independent variables were simultaneously tested (i.e. fragment size and matrix disturbance). We included only the effect of one of the variables keeping constant the other one, and choosing the one with fewer entries in the data set to equilibrate the number of entries per component of landscape alteration.

In total, 58 publications (37 on landscape alteration and 21 on biological invasions) met our primary criteria (see Appendix S1 in Supporting Information). Our data set had 143 entries, 87 on landscape alteration and 56 on invasions (45 on plant invasions and 11 on animal invasions). Sixty refer to impacts on the whole pollinator community, while the remainder (83) refer to specific taxonomic groups, mostly insects, but also birds and bats. To have enough entries of each pollinator taxonomic group, we grouped them as: bees (32), bumblebees (16), other insects (23) and vertebrates (12). For the same reason, ecosystem types were also grouped into three general types: forests (67), shrublands (23) and grasslands (53). Regarding the type of study, 46 were experimental and 97 observational.

Only one of the 58 publications (Bartomeus, Vilà & Steffan-Dewenter 2010, see Appendix S1) simultaneously studied the effect of both global change components and their interaction. Therefore, we could not explore how these global change components act together as we did not have enough entries to include the interaction in the analysis.

META-ANALYSIS

For each response variable, we recorded sample size (*N*), mean and standard deviation (SD) for the control and experimental groups. If standard error (SE) or 95% confidence intervals (CI) were given, we transformed them to SD. When only figures were given, the software DATATHIEF III (Tummers 2006) was used to extract these parameters from the graphs. When necessary, we asked authors for the missing data. In a couple of papers, the exact *N* values were not given, but rather ranges of values. In those cases, we opted for the more conservative solution and chose the lowest *N* values.

For each entry of the data set, we calculated *Hedges'd* as a measure of effect size. *Hedges'd* is an estimate of the standardized mean difference between control and experimental groups that is not biased by small sample sizes and unequal sampling variances (Rosenberg, Adams & Gurevitch 2000).

Hedges'd is a unit-free index that ranges from $-\infty$ to $+\infty$ and estimates the magnitude of the effect and its direction. As in classical statistical analysis, the highest effect sizes are from those studies showing large differences between control and treatment groups. Zero *d* values signify no difference in the response variable between nonaltered and altered plots or between noninvaded and invaded plots. Positive and negative *d* values denote a general trend following landscape alteration or invasion for an increase or a decrease, respectively. *Hedges'd* calculations and statistical analysis were conducted using the METAWIN v2.1 Software (Rosenberg, Adams & Gurevitch 2000).

We first tested whether effect sizes across studies were homogeneous, using the Q_{total} statistic. A significant Q_{total} indicates that the variance among effect sizes is greater than that expected by sampling error alone (i.e. effect sizes are not equal across studies). On the other hand, a non-significant Q_{total} does not preclude the possibility of heterogeneity among studies. To assess the effect of different grouping variables (invasion versus landscape alteration, differences between ecosystem types, pollinator taxonomic groups, etc.), we developed categorical random-effects meta-analysis. These models, unlike fixed-effects models, incorporate a random component in the effect size variation apart from the sampling error; that is, they do not assume a real effect size shared by all studies, which is not likely to be satisfied in ecological studies (Gurevitch & Hedges 1999). For each grouping category, a cumulative effect size (d_{++}) and a 95% confidence interval were calculated. A cumulative effect size is considered significant when its 95% confidence interval does not overlap zero. Confidence intervals were calculated using bias-corrected bootstrap resampling procedures with 3000 iterations from the effect sizes and their non-parametric variances according to Adams, Gurevitch & Rosenberg (1997) for groups of 10 or more entries. For groups with small sample sizes (< 10 entries), bootstrap procedures were not used because they are biased due to resampling from the same small set of values (Bancroft, Baker & Blaustein 2007), and the more conservative parametric 95% confidence interval were used.

For categorical comparisons, we examined the p_{random} values associated with the $Q_{between}$ statistic, which describes the variation in effect sizes that can be attributed to differences between categories. We also tested whether the remaining within-group heterogeneity (Q_{within}) was significant using a chi-square test (Rosenberg, Adams & Gurevitch 2000).

Non-independence of effect sizes and publication bias, two of the more important and frequent problems that arise when doing a meta-analysis (Gurevitch & Hedges 1999) were tested by METAWIN v2.1 Software (Rosenberg, Adams & Gurevitch 2000) (see detailed analysis and results in Appendix S2).

Results

Pollinator abundance was negatively affected by landscape alteration as indicated by $d_{++} = -0.95$, and a CI of mean effect sizes that did not overlap zero. A similar trend was not observed for invasions as CI overlapped zero. Neither landscape alteration nor invasions had a significant effect on pollinator richness. In contrast, both factors reduced

significantly visitation rates (d_{++} = −0.61 and −0.62 for landscape alteration and invasions, respectively) (Fig. 1).

The overall effect of landscape alteration was not significantly different from the effect of biological invasions on pollinators' abundance ($Q_{between}$ = 2.04, p_{random} = 0.19), pollinators' richness ($Q_{between}$ = 0.83, p_{random} = 0.56) or visitation rates ($Q_{between}$ = 0.00, p_{random} = 0.98). This lack of difference is possibly a result of considerable variability in the effect sizes among studies (Table 1).

LANDSCAPE ALTERATION

The effect of landscape alteration was not significantly different depending on whether it was measured for the whole pollinator community or for specific taxa for abundance ($Q_{between}$ = 1.60, p_{random} = 0.15), richness ($Q_{between}$ = 0.12, p_{random} = 0.82) or visitation rates ($Q_{between}$ = 0.22, p_{random} = 0.67). Focusing on specific pollinator taxa, there were only marginally significant differences in visitation rates with vertebrates being most negatively affected (Table 2, Fig. 2).

Except for visitation rates, the effect of landscape alteration on pollinators was dependent on the type of ecosystem (Table 2, Fig. 3). Pollinator abundance decreased significantly in altered forests, but not in altered grasslands. The opposite trend was found for pollinator richness: it was negatively affected in grasslands but not in forests. Visitation rates were negatively affected in both ecosystems.

Pollinator abundance and visitation rates were not significantly different between experimental and observational
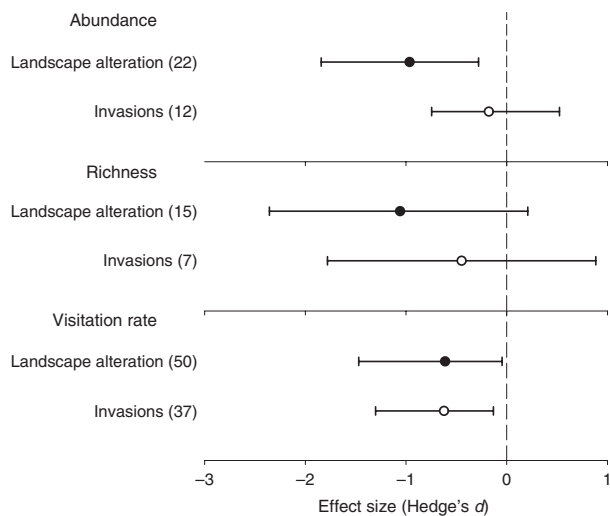

Fig. 1. Overall cumulative effect sizes of landscape alteration (black circles) and invasions (open circles) on pollinators' abundance, richness and visitation rates. The bars around the means denote 95% CI (bias-corrected bootstrap for grouping variables with ≥10 entries and parametric ones for grouping variables with < 10 entries). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than altered and invaded habitats. In brackets, the number of studies for each grouping variable is indicated.

Table 1. Q_{total} and associated P values on the effect of landscape alteration and invasions to pollinator abundance, richness and visitation rates

	Abundance		Richness		Visitation rates	
	Q_{total}	P	Q_{total}	P	Q_{total}	P
Landscape alteration	15.07	0.82	29.24	0.01	41.06	0.78
Invasions	15.91	0.14	6.40	0.38	62.59	< 0.01

studies. However, despite this lack of significance, abundance was found to be negatively affected in observational but not in experimental studies (Table 2). We could not compare pollinator richness because only one study was experimental.

Pollinator visitation rates were affected differently depending on the component of landscape alteration considered. Matrix disturbance had a significant negative effect on visitation rates, while the reduction in fragment size did not (Table 2, Fig. 4).

BIOLOGICAL INVASIONS

The effect of biological invasions on pollinator abundance did not differ whether it was measured on the whole pollinator community or on specific taxonomic groups ($Q_{between}$ = 3.67, p_{random} = 0.13). However, there were significant differences in pollinator richness ($Q_{between}$ = 31.88, p_{random} = 0.03). Pollinator richness of particular taxa was negatively affected by invasions (d_{++} = −1.60, CI = −2.69 to −0.51, N = 3), while no effect was found on the whole community (d_{++} = 0.42, CI = −0.38 to 1.23, N = 4). Visitation rates were not differently affected whether they were measured for the whole pollinator community or only for specific taxa ($Q_{between}$ = 2.43, p_{random} = 0.25) possibly because there was large variation in the effect sizes within each grouping category (Q_{within} = 60.69, P = 0.01). While visitation rates in bees were not affected consistently, visitation rates of other insects decreased with invasion (Fig. 5).

The effect of invasions was not ecosystem-dependent (i.e. forest, grassland or shrubland) for either abundance or visitation rates (Table 2, Fig. 6), but for the latter, heterogeneity within studies was significant (Q_{within} = 59.49, P < 0.01). Pollinator abundance decreased with invasion in observational studies but did not in experimental studies (Table 2). As with landscape alteration, these analyses could not be conducted for pollinator richness due to the small sample size.

Whether the invasive organism was an animal or a plant did not affect differently pollinator visitation rates (Table 2, Fig. 7) possibly due to the large variation in the effect sizes within each grouping category (Q_{within} = 57.32, P = 0.01). While visitation rates decreased in habitats invaded by animals, a nonconsistent effect for invasive plants was found. Differences between plant and animal invasions could not be compared for pollinator abundance and richness because of the scarcity of studies on animal invaders.

Table 2. Meta-analysis of the effect of landscape alteration and biological invasions on pollinator abundance, richness and visitation rates for each grouping variable considered. For each grouping variable, $Q_{between}$ and p_{random} are given. Some analysis could not be conducted due to small sample sizes

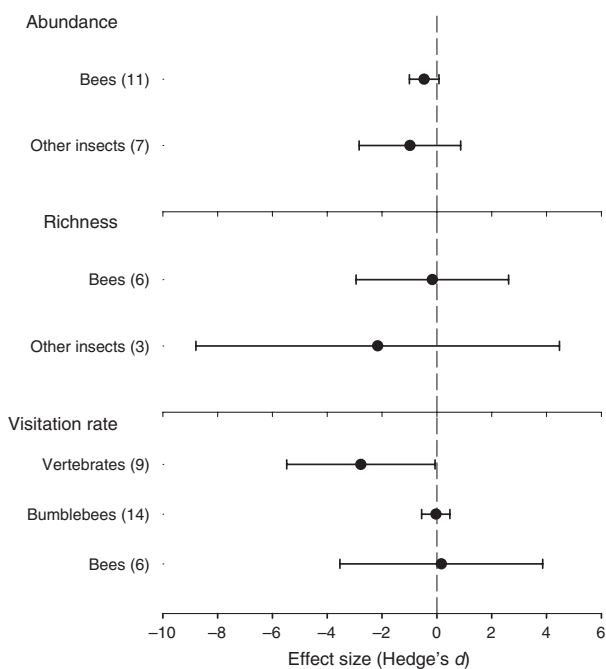|	Categorical variable	Levels	Abundance		Richness		Visitation rates	
			$Q_{between}$	p_{random}	$Q_{between}$	p_{random}	$Q_{between}$	p_{random}
Landscape alteration	Pollinator taxa	Bees	1.05	0.20	1.12	0.47	4.12	0.05
		Other insects						
		Bumblebees						
		Vertebrates						
	Type of study	Observational	2.26	0.09	–	–	0.21	0.67
		Experimental						
	Type of ecosystem	Forest	5.74	0.01	22.82	0.01	1.95	0.19
		Grassland						
	Component of landscape alteration	Fragment size	–	–	–	–	7.12	0.02
		Matrix disturbance						
Invasions	Pollinator taxa	Bumblebees	–	–	–	–	15.65	0.01
		Bees						
		Other insects						
	Type of study	Observational	7.36	0.04	–	–	0.29	0.69
		Experimental						
	Type of ecosystem	Forest	0.96	0.70	–	–	3.97	0.34
		Grassland						
		Shrubland						
	Type of invader	Plant	–	–	–	–	5.66	0.06
		Animal						

Fig. 2. Overall cumulative effect sizes of landscape alteration on pollinators' abundance, richness and visitation rates depending on the taxonomical group they belong to. The bars around the means denote 95% CI (bias-corrected bootstrap for grouping variables with ≥10 entries and parametric ones for grouping variables with < 10 entries). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than altered habitats. In brackets, the number of studies for each grouping variable is indicated.

Discussion

The magnitude of the impact of landscape alteration and biological invasions on pollinators was similar. Across studies, there was a consistent negative effect of both components of global change on visitation rates. Landscape alteration also decreased pollinator abundance.

However, we could not explore how these global change components interact due to the limited number of publications that simultaneously examine both components. Didham *et al.* (2007) reviewed the literature available on the effect of invasions and habitat modification on biodiversity and also found that only 1.2% of these publications considered both global change components (and not necessarily their interaction). Despite the scarcity of studies, there is direct (see Bartomeus, Vilà & Steffan-Dewenter 2010) and indirect (e.g. Aizen & Feinsinger 1994; Brosi *et al.* 2008) evidence for interactions between landscape alteration and invasions. These interactions are not necessarily additive but rather synergistic or antagonistic (Sala *et al.* 2000; Didham *et al.* 2005, 2007). Realistic and robust projections of the future of pollinator communities will require improved understanding about interactions among these (and others) global change components (Sala *et al.* 2000).

TAXONOMICAL DIFFERENCES

Visitation rates by vertebrate pollinators (birds and bats) was the factor most affected by landscape alteration. Response differences between vertebrates and insects might be due to
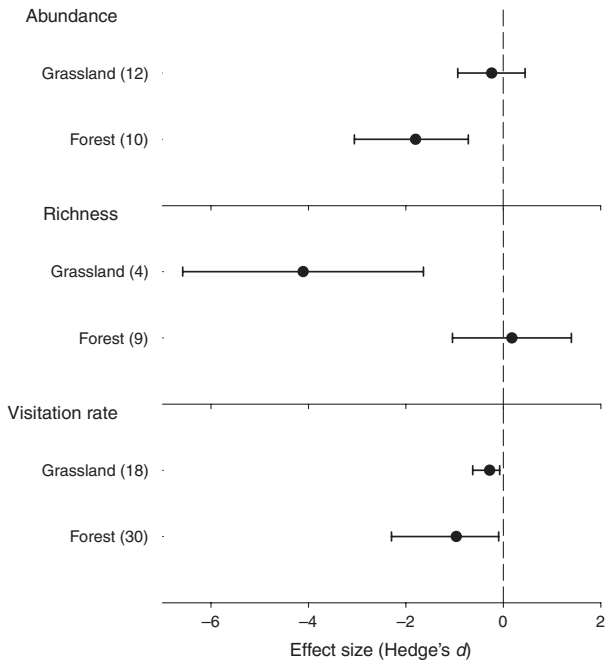
Fig. 3. Overall cumulative effect sizes of landscape alteration on pollinators' abundance, richness and visitation rates depending on the type of ecosystem altered. The bars around the means denote 95% CI (bias-corrected bootstrap for grouping variables with ≥10 entries and parametric ones for grouping variables with <10 entries). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than altered habitats. In brackets, the number of studies for each grouping variable is indicated.
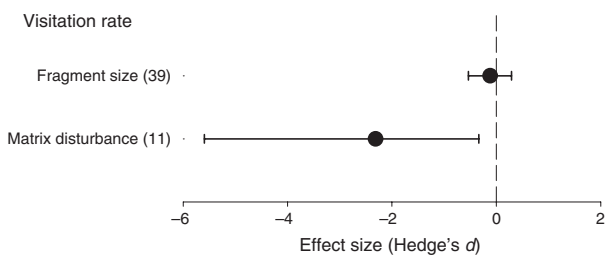

Fig. 4. Overall cumulative effect sizes of different components of landscape alteration on pollinators' visitation rates. The bars around the means denote 95% CI (bias-corrected bootstrap). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than altered habitats. In brackets, the number of studies for each grouping variable is indicated.

differences in their foraging distances. Foraging distances up to 2 km have been described for medium sized bees (Bommarco *et al.* 2010) and up to 5 km for bumblebees (Osborne *et al.* 2008), while flower-visiting birds and bats have larger foraging areas compared with most insect pollinators, given that they have greater energy requirements due to their endothermic metabolism (Fleming, Geiselman & Kress 2009). Bats and birds are recognized as excellent promoters of outcrossing
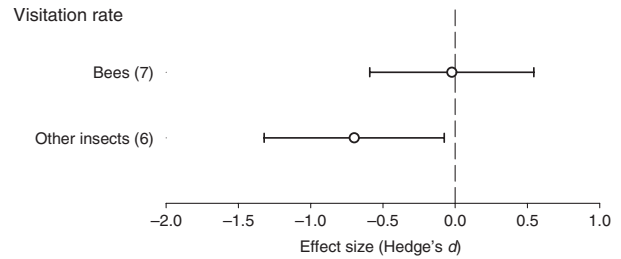

Fig. 5. Cumulative effect sizes of invasions on pollinators' visitation rates depending on the taxonomical group they belong to. The bars around the means denote 95% parametric CI. A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than invaded habitats. In brackets, the number of studies for each grouping variable is indicated.
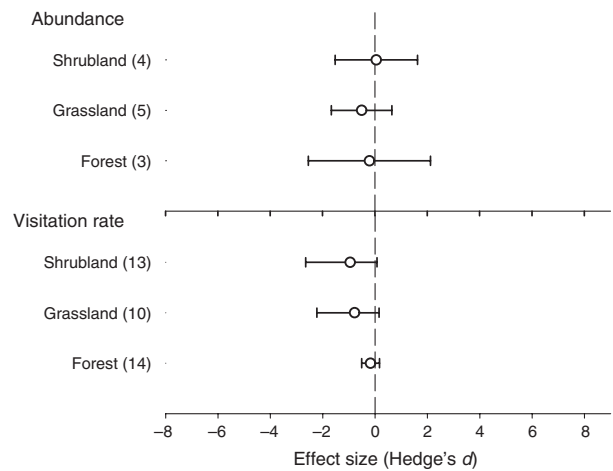
Fig. 6. Cumulative effect sizes of invasions on pollinators' abundance and visitation rates depending on the type of invaded ecosystem (forests or grasslands). The bars around the means denote 95% CI (bias-corrected bootstrap for grouping variables with ≥10 entries and parametric ones for grouping variables with <10 entries). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than invaded habitats. In brackets, the number of studies for each grouping variable is indicated.

(Fleming, Geiselman & Kress 2009; Phillips, Hopper & Dixon 2010). Hadley & Betts (2009) tracked hummingbirds and found larger movement ranges in fragmented landscapes than in continuous forested areas. Therefore, different remaining patches of nonaltered habitat can be included in the foraging areas of bats and birds but they are less intensively exploited than nonaltered landscapes. Conversely, the smaller foraging areas of insects might be disrupted to a lower extent than in vertebrates.

However, if landscape alteration is extreme, a larger decrease in visitation rates will be expected in insects. Our results agree with Winfree *et al.* (2009) who also did not find a significant decrease in bee abundance and richness when moderate habitat loss was considered, although this effect became significant when habitat loss was extreme (defined as

Visitation rate

Invasive plants (28)

Invasive animals (9)

−3   −2   −1   0   1

Effect size (Hedge's *d*)

Fig. 7. Cumulative effect sizes of plant and animal invasions on pollinator visitation rates. The bars around the means denote 95% CI (bias-corrected bootstrap for grouping variables with ≥10 entries and parametric ones for grouping variables with < 10 entries). A cumulative effect size is significantly different from zero when its CI do not bracket zero. Negative cumulative effect sizes indicate that the control plots had on average greater values than invaded habitats. In brackets, the number of studies for each grouping variable is indicated.
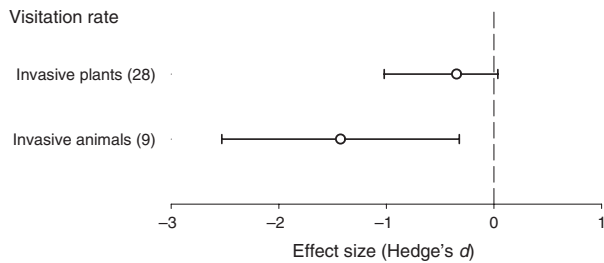
remaining fragments ≤1 ha or ≤5% natural habitat remaining in the surrounding matrix). The 66.67% and 61.54% of the entries included in our analysis reporting the effects on pollinator abundance and richness, respectively, refer to moderate (percentages calculated when possible according to the former definition) habitat fragmentation scenarios, which might be more representative of the global situation than the extreme ones (Winfree *et al.* 2009).

Another, and not mutually exclusive, explanation for the higher decrease in visitation rates of vertebrate pollinators compared with insect pollinators is the difference on diet breadth. Landscape alteration is more likely to have an effect in specialist pollinators, which depend exclusively on one or a few plant taxa as food sources, than on generalist pollinators, which are able to feed on a wider array of flower species (Kunin 1993; Winfree, Bartomeus & Cariveau 2011). Although it is not universal that vertebrate pollinators are more specialized than insect pollinators, in our review the insect pollinators included both bumblebees and other bees. From the six entries of other bees but bumblebees, three reported the effect of landscape alteration on the honey bee (*Apis mellifera*), which is known for its generalized diet (Huryn 1997). In the case of the bumblebees, we do not know the species identity of most of the entries; therefore, we cannot consider the diet breadth of the particular species studied. However, there are bumblebees that have been reported as generalists (excepting long-tongued bumblebees) and it is these species which are less affected by habitat loss, fragmentation and degradation (Goulson, Lye & Darvill 2008). Moreover, both *A. mellifera* and some species of *Bombus* have the capacity to broaden their diets including new food resources like alien plants (Stout, Kells & Goulson 2002; Simpson, Gross & Silberbauer 2005; Gross *et al.* 2010) or mass-flowering crops (Goulson *et al.* 2002). Therefore, we can assume that the vertebrate pollinators in our review (bats and birds) could have narrower diet breadths than these insect groups. Flowers visited by bats satisfy the criteria for a set of syndromes (nocturnal anthesis, large nectar reward, cauliflory, etc.; Fleming, Geiselman & Kress 2009), as do bird-visited ones (red-orange-yellow corolla colours,

abundant dilute nectar, diurnal anthesis, absent scent and landing platform and long corollas; Valido, Dupont & Olesen 2004; Curti & Ortega-Baes 2011). These vertebrate pollinators would not be expected to significantly broaden their diet, but rather to forage for food resources in other sites. In contrast, the generalized pollinator systems of most of the insects included in this analysis might buffer the effects of landscape alteration by including the most abundant and new floral resources in their diet.

In invaded sites, pollinator abundance and richness were not affected, while pollinator' foraging behaviour was modified, thereby reducing their visitation rates. Visitation rates of insect species, not including bees, were the most negatively affected. Compared with bees, the other insects might be more specialized (Winfree, Bartomeus & Cariveau 2011) and thus might not include new alien plant species in their diets. If alien plants displace their food resources, they should look for them further afield and exploit resources which are still available nearby less intensively. In the case of animal invasions, the narrower foraging areas and periods of insects apart from bees, might easily overlap with the alien species that usually have generalist diets, large foraging areas and periods, both during the day and throughout the year (Stout, Kells & Goulson 2002; Gross *et al.* 2010).

In general, although the number of studies suitable for meta-analysis was low for invasive animals, we found a trend towards a more negative effect of invasive animals than invasive plant species. Invasive plant species become well integrated into the native plant–pollinator networks (Vilà *et al.* 2009) through repeated visits by native pollinators and large effects are expected to occur on native plants rather than on native pollinators (Bjerknes *et al.* 2007). In contrast, alien pollinators can directly compete with native pollinators, for nest sites and floral resources because their niches can overlap (Gross & Mackay 1998; Kato *et al.* 1999; Goulson 2003). In the case of honey bees and bumblebees, which are the most studied alien pollinators (six of nine entries of this meta-analysis), feeding niche overlap can be due to their polylectic diet, relatively large flight and foraging distances, relatively large vital cycles, capacity to start foraging earlier and their capacity to find and exploit food resources more rapidly (Goulson 2003). Alien insects can also interfere with native insects by transmitting parasites or pathogens (Goulson 2003) or by direct exclusion. For example, invasive ants (three studies in this meta-analysis) can exclude native pollinators in the plants they host, reducing their abundance and diversity (Cole *et al.* 1992).

ECOSYSTEM TYPE DIFFERENCES

The decrease in pollinator abundance was mainly found in altered forest (even though 85.71% of the entries belonged to moderate landscape alterations according to Winfree *et al.* 2009), but not in altered grasslands. Mid-successional habitats and more open areas with intermediate disturbance regimes seem to offer more nesting and feeding resources to most pollinator communities than forests (Steffan-Dewenter &

Tscharntke 2002; Steffan-Dewenter & Westphal 2008). Forest pollinators might be more specialized and therefore vulnerable to landscape alteration (Steffan-Dewenter & Westphal 2008). Despite this, moderate and non-extreme landscape alteration might prevent species from totally disappearing, which may be the reason why we did not find a negative effect for richness; although changes in community composition might occur (Brosi *et al.* 2008). In grasslands, the opposite trends were observed, that is, while pollinator abundance was not affected, pollinator richness significantly decreased. The loss of pollinator species in altered grassland ecosystems could be replaced by generalist pollinators like managed honey bees (Aizen & Feinsinger 1994), thereby maintaining abundance levels.

On the contrary, the effect of invasions on pollinators was not influenced by ecosystem type. However, many aspects in the patterns of invasion and their ecological impacts are ecosystem-dependent (Vilà *et al.* 2006; Chytrý *et al.* 2009). It is possible that pollination patterns are more community context-dependent than ecosystem-dependent (Lonsdale 1999; Vilà *et al.* 2009), as there was a large variation in the effect sizes between studies (i.e. significant Q_{within} for visitation rates).

OBSERVATIONAL VERSUS EXPERIMENTAL STUDIES

Only pollinator abundance after invasions differed between observational and experimental studies. In observational studies invasion reduced pollinator abundance, whereas this was not the case in experimental studies. This is perhaps due to the short duration of most field manipulative studies compared with the long-term dynamics associated with natural communities. Pollinators might change their foraging behaviour quickly, just after the introduction of the alien species, but the effects on pollinator populations might have a lag-time before being detected (Kuussaari *et al.* 2009). The existence of such a lag-time could also explain the lack of a significant effect of invasion on pollinator abundance and richness.

Furthermore, experimental studies isolate the effect of the global change component of interest, whereas in observational studies other components could be simultaneously acting, producing additive or synergistic effects with invasions (Sala *et al.* 2000).

DIFFERENCES AMONG LANDSCAPE ALTERATION COMPONENTS

The component of landscape alteration that primarily influenced pollinator patterns was disturbance of the surrounding matrix. The characteristics of the matrix could possibly lessen the effects of patch size reduction in nonaltered habitat on visitation rates, thereby allowing the pollinators to persist in the area to reach other foraging areas or even exploit the matrix. As the nature of the matrix becomes more hostile, pollinators are more vulnerable and achieve fewer visits, probably due to a decrease in their abundance. In our study, 63.63% of the

entries relating to the effect of matrix disturbance refer to matrices converted on agricultural land. In intensively managed agricultural lands, pollinator abundances have been reported to decrease within a 150-m zone outside remaining natural patches (Kohler *et al.* 2008), while more extensive croplands, such as those with semi-natural vegetation in fields margins, can offer foraging areas for pollinators (Pywell *et al.* 2005) generating less hostile landscapes and buffering the effect of the reduction of fragment size.

Conclusions

Our review found that pollinator communities are affected by landscape alteration and biological invasions similarly. Responses of pollinators to these two global change components vary among taxa and ecosystem types. Despite the fairly large amount of literature concerning the effects of landscape alteration and invasions on different steps of the plant reproduction process, from pollinator abundance to fruit and seed set (Aizen & Feinsinger 1994), there are few studies exploring the impact on plant–pollinator networks (Aizen, Morales & Morales 2008; Vilà *et al.* 2009), and on plant and pollinator progeny performance (Gonzalez-Varo *et al.* 2010; Potts *et al.* 2011).

Our results point to larger effects due to invasive animals than invasive plants. Many studies have investigated the effect of domestic honey bees and bumblebees on native pollinators (e.g. Dupont *et al.* 2004; Ings, Ward & Chittka 2006; Nagamitsu *et al.* 2010), however, a large number of these studies lack reference plots that prevented us from including many entries in the meta-analysis.

Bees and bumblebees are also the main studied species responding to invasion and landscape alteration. Although the growing concern on the pollination crisis focuses on these two groups of pollinators, more attention should be paid to vertebrate pollinators as they are the most affected by landscape alteration.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of studies for meta-analysis on landscape alteration and biological invasions impacts on pollinators.

Appendix S2. Exploration of publication bias (i.e. funnel plots, Spearman rank correlations and fail-safe numbers) for the effect of landscape alteration and biological invasions on pollinator abundance, richness and visitation rates.

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