



# **Asymmetric effects of biological invasions on pollination interactions**

Seminario de Título entregado a la Universidad de Chile en el cumplimiento parcial de  
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### **Asymmetric effects of biological invasions on pollination interactions**

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Gracias a mi familia que me ha aguantado todo este tiempo, por el apoyo y la comprensión.

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**Table S1.** Coefficients of the best models (lowest BIC, see Table 1) obtained for invasive animals ( $Q_{\text{between}} = 338.20$ ,  $df = 19$ ,  $P < 0.001$ ,  $Q_{\text{total}} = 602.85$ ,  $df = 69$ ,  $P < 0.001$ ). Bold values represent significant coefficients at  $\alpha \leq 0.05$ . Abbreviations:  $\beta$  = estimate, SE = standard error, CI = 95% confidence interval, m = metric, RAD = native pollinator diversity, lat = latitude, tmp = temperature, pp = precipitation.

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= standard error, m = metric, RAD = native pollinator diversity, lat = latitude, tmp = temperature, pp = precipitation.

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**Figure 4.** Meta-regression plots of latitude against pollination (left panels) and pollinator (right panels) metrics for invasive animals. The figure shows that for most metrics (all except effectiveness), negative effects are more likely to be detected closer to the tropics and positive effects are more likely to be detected at greater latitudes.

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**Figure 7.** Funnel plot obtained for the invasive animal dataset. Gray scale represents the confidence intervals at 90, 95 and 99%.

**Figure 8.** Funnel plot obtained for the invasive plant dataset. Gray scale represents the confidence intervals at 90, 95 and 99%.

## RESUMEN

Las invasiones biológicas son un importante motor de pérdida de biodiversidad. Ciertas especies exóticas invaden exitosamente las comunidades y alteran los patrones locales de interacciones ecológicas, afectando el funcionamiento de los ecosistemas (por ej. polinización). En este trabajo nosotros sintetizamos estudios realizados alrededor del mundo (N=368), para evaluar el efecto de las especies invasoras de plantas y animales en los polinizadores (tasa de visitas y diversidad) y en la polinización (efectividad, producción de frutos y semillas). Mostramos que las plantas invasoras poseen un riesgo mayor para los polinizadores y el funcionamiento ecosistémico que animales invasores, pero estos efectos dependen del clima. En regiones templadas, el efecto general de los polinizadores invasores fue positivo para los polinizadores nativos y en el éxito de polinización. Estos hallazgos sugieren que se requiere una mayor inversión para prevenir y manejar las plantas invasoras, y recalcan el mayor riesgo que representan para los ecosistemas tropicales. Nuestra síntesis se basa en nuestro conocimiento actual acerca de los efectos de invasores en la polinización en tres mayores aspectos: (1) la polinización es influenciada por efectos asimétricos en plantas y polinizadores invasores, (2) los estudios realizados a nivel de comunidad muestran un escenario diferente que aquellos basados en una sola especie, y (3) el efecto de especies invasoras en la polinización es contexto-dependiente, variando con la latitud, temperatura y precipitación. Aceptar la complejidad que tienen las especies invasoras es crucial al momento de entender sus efectos globales y tomar acciones de conservación apropiadas.

## ABSTRACT

Biological invasions are a major driver of biodiversity loss. Certain exotic species successfully invade communities and alter the pattern of local ecological interactions, affecting ecosystem functioning (e.g., pollination). Here we synthesized studies throughout the world (N=368) to evaluate the effects of invasive plant and pollinator species on native pollinators (visitation rates and diversity) and pollination success (effectiveness, fruit set, and seed set). We show that invasive plants pose a greater risk to native pollinators and ecosystem functioning than invasive pollinators, but such effects largely depend on climate. In tropical regions, both invasive plants and pollinators consistently negatively impacted on native pollinators and pollination success. However, in temperate regions, the overall effect of invasive pollinators was positive on native pollinators and pollination success. These findings suggest that more investment is required to prevent and manage plant invasions and highlight the higher risk posed to tropical ecosystems. Our synthesis builds upon our current knowledge about invasive effects on pollination in three major aspects: (1) pollination is influenced by asymmetric effects on invasive plants and pollinators, (2) studies conducted at community level depict a different scenario than those based on a single species, and (3) the effects of invasive species on pollination are context-dependent, varying with latitude, temperature, and precipitation. Embracing the complexity that invasive species have is crucial to understand its global effects and take appropriate conservation actions.

## INTRODUCTION

Biological invasions are one of the main drivers of biodiversity loss worldwide. Altogether with climate and land-use changes, invasive species are leading to a global decline of pollinators (Potts et al. 2010; Aizen et al. 2008) and pollination services (González-Varo et al. 2013; Pejchar and Mooney 2009). Invasive species can rapidly integrate into pollination networks via generalist flower visitors and morphological trait similarity (Stouffer et al. 2014; Arroyo-Correa et al. 2020), affecting native species in many possible ways. For example, invasive species can increasing facilitation or competition interactions, alter the structure of pollination networks, and strongly affect specialized or rare species (González-Varo et al. 2013; Carvalheiro et al. 2008; Bartomeus et al. 2008b; Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002; Montero-Castaño and Vilà 2017). In the past decades, our understanding of how an exotic species succeed to establish has improved (Rejmanek and Richardson 1996; Sakai et al. 2001) and shifted from a species perspective to a community perspective (Memmott and Waser 2002; Bartomeus et al. 2010). However, while many syntheses have looked for general patterns of invasive plants (e.g., Morales and Traveset 2009; Vilà et al. 2011; Montero-Castaño and Vilà 2012), the impacts of invasive pollinators remain less studied, and our knowledge on them is usually are related to croplands (e.g., Montero-Castaño et al. 2016) due to their economic importance (Klein et al. 2007).

Managed pollinator species, like *Apis mellifera* and *Bombus terrestris*, are highly efficient crop pollinators and sometimes are introduced to compensate for wild pollinator deficit (Klein et al. 2007; Trillo et al. 2018). Generally, those pollinators are used because

they are cheap, versatile, and generalist (Klein et al. 2007), reaching high abundances in short times (González-Varo et al. 2013). On the other hand, invasive plants require long time-lags to reach a significant abundance in the invaded community (González-Varo et al. 2013). Therefore, successful invasive plants probably have long flowering periods, allowing them to ensure proper pollination and reproductive success (as Memmott and Waser 2002 discuss). Nevertheless, little is known about the differential effects that invasive plants and pollinators exert on pollinator communities and pollination interactions, as those factors are rarely assessed simultaneously. Moreover, while the previous synthesis works on the impact of invasive plants on pollination have shown negative impacts on visitation rates and reproductive success of native plants (Morales and Traveset 2009; Vilà et al. 2011), they also show that the impact is highly context-dependent among species and ecosystems (Carvalho et al. 2014; Bartomeus et al. 2008b; Vilà et al. 2009; Charlebois and Sargent 2017). Thus, different studies report contrasting results, as in some cases, the effect is positive (e.g., Lopezaraiza-Mikel et al. 2007) and in others negative (e.g., Kandori et al. 2009). When invasive plant species integrate into native ecological networks, topology alterations are expected as invasive species usually establish strong links with their counterparts, acting as super-generalists (Montero-Castaño and Vilà 2017; Bartomeus et al. 2008b; Bartomeus et al. 2010). Similarly, invasive animal species rapidly become the most abundant pollinator, acting as super-generalists, and sometimes the most effective pollinators (Medel et al. 2018; González-Varo et al. 2013).

Besides the trophic level, the geographic context is also rarely assessed in studies on the impacts of invasive species' effect on pollination. Latitudinal and climatic

differences between regions can have an important influence on the strength of biological effects. Abiotic factors, as precipitation and temperature, may affect both flowering phenology and pollen vectors (Rathcke and Lacey 1985; Fenner 1998). Also, the temperature has a direct effect on germination times, increasing competition by positively selecting plants with the earliest germination (Rathcke and Lacey 1985). In temperate zones, both temperature and precipitation are likely to affect flowering times. Contrarily, in tropical regions, precipitation is usually the determinant factor as the temperature is stable around the year (Fenner 1998). In temperate zones, flowering and pollination activity is concentrated in one season (i.e., spring), which may promote either facilitation (e.g., earlier flowering may increase visitation rates to later plants) or competition for floral resources and pollinators (Rathcke and Lacey 1985). Therefore, these conditions promote generalist plant-pollinator systems (Johnson and Steiner 2000; Armbruster and Baldwin 1998). Invasive pollinators, like honeybees and bumblebees, can start foraging earlier, flying longer distances (Montero-Castaño and Vilà 2012).

Invasive pollinators could exert adverse effects by increasing competition with native species due to feeding niche overlap, while invasive plants may be welcomed by generalist pollinators, reducing pollination services on native plants (Morales and Traveset 2009; González-Varo et al. 2013). Also, temperate systems are less diverse than tropical ones making them more susceptible to invaders, as the biotic resistance hypothesis states (Jeschke 2014). Contrarily, tropical regions are more diverse, making them less susceptible to invaders, and have a long period of flowering time with suitable conditions for plant reproduction and insect activity (Seymour et al. 2003). Because of this, overlapping in flowering times can be reduced, decreasing the competition within the

community (Fenner 1998). This temporality may promote specialization and niche segregation (Armbruster 2014; Pauw 2013), making tropical communities less susceptible to the effects of invasive plants, but as happens in temperate systems, invasive pollinators may act as robbers, negatively affecting native plant and pollinators (Dohzono et al. 2008; Saez et al. 2017).

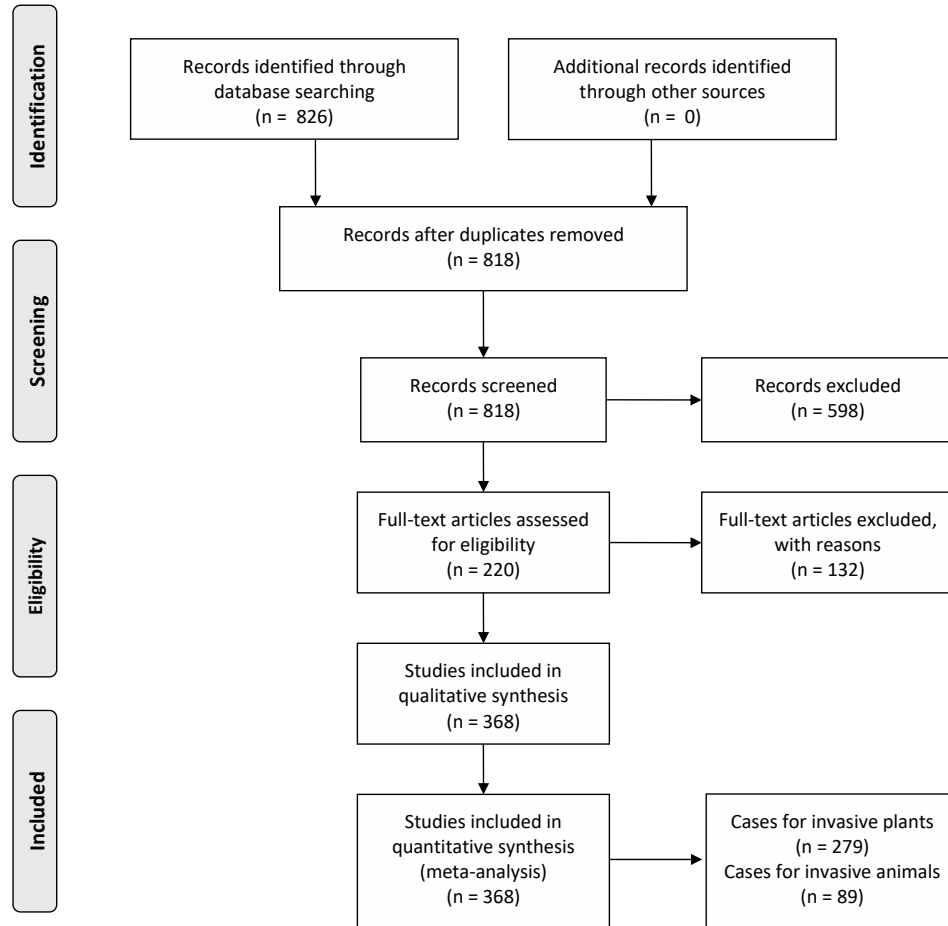
Hence, we hypothesized that (1) both invasive plant and pollinator species would exert negative effects on pollinators and pollination success, and (2) according to the biotic resistance hypothesis (Jeschke 2014), temperate communities would be more susceptible than tropical ones. Here we performed a meta-analysis (based on 368 study cases: 89 for animals and 279 for plants) to compare the global effects of biological invasions on pollinators and pollination, comparing the consequences of top-down (animal-mediated) and bottom-up (plant-mediated) effects. More specifically, we tested if invasive plants and animals have similar effects (1) on pollinators, and (2) on pollination, and (3) if those effects vary with the latitude, temperature, and precipitation.

## MATERIAL AND METHODS

### *Literature survey and inclusion criteria*

We surveyed the literature on the topic of interest using the ISI Web of Science, Scopus, and ScienceDirect databases (January 1988-December 2019). For building the database, we used the following search terms: “pollinat\*” + “nativ\*” + one of the following: “exotic\*”, “invasive”, or “alien”, resulting in three different batches of results. From those search keywords, we obtained 826 papers reporting the effects of invasive plants and invasive pollinators on pollination. Since we had three different batches, the same paper could appear in more than one batch, so we removed duplicates obtaining a total of 818 papers. After reading those 818 papers, we excluded 598 and 220 met our inclusion criteria, defined as follows: (i) studies focused on biotic pollination *sensu lato*, (ii) studies comparing invaded (treatment) and uninvaded (control) areas, reporting at least one measurement of pollination success (pollination effectiveness, fruit set, seed set, and) or pollinators (visitation rates and pollinator diversity), (iii) studies reporting mean, sample size and any dispersion measurement (standard deviation, standard error or confidence intervals). We also distinguished the scale of the studies, separating cases in species-level and community level (i.e., studies reporting the impact in a whole community, instead of a particular specie). Literature search procedures followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) statement (Moher et al. 2009). In concordance with the PRISMA statement, we prepared a standardized flowchart (Fig. 1).

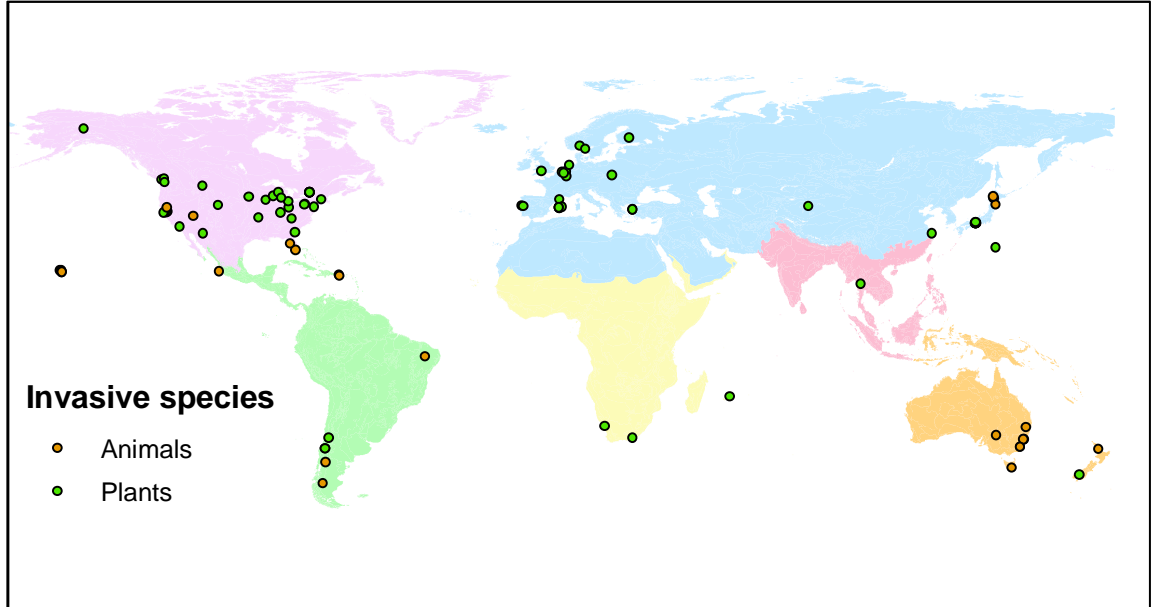




**Figure 1.** Preferred Reporting Items for Systematic Reviews and Meta-Analysis (PRISMA) flowchart, summarizing the information gathering and selection procedures.

Also, we followed the recommendations of Nakagawa et al. (2017) to get informative results by taking data independence, publication bias, and the potential effects of outliers. We obtained 368 case studies from the 220 articles that fulfilled our inclusion criteria (some papers provide more than one case study). From those, 279 case studies were for invasive plants (from 66 different papers), and 89 case studies were for invasive pollinators (from 22 different papers) from the five continents (Fig. 2). In detail, from

invasive plant cases, ten were from tropical regions (which include five community-level studies and five species-level studies), and 269 are from temperate ones (209 species-level studies and 60 community-level). Among the invasive pollinator cases, 56 were from temperate zones (11 community-level studies and 45 species-level studies), and 33 were from tropical regions (27 species-level studies and six community-level studies). As some papers presented more than one case study, we consider them as independent cases when reporting different areas, species, or response metrics, but not different sampling events in time (in this case, we considered only one event). In the case of many areas with different levels of invasion were reported, we contrasted the extreme situations. When data were presented only as graphics, we used GraphClick 3.0 software (Arizona Software, Switzerland) to extract the information required. Two persons (FEF and VGS) performed paper screening independently. Therefore, to assess between-reviewer agreement, we calculated Cohen's kappa coefficient, which was 95.6% (confidence interval 93-98%), based on the papers selected for a full-text screening or rejected because they fail to meet our inclusion criteria (Nakagawa et al. 2017).



**Figure 2.** World map with the geographic regions showing the locations of the case studies included in the meta-analysis.

### *Pollinator and pollination metrics*

To evaluate if invasive plants and animals have similar effects on pollinators (objective 1), we considered following metrics: species diversity (including native species richness, abundance, and diversity indices, as explained above), and visitation rate (visitation events per unit of time, being variable among studies). To evaluate if invasive species have similar effects on pollination (objective 2), we considered the following metrics: pollination effectiveness (including proportion of flowers pollinated, pollen deposition, % conspecific pollen), fruit set (i.e., the proportion of flowers producing fruits), and seed set (i.e., number of seeds produced by flower).

For each study and metric described above, we calculated the effect size of the impact of invasive species using the formula of the Hedges' unbiased standardized mean difference (Hedges'  $d$ , Hedges & Olkin 1985):

$$d = \left( \frac{X_E - X_C}{S_{EC}} \right) * J$$

where  $X_E$  is the mean value of the invaded area,  $X_C$  is the mean value of the control area,  $S_{EC}$  is the pooled standard deviation of both treatments and  $J$  is a term that corrects effect sizes according to the sample size (particularly useful in situations where part of the studies has low sample sizes). Hedges'  $d$  has been largely applied in meta-analyses performed to answer ecological questions, where the aim is to estimate the magnitude of the effects of a given treatment (in this case, biological invasions) contrasting the results to a control situation (Gurevitch *et al.* 2001). Negative  $d$  values are interpreted as a reduction of the response metric in the invaded area, and positive values mean the opposite. Mean absolute effects can be classified as: small ( $d \geq 0.2$ ), moderate ( $d \geq 0.5$ ) or large ( $d \geq 0.8$ ) (Koricheva *et al.* 2013).

#### *Latitude and environmental variables*

We extracted the geographic coordinates of each case study (in the cases that precise coordinates were not provided, we estimated them using the centroid of the reference area in Google Earth Pro) and considered absolute latitude (i.e., all positive values, considering the difference to the Equator irrespectively of north or south, ranging from 18.43 to 64.71 decimal degrees). Using the geographic coordinates of each case study, we obtained average temperature (ranging from -3.34 to 24.28 °C) and precipitation (ranging from

105.25 to 1882.00 mm) values from WorldClim database version 2.0 (Fick and Hijmans 2017), which is freely available at [www.worldclim.org](http://www.worldclim.org).

### *Model fitting and selection*

We performed all analyses using the *metafor* package (Viechtbauer 2010) in R 3.6.0 (R Development Core Team 2019). To evaluate if invasive plants and pollinators have similar effects on native pollinators and pollination success, we fitted weighted mixed-effects models (using the R function ‘*rma.mv*’ from the *metafor* package) with a maximum likelihood estimation, to analyze how effect size (related each metric) changes with plant or pollinator invasive species as recommended by Borenstein et al. (2009). We run separate models for the effect of plants (bottom-up effects) and the effect of animals (top-down effects), using each pollinator/pollination success metric as the explanatory variable.

As some studies provided more than one case study (as described above), and some invasive species were present in more than one study, we included study ID and the ID of the invasive species as random effects. To account for taxonomic scale variability (either species or community level), we included scale as a covariate, along with the interaction between metric and scale in the models. As we included community-level studies, we were unable to perform a formal phylogenetic control. However, instead we included invasive species as a random factor (as explained above) to account for potential inter-species bias.

Climatic conditions can also influence the effect of the invasion and are not solely dependent on latitude. Therefore, to assess if the impact of invasive species depends on climate and latitude, we included latitude (as an absolute value), temperature, and precipitation as covariates. To obtain the model with the best explanatory power for both

invasive pollinators and plants, we conducted a model selection procedure. For model selection, we considered 76 candidate models, including a null model (i.e., with no explanatory variables). We ranked all models using the Bayesian Selection Criterion (BIC) to select the most parsimonious model (Burnham and Anderson 2004). We evaluated the effects of latitude, temperature, and precipitation using meta-regressions (Gurevitch et al. 2001). For presenting the results in forest plots, we decided to split our results in tropical and temperate (using the average values of latitude, temperature and annual precipitation values of each data set for visualization purposes). Average values for invasive pollinators are: (a) tropical zone: latitude = 17.49°, temperature = 21.00°C, precipitation = 1614.13 mm, (b) temperate zone: latitude = 39.69°, temperature = 10.40°C, precipitation = 1012.59; for invasive plants are: (a) tropical zone: latitude = 19.75°, temperature = 21.22°C, precipitation = 1445.23 mm, (b) temperate zone: latitude = 42.53°, temperature = 10.97°C, precipitation = 851.26 mm. We assessed heterogeneity on the fitted models using the  $Q$ -statistic, which is a  $\chi^2$ -distributed metric and tests if there is a common effect among the case studies included in the meta-analysis model. Large  $Q$  values suggest that effect size differences across case studies do not have a common mean, may vary for other reasons than sampling error (e.g., environmental factors; Hedges and Olkin 1985).

### *Publication bias*

We used the funnel plot approach (Hedges and Vevea 1996) to assess publication bias through the graphical representation of the relationship between effect size and sample

size. In the case that we observe funnel plot asymmetries, we conducted a sensitivity analysis by removing four ‘outlier’ cases with Hedges’  $d < -5$  values, which may be causing bias and potentially altering our results (Nakagawa et al. 2017). As we used mixed-effects models with multiple variables (i.e., ‘`rma.mv`’ objects), we were unable to conduct other bias assessments tests (e.g., fail-safe number calculation, trim-and-fill analysis) as they are not implemented yet for this kind of models.

## RESULTS

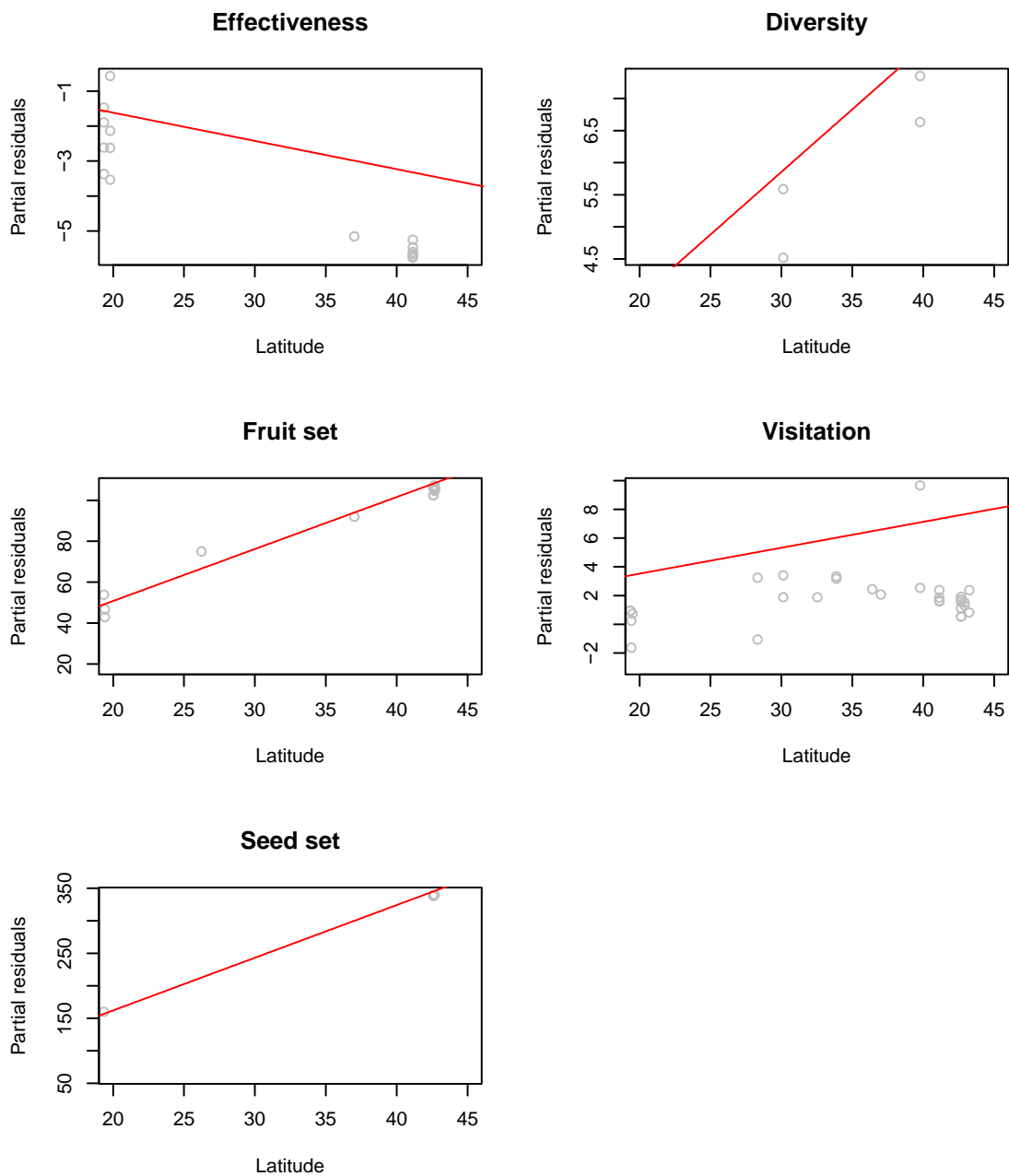
Overall, we found that the effects of biological invasions depend on the trophic level of the invader, with contrasting results being detected for exotic animals and plants, as well as between species- and community-level studies, and between tropical and temperate zones. Results from model selection are presented in Table 1. The results of the model selection for invasive animals are presented in Table S1, and for invasive plants in Table S2. We found significant heterogeneity at both animal ( $Q_{\text{between}} = 338.20$ ,  $df = 19$ ,  $P < 0.001$ ,  $Q_{\text{total}} = 602.85$ ,  $df = 69$ ,  $P < 0.001$ ) and plant ( $Q_{\text{between}} = 400.89$ ,  $df = 32$ ,  $P < 0.001$ ,  $Q_{\text{total}} = 3288.54$ ,  $df = 246$ ,  $P < 0.001$ ) models, indicating that there is not a common effect size across case studies.

For invasive animals (which were mainly represented by three species: *Bombus terrestris*, *Bombus ruderatus* and *Apis mellifera* invading both tropical (e.g., Puerto Rico or Hawaii) and temperate (e.g., Japan, Argentina, or New Zealand) systems, making 83% of the case studies), we found that the effects on pollinators and pollination became more accentuated with increasing absolute value of latitude, the exception being effectiveness where effects were more accentuated towards the tropics (Fig. 3). Similarly, the effects of invasive plants became less accentuated farther from the tropics (Fig. 4). We also found effects of climate that were detected over the effects of latitude, affecting all pollinator and pollination metrics assessed (Table S2). To illustrate such interactive effects, in Figs. 5 and 6 we present the detailed effects on pollinators and pollination under two geographic scenarios, one typical from tropical conditions and another typical from temperate conditions.

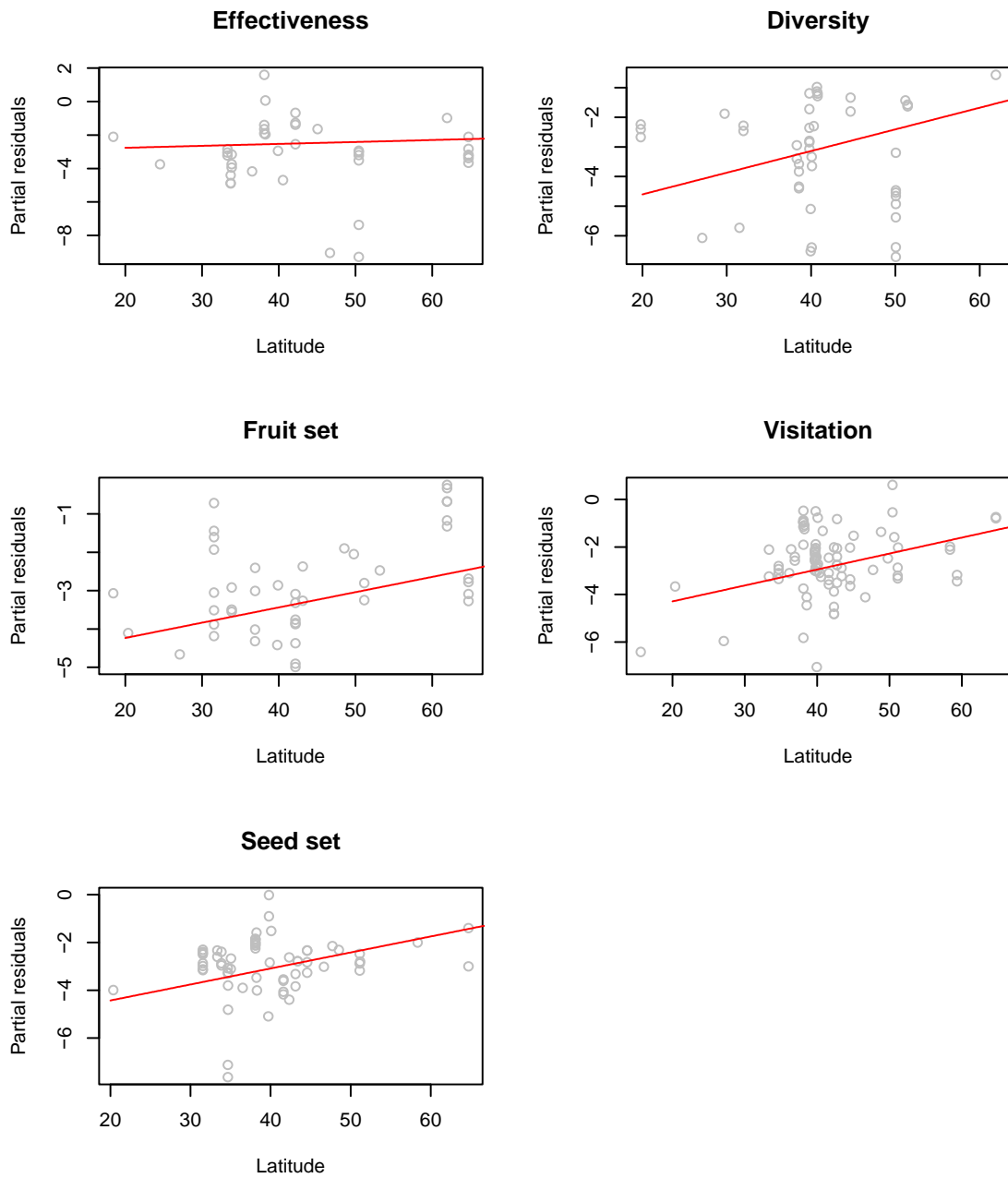


**Table 1.** Model selection results for effects of latitude (lat), temperature (tmp), precipitation (pp) and taxonomic scale (species or community) on the different metrics of pollinators and pollination here evaluated. Model selection was based on Bayesian Information criterion (BIC), and variation of BIC from each model to the most parsimonious model ( $\Delta\text{BIC}$ ) is also presented along with model weights ( $\omega_i$ ). LLV = log-likelihood value. For each case (invasive animals or plants) we present  $\Delta\text{BIC} \leq 2$  models and the null model.

Rank	Model	LLV	BIC	$\Delta\text{BIC}$	$\omega_i$
Animal					
m67	rma.mv(d~metric*lat+metric*tmp+metric*pp+pp*scale)	-255.95	610.65	0.00	0.77
m63	rma.mv(d~metric*lat*scale+metric*scale+pp*metric)	-255.59	614.42	3.77	0.12
m73	rma.mv(d~metric*lat+metric*tmp+metric*pp+pp*scale+tmp*scale)	-255.62	614.47	3.83	0.11
mNull	rma.mv(d~1)	-347.58	708.63	97.99	0.00
Plant					
m55	rma.mv(d~metric*lat*scale+metric*tmp*scale+metric*pp)	-1199.45	2595.99	0.00	0.72
m57	rma.mv(d~metric*lat*scale+metric*tmp*scale+metric*pp+pp*scale)	-1198.41	2599.10	3.10	0.15
m56	rma.mv(d~metric*lat*scale+metric*tmp*scale+metric*pp*scale)	-1195.37	2599.53	3.54	0.12
mNull	rma.mv(d~1)	-1399.29	2815.47	219.48	0.00



**Figure 3.** Meta-regression plots of latitude against pollination (left panels) and pollinator (right panels) metrics for invasive animals. The figure shows that for most metrics (all except effectiveness), negative effects are more likely to be detected closer to the tropics and positive effects are more likely to be detected at greater latitudes.



**Figure 4.** Meta-regression plots of latitude against pollination (left panels) and pollinator (right panels) metrics for invasive animals. The figure shows that for most metrics (all except effectiveness), negative effects are more likely to be detected closer to the tropics and positive effects are more likely to be detected at greater latitudes.

### *Effects on pollinators*

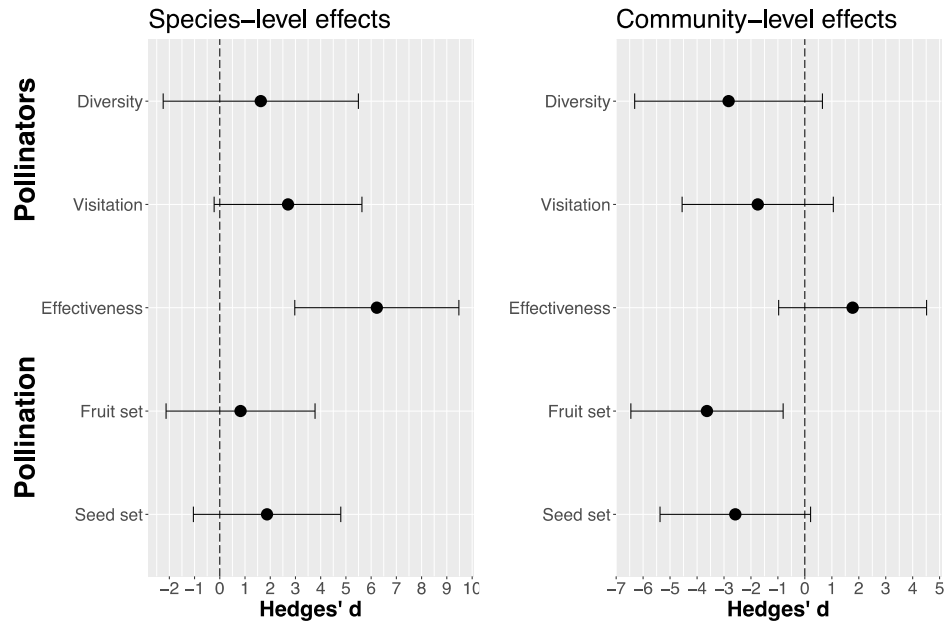
We found no significant impact on both pollinator diversity and visitation rates in tropical regions (Fig. 5a). In temperate zones, however, we found that invasive pollinators have a positive effect on pollinator diversity and visitation rates, and these effects were most accentuated in studies conducted at the species level (Fig. 5b).

For invasive plants, we found a negative effect on native pollinators in tropical zones, on pollinator diversity at the species level and visitation rates at the community level (Fig.6a). As we detected for invasive pollinators in temperate zones, we found a positive effect of invasive plants on pollinator diversity (significant at the species level, Fig.6b).

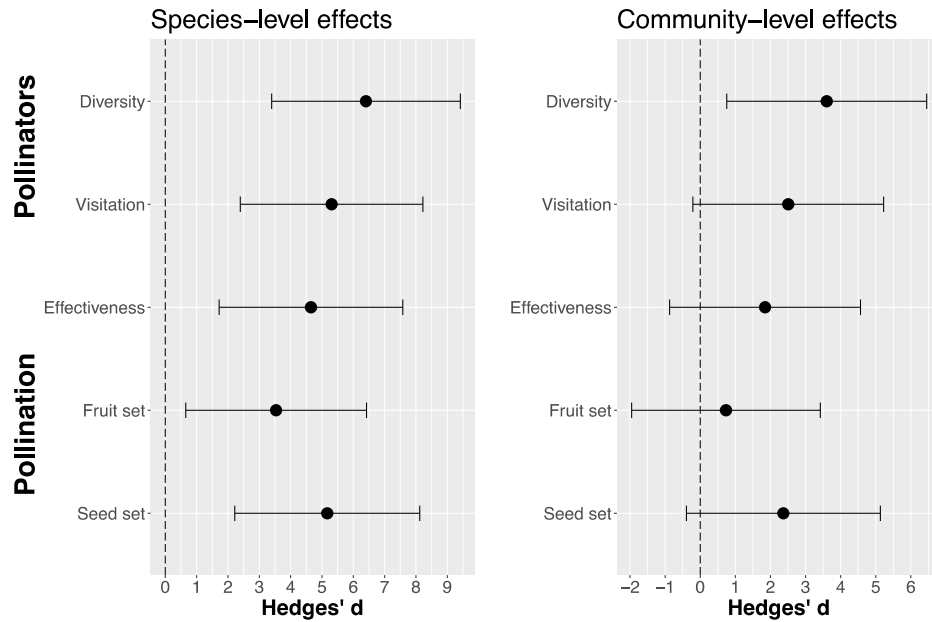
### *Effects on pollination*

In both tropical and temperate regions, we detected positive effects of invasive animals (Fig. 5) on pollination effectiveness for those studies conducted at the species level, but not at the community level. In turn, we found negative effects on fruit set (at community-level studies) in tropical zones, but a positive effect on fruit and seed set at temperate zones (at species-level studies). Regarding invasive plants (Fig. 6), we found a negative effect on pollination effectiveness in temperate zones (at community level), and negative effects on fruit and seed set in all cases.

### (a) Tropical

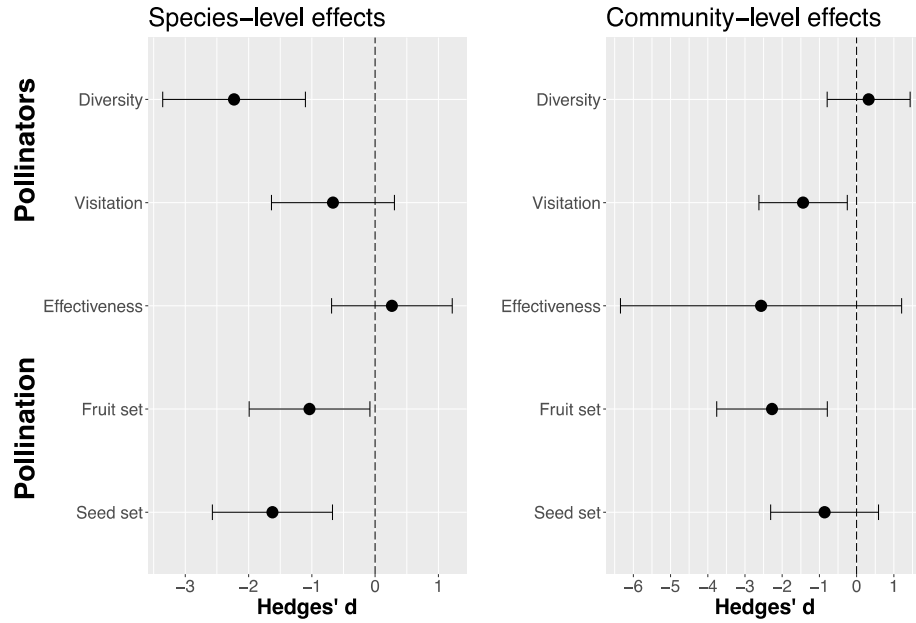


### (b) Temperate

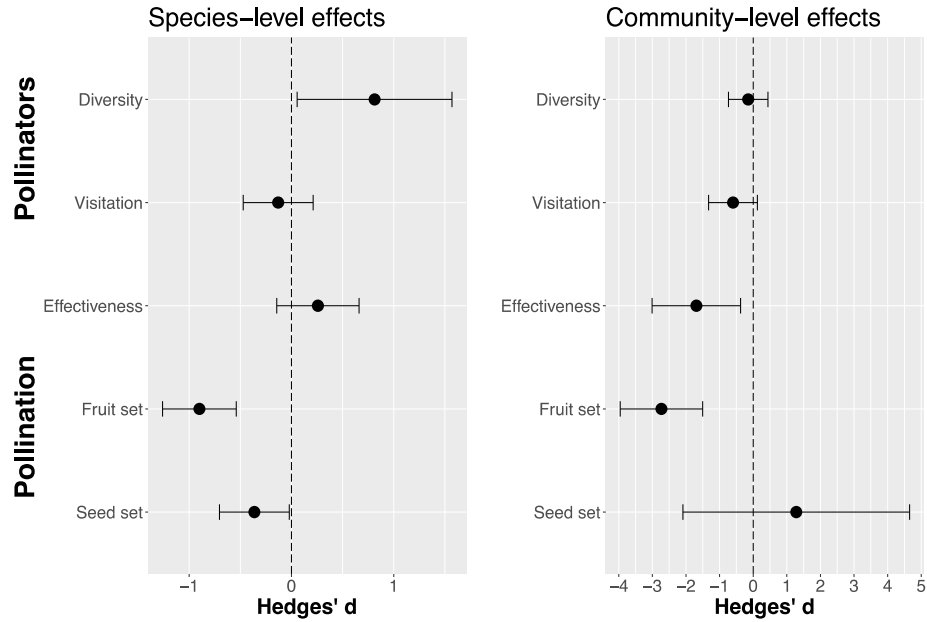


**Figure 5.** Effects of invasive animals. (a) Mean effects at temperature = 20.68°C, precipitation = 1726 mm, latitude = 18.85° (tropical conditions), and (b) temperature = 10.32°C, precipitation = 1012 mm, latitude = 39.75° (temperate conditions), contrasted between species and community levels. Error bars represent the 95% confidence interval. Estimates were extracted from best model obtained.

### (a) Tropical



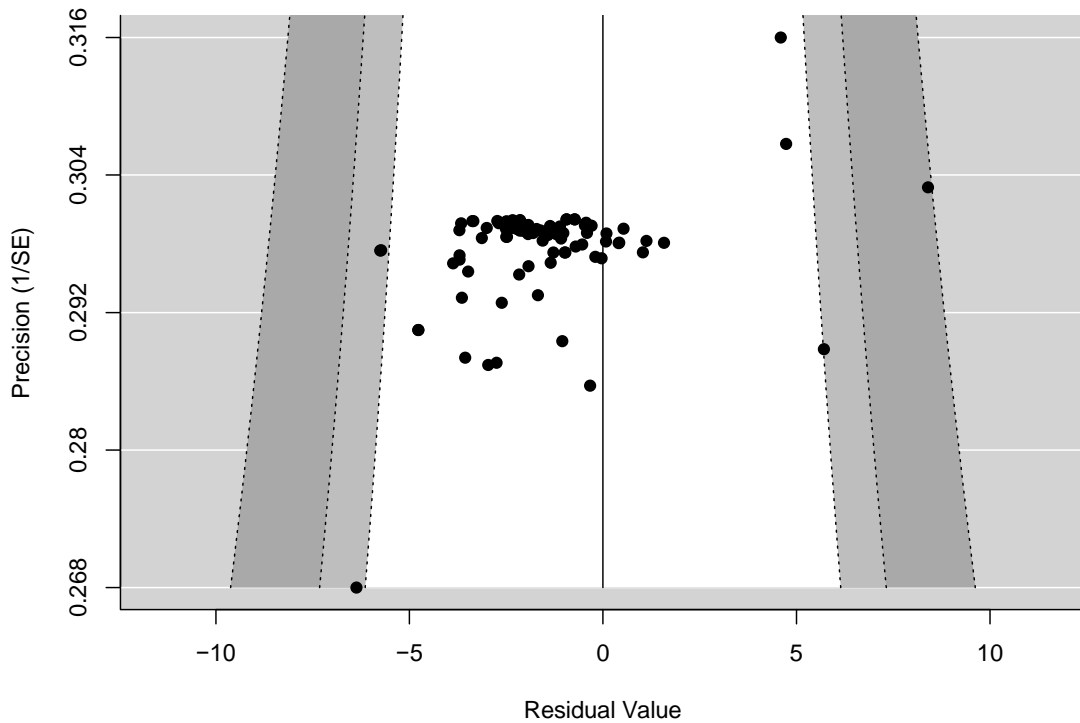
### (b) Temperate



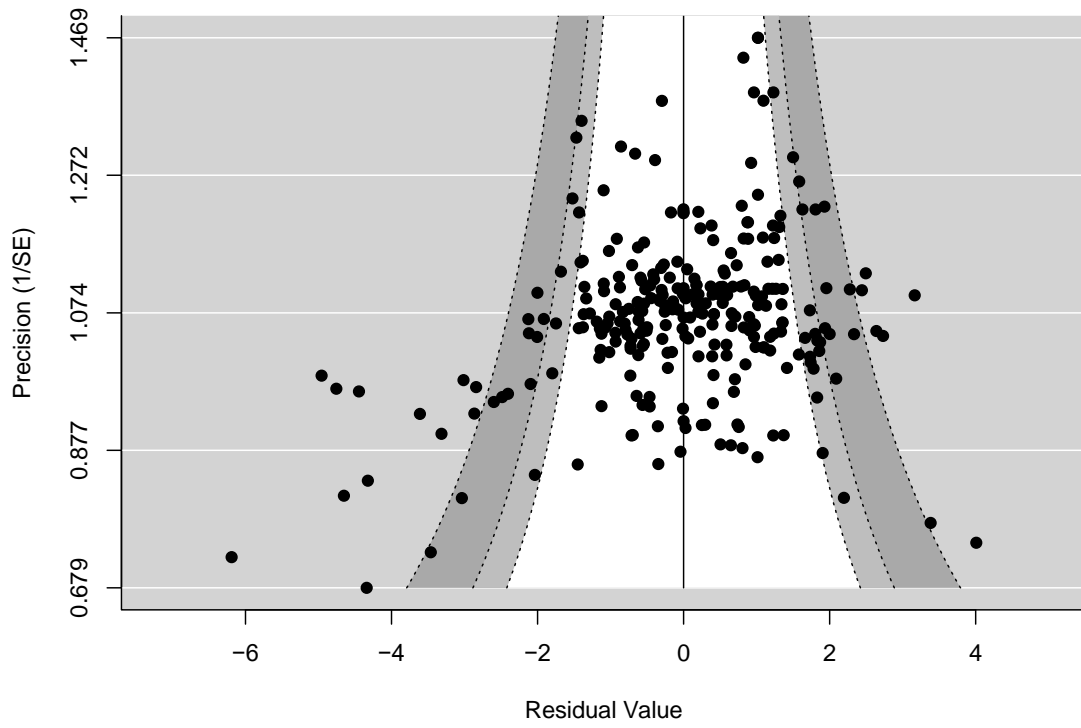
**Figure 6.** Effects of invasive plants. (a) Mean effects at temperature = 21.22°C, precipitation = 1445 mm, latitude = 19.75° (tropical conditions), and (b) temperature = 10.97°C, precipitation = 851 mm, latitude = 42.53 ° (temperate conditions), contrasted between species and community levels. Error bars represent the 95% confidence interval. Estimates were extracted from the best model obtained.

*Publication bias*

The funnel plot from invasive pollinator data (Fig. 7) showed symmetric distribution with no outlier points. However, we observed asymmetry in the funnel plot from invasive plant data (Fig. 8) resulting from four outlier points. Therefore, we conducted a sensitivity analysis and estimated all coefficients again, excluding that points, but results obtained have not changed their direction or significance (Table S3), indicating that our results are robust and not affected by these outliers.



**Figure 7.** Funnel plot obtained for the invasive animal dataset. Gray scale represents the confidence intervals at 90, 95 and 99%.



**Figure 8.** Funnel plot obtained for the invasive plant dataset. Gray scale represents the confidence intervals at 90, 95 and 99%.



## DISCUSSION

Despite the importance of pollinators for ecosystem functioning and the recognized influence of climate on biodiversity patterns, little was known on how variable the impacts of invasive species were on pollinators and pollination between tropical and temperate regions. Here we show that invasive plants are more likely to impact pollinators and pollination success than invasive pollinators (mainly commercial bees), and those negative impacts (of both plants and pollinators) are more likely to be detected in tropical regions. Below, we discuss the effects of these two main groups of invasive species on native pollinators and pollination success, as well as the implications for conservation.

### *Effects on native pollinators*

The asymmetric effects of invasive pollinators on native pollinators detected between tropics (no significant effect) and temperate regions (positive effect) could be related to the higher level of generalization of temperate communities (Armbruster and Baldwin 1998; Johnson and Steiner 2000). Such high levels of generalization may facilitate the integration of exotic animal species within native communities (Molina-Montenegro et al. 2008; Traveset and Richardson 2014; Emer et al. 2016).

The resource concentration of in a short time that occurs in temperate systems may also result in stronger direct competition between native and exotic pollinators (Kenta et al. 2007), especially if the exotic pollinators are super-generalists with wide niches that overlap with those from the native ones (Nishikawa and Shimamura 2016; González-Varo et al. 2013). Additionally, the apparent competition via shared pathogens (Morales et al. 2013; Arbetman et al. 2013) could worsen the effects of invasive pollinators on the native

pollinator assemblage on both temperate and tropical systems. Those effects can reduce the native pollinator diversity and visitation rates (Montero-Castaño and Vilà 2012) due to an increase in mortality of native pollinators and the reduction of foraging time and distance (González-Varo et al. 2013; Vanbergen et al. 2018). However, our results indicate the opposite, as negative effects being less accentuated or even positive (on diversity) in temperate systems. Such positive effects may have two non-mutually exclusive explanations: (1) many bees rely on visual cues to locate floral resources, and invasive bees may be “helping” naïve native bees to locate floral resources (Orban and Plowright 2014); and (2) in temperate systems there is a greater abundance of native pollinator species that are closely related to invasive species (e.g., *Bombus* species).

As with invasive pollinators, the high levels of generalization (in this case of the pollinators) in temperate regions may facilitate the integration of invasive plant species within native communities (Molina-Montenegro et al. 2008; Traveset and Richardson 2014). The asymmetric effects of invasive plants on native pollinators on tropical and temperate regions might be due to the differences in seasonality of the two climatic regions. While in temperate zones, flowering is concentrated in one season being mainly associated with generalist pollinators, in tropical zones, plants have more diverse phenologies that are typically associated with specialized pollinators (Armbruster 2014; Pauw 2013; Benadi et al. 2014). Moreover, due to the concentration of floral resources in a single season (Pauw 2013; Armbruster and Baldwin 1998), competition for pollinators between landscapes might be more significant in temperate systems, and a beneficial magnet effect caused by invasive species might occur more often (Molina-Montenegro et al. 2008; Muñoz and Cavieres 2008). Additionally, facilitation interactions among

invasive species may be occurring, whereby the presence of invasive pollinators (common in tropical systems, particularly *Apis mellifera* that is widely distributed) may be facilitating invasive plants and worsening community effects (the invasional meltdown hypothesis, Simberloff 2006; Simberloff and Von Holle 1999).

#### *Effects on pollination success*

Invasive plants negatively affected pollination success of native plants (primarily impacting fruit and seed set). Their effect on natural communities is expected to be stronger if invasive species are morphologically similar to native ones (Bjerknes et al. 2007), which may facilitate their integration into pollination networks (Da Silva and Sargent 2011; Montero-Castaño and Vilà 2017), resulting in competition or facilitation processes. However, our results show that competition prevails over facilitation, even in temperate systems where positive effects on pollinator diversity (possibly a magnet effect as discussed above) were detected in response to invasive plants. Such competition could be due to a reduction of flower visitation to native plants caused by the presence of more productive floral resource in exotic species (e.g., more nectar; stronger scents), which makes them more attractive to native pollinators than the native species with overlapping flowering phenology (Bjerknes et al. 2007; Brown and Mitchell 2001; Albrecht et al. 2016). Alternatively, or in combination, the presence of exotic plants may increase the deposition of heterospecific pollen (Ashman et al. 2004; Arceo-Gomez and Ashman 2016), reducing fruit and seed set even if visitation is increased (Bartomeus et al. 2008a). Our results show more accentuated effects of invasive plants on fruit set at temperate systems, supporting the heterospecific pollen interference hypothesis.

As detected for native pollinators, there is a clear asymmetric effect of invasive animals on pollination between tropical (negative effect) and temperate system (positive effect). The positive effect in temperate regions could either be a result of direct and efficient pollination by invasive species, or an indirect effect caused by the positive effect on native pollinators. As discussed, most invasive species come from Europe (i.e., temperate systems; Kenta et al. 2007; Madjidian et al. 2008) and more related to native pollinator communities at invaded temperate systems (e.g., North and South America) than at invaded tropical systems. Apart from working as visual clues for closely related species, this may make invasive pollinators more suitable replacing native ones for the native plant community (Medel et al. 2018; González-Varo et al. 2013). Further field and experimental studies would be required to understand the mechanisms behind these patterns better.

Overall, the negative impacts were more accentuated for pollination success than for pollinators (cf. Figs. 2 and 3), and even where pollinators were positively affected, pollination benefits were far less accentuated (Fig 2b). This could be explained by the fact that even when pollinators visit native plants more frequently (due to the introduction of an invasive pollinator, or due to facilitation caused by an invasive plant), this may not affect fruit or seed set if those visits usually have lower effectiveness (Trillo et al. 2018; Saez et al. 2017). Such lack of efficiency could be related to robbing (i.e., rewards are taken, but no pollen is transferred; Dohzono et al. 2008), and from high loads of heterospecific pollen carried by this super-generalists that can visit many different species (Bartomeus et al. 2008b; Magrach et al. 2017).

### *Climate covariation*

Large-scale variations in environmental conditions may be modulating biological invasions and leading to non-consistent results found in previous studies (Charlebois and Sargent 2017). Such effects may be strong, but not solely related to latitudinal effects (e.g., tropical vs. temperate regions). Indeed, the latitudinal effects could be related to differences in biodiversity (Armbruster 2014; Armbruster and Baldwin 1998), and climate might greatly vary with longitudinal and altitude gradients (Schleuning et al. 2012). However, so far, climate and latitude have rarely been considered in studies evaluating the impacts of exotic species on pollinators and pollination success.

Our results show that temperature and precipitation influenced the effects of invasive species beyond the effects of latitude, and the negative effects being more accentuated in warmer and wetter regions (i.e., for most metrics; see Figs. S2 and S3, and Tables S4 and S5). Warmer and wetter places may have positive effects on the establishment and reproduction of invasive pollinators, potentiating negative effects. Also, temporal mismatches (due to changes in phenology) between native plants and their pollinators caused by ongoing global climate change are more likely to occur in regions with warmer climates (González-Varo et al. 2013). Such mismatches may favor the integration of exotic species into the pollination networks, because those exotic pollinators are often generalists, with longer activity seasons, foraging times, and distances, which are more resilient to phenology changes and capable of using alternative floral resources (Memmott et al. 2007; Montero-Castaño and Vilà 2012; Benadi et al. 2014).

Latitude effects are likely to be correlated to temperature and precipitation effects. Previous studies (e.g., Lonsdale 1999) found a positive correlation between latitude and

the presence of exotic species. Thus, plant-pollinator communities at higher latitudes are usually dominated by generalist species and, therefore, more prone to be invaded (Traveset and Richardson 2014), as invasive species can easily integrate into less diverse and connected pollination networks (Olesen and Jordano 2002; Lopezaraiza-Mikel et al. 2007). Yet, our results show that negative effects were more accentuated in lower latitudes (i.e., closer to the tropics). This suggests that invasive species are more likely to be beneficial to pollinators and pollination success in less diverse and more generalized systems (i.e., temperate systems).

#### *Effect of taxonomic scale*

If all species within a community were studied, the impacts of invasive species at the community level should be an average of the effects at the species level. Consequently, no effect of taxonomic scale would be expected. However, in tropical regions, the negative effects of invasive animals on pollinators and pollination were more severe at the community level. In temperate regions, positive effects became more accentuated at this community level too. This suggests that, worldwide, species-level studies tend to be focused on plants that have generalist flower morphology being easily integrated into the diet of invasive species. Our results support this idea, as most of the invasive plants included in the reviewed case studies have generalist morphologies (e.g., *Ranunculus* sp. and *Taraxacum* sp.), which have more opportunities to be rapidly integrated into plant-pollinator networks and become highly connected nodes.

When evaluating the effects of exotic plants, negative effects became less accentuated at the community level, at least for tropical systems. This suggests that

researchers have focused on the impacts of invasive species in tropical regions that are more likely to focus (or publish their results) on species that compete for pollinators with the invasive species (i.e., a taxonomic bias). Also, previous studies have shown that plants that are phylogenetically closer are more likely to influence each other visitation rates (Carvalho et al. 2014). Studies focused on single species may tend to select plant species that are closely related to the studied invasive species (e.g., Kandori et al. 2009; Vervoort et al. 2011; Powell et al. 2011; Beans and Roach 2015). Alternatively, it could be that species-level studies are conducted within communities where generalist pollination interactions are dominant, and hence impacts are likely to be more accentuated (Traveset and Richardson 2014).

Several studies aimed to explain the effects of invasive species on native pollination success and pollinators (Vilà et al. 2011; Montero-Castaño and Vilà 2012; Morales and Traveset 2009; Traveset and Richardson 2014; Charlebois and Sargent 2017). This is a complex issue because of multiple factors converging on it. Some of them are mentioned here (the taxonomic scale, trophic level, and climatic covariation), but there are other factors to be explored in future studies. One of them is the phylogenetic relatedness, which has demonstrated to be a crucial element for the understanding of the impact of invasive species (Carvalho et al. 2014; Morales and Traveset 2009). Despite that, our study provides a wider view of the impact of invasive species since it allows us to detect asymmetric patterns depending on the type of climate being invaded and the invader's trophic level. Our results describe a consistent and detailed pattern. However, to expand our understanding of this issue, it is urgent to decrease the research asymmetry not only between trophic levels but also among climatic regions.

## CONCLUSIONS AND PERSPECTIVES

Our meta-analysis adds three major evidence lines to what previous synthesis works have developed upon the effects of invasive species on pollination: (1) we found that pollination is influenced by asymmetric effects on invasive plant and pollinator species, (2) we found that studies conducted at community level depict a different scenario than those based on a single species, and (3) the outcome of invasive species effects on pollination is context-dependent as it varies with latitude, temperature, and precipitation. To the best of our knowledge, this is the first study assessing those aspects simultaneously.

Overall, our results partially contradict the biotic resistance hypothesis (Jeschke 2014) since we show that more diverse communities (i.e., those from tropical systems) are more susceptible to (i.e., negatively affected by) biological invasions than less diverse communities (i.e., temperate systems). Besides, our analyses allowed us to detect that invasive plants pose a greater risk to native pollinators and plant communities than invasive animals. Such information provides a wider view on the impacts of exotic species, allowing to detect general patterns that otherwise may be interpreted as non-consistent results, as Charlebois and Sargent (2017) argued. By showing that tropical communities are more susceptible than we thought, and functioning is more impacted than species, our study stresses shifting from a species-based to an ecosystem-based approach (Harvey et al. 2017). While invasion effects can be partially reversible (Kaiser-Bunbury et al. 2017), clearly, the asymmetric effects of exotic plants and animals should be considered in future restoration studies.



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## SUPPORTING INFORMATION

**Table S1.** Coefficients of the best models (lowest BIC, see Table 1) obtained for invasive animals ( $Q_{\text{between}} = 338.20$ ,  $df = 19$ ,  $P < 0.001$ ,  $Q_{\text{total}} = 602.85$ ,  $df = 69$ ,  $P < 0.001$ ). Bold values represent significant coefficients at  $\alpha \leq 0.05$ . Abbreviations:  $\beta$  = estimate, SE = standard error, CI = 95% confidence interval, m = metricRAD = native pollinator diversity, lat = latitude, tmp = temperature, pp = precipitation.

<b>Coefficient</b>	<b>Beta</b>	<b>SE</b>	<b>z</b>	<b>P</b>	<b>CI low</b>	<b>CI up</b>
Intercept	6.603	1.863	3.544	<0.001	2.951	10.254
m(Fruit set)	23.598	4.300	5.488	<0.001	15.170	32.026
m(RAD)	-9.264	1.812	-5.111	<0.001	-12.817	-5.712
m(Seed set)	4.544	2.054	2.212	<b>0.027</b>	0.518	8.570
m(Visitation)	-5.005	1.951	-2.565	<b>0.010</b>	-8.830	-1.180
Latitude	-0.081	0.026	-3.137	<b>0.002</b>	-0.131	-0.030
Temperature	-0.196	0.038	-5.164	<0.001	-0.270	-0.122
Precipitation	0.000	0.000	1.447	0.148	0.000	0.001
Scale(sp)	-2.824	0.561	-5.033	<0.001	-3.924	-1.724
jm(Fruit set)*lat	-0.306	0.064	-4.757	<0.001	-0.432	-0.180
m(RAD)*lat	0.276	0.055	5.006	<0.001	0.168	0.384
m(Seed set)*lat	0.046	0.031	1.460	<b>0.144</b>	-0.016	0.107
m(Visit)*lat	0.176	0.033	5.296	<0.001	0.111	0.241
m(Fruit set)*tmp	-0.746	0.141	-5.286	<0.001	-1.023	-0.469
m(Seed set)*tmp	-0.015	0.051	-0.299	<b>0.765</b>	-0.116	0.085
m(Visit)*tmp	0.140	0.049	2.884	<b>0.004</b>	0.045	0.236
m(Fruit set)*pp	-0.005	0.001	-5.920	<0.001	-0.007	-0.003
m(Seed set)*pp	-0.006	0.001	-6.271	<0.001	-0.008	-0.004
m(Visit)*pp	-0.003	0.001	-5.125	<0.001	-0.004	-0.002
Scale(sp)*pp	0.003	0.001	5.217	<0.001	0.002	0.004

**Table S2.** Coefficients of the best models (lowest BIC, see Table 1) for invasive plants ( $Q_{\text{between}} = 400.89$ ,  $df = 32$ ,  $P < 0.001$ ,  $Q_{\text{total}} = 3288.54$ ,  $df = 246$ ,  $P < 0.001$ ). Bold values represent significant coefficients at  $\alpha \leq 0.05$ . Abbreviations:  $\beta$  = estimate, SE = standard error, CI = 95% confidence interval, m = metric, RAD = native pollinator diversity, lat = latitude, tmp = temperature, pp = precipitation.

Coefficient	Beta	SE	z	P	CI low	CI up
Intercept	7.328	4.284	1.711	0.087	-1.068	15.725
m(Fruit set)	-37.530	5.939	-6.319	<b>&lt;0.001</b>	-49.170	-25.890
m(RAD)	-5.962	4.473	-1.333	0.183	-14.728	2.804
m(Seed set)	2.271	2.571	0.883	0.377	-2.767	7.309
m(Visitation)	-15.117	3.793	-3.985	<b>&lt;0.001</b>	-22.551	-7.682
Latitude	-0.127	0.060	-2.116	<b>0.034</b>	-0.245	-0.009
Temperature	-11.076	4.235	-2.615	<b>0.009</b>	-19.377	-2.775
Precipitation	-0.485	0.162	-2.994	<b>0.003</b>	-0.802	-0.167
Scale(sp)	0.002	0.001	2.336	<b>0.019</b>	0.000	0.003
m(Fruit set)*lat	0.526	0.084	6.256	<b>&lt;0.001</b>	0.361	0.691
m(RAD)*lat	0.099	0.060	1.654	0.098	-0.018	0.217
m(Seed set)*lat	0.036	0.027	1.307	0.191	-0.018	0.089
m(Visit)*lat	0.257	0.061	4.201	<b>&lt;0.001</b>	0.137	0.377
m(Fruit set)*S(sp)	31.417	5.667	5.543	<b>&lt;0.001</b>	20.309	42.525
m(RAD)*S(sp)	14.473	4.794	3.019	<b>0.003</b>	5.077	23.869
m(Seed set)*S(sp)	-3.749	2.059	-1.821	0.069	-7.784	0.286
m(Visit)*S(sp)	14.925	3.488	4.279	<b>&lt;0.001</b>	8.089	21.761
Latitude*Scale(sp)	0.182	0.065	2.792	<b>0.005</b>	0.054	0.309
m(Fruit set)*tmp	1.209	0.176	6.885	<b>&lt;0.001</b>	0.865	1.553
m(RAD)*tmp	0.516	0.165	3.122	<b>0.002</b>	0.192	0.840
m(Seed set)*tmp	-0.015	0.047	-0.317	0.751	-0.108	0.078
m(Visit)*tmp	0.645	0.128	5.033	<b>&lt;0.001</b>	0.394	0.897
Scale(sp)*tmp	0.495	0.174	2.840	<b>0.005</b>	0.153	0.837
m(Fruit set)*pp	0.001	0.001	1.759	<b>0.079</b>	0.000	0.003
m(RAD)*pp	-0.003	0.001	-2.842	<b>0.004</b>	-0.004	-0.001
m(Seed set)*pp	-0.001	0.001	-0.649	0.517	-0.002	0.001
m(Visit)*pp	-0.001	0.001	-1.382	0.167	-0.003	0.000
m(FS)*lat*S(sp)	-0.453	0.084	-5.409	<b>&lt;0.001</b>	-0.617	-0.289
m(RAD)*lat*S(sp)	-0.164	0.069	-2.385	<b>0.017</b>	-0.299	-0.029
m(Visit)*lat*S(sp)	-0.247	0.063	-3.949	<b>&lt;0.001</b>	-0.370	-0.124



m(FS)*tmp*S(sp)	-1.149	0.187	-6.151	<0.001	-1.515	-0.783
m(RAD)*tmp*S(sp)	-0.791	0.193	-4.095	<0.001	-1.169	-0.412
m(Visit)*tmp*S(sp)	-0.609	0.142	-4.272	<0.001	-0.888	-0.330

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**Table S3.** Sensitivity analysis of the best model for plants, by removing four outlier points with Hedges'  $d < -5$  values, with a comparison of the original and the adjusted models. Bold values represent significant coefficients at  $\alpha \leq 0.05$ . Abbreviations:  $\beta$  = estimate, SE = standard error, m = metric, RAD = native pollinator diversity, lat = latitude, tmp = temperature, pp = precipitation.

Coefficient	Original model			Adjusted model		
	$\beta$	SE	P	$\beta$	SE	P
Intercept	7.328	4.284	0.087	5.067	4.257	0.234
m(Fruit set)	-37.530	5.939	< <b>0.001</b>	-34.245	5.928	< <b>0.001</b>
m(RAD)	-5.962	4.473	0.183	-3.585	4.446	0.420
m(Seed set)	2.271	2.571	0.377	0.591	2.556	0.817
m(Visitation)	-15.117	3.793	< <b>0.001</b>	-12.128	3.787	<b>0.001</b>
Latitude	-0.127	0.060	<b>0.034</b>	-0.096	0.060	0.109
Temperature	-11.076	4.235	<b>0.009</b>	-7.775	4.213	0.065
Precipitation	-0.485	0.162	<b>0.003</b>	-0.361	0.161	<b>0.025</b>
Scale(sp)	0.002	0.001	<b>0.019</b>	0.002	0.001	<b>0.027</b>
m(Fruit set)*lat	0.526	0.084	< <b>0.001</b>	0.482	0.084	< <b>0.001</b>
m(RAD)*lat	0.099	0.060	0.098	0.067	0.060	0.260
m(Seed set)*lat	0.036	0.027	0.191	0.048	0.027	0.081
m(Visit)*lat	0.257	0.061	< <b>0.001</b>	0.215	0.061	< <b>0.001</b>
m(Fruit set)*S(sp)	31.417	5.667	< <b>0.001</b>	27.575	5.661	< <b>0.001</b>
m(RAD)*S(sp)	14.473	4.794	<b>0.003</b>	11.072	4.770	<b>0.020</b>
m(Seed set)*S(sp)	-3.749	2.059	0.069	-2.920	2.035	0.151
m(Visit)*S(sp)	14.925	3.488	< <b>0.001</b>	11.246	3.489	<b>0.001</b>
Latitude*Scale(sp)	0.182	0.065	<b>0.005</b>	0.135	0.065	<b>0.036</b>
m(Fruit set)*tmp	1.209	0.176	< <b>0.001</b>	1.067	0.176	< <b>0.001</b>
m(RAD)*tmp	0.516	0.165	<b>0.002</b>	0.390	0.164	<b>0.017</b>
m(Seed set)*tmp	-0.015	0.047	0.751	0.015	0.047	0.752
m(Visit)*tmp	0.645	0.128	< <b>0.001</b>	0.510	0.128	< <b>0.001</b>
Scale(sp)*tmp	0.495	0.174	<b>0.005</b>	0.345	0.173	<b>0.046</b>
m(Fruit set)*pp	0.001	0.001	<b>0.079</b>	0.001	0.001	0.098
m(RAD)*pp	-0.003	0.001	<b>0.004</b>	-0.003	0.001	<b>0.005</b>
m(Seed set)*pp	-0.001	0.001	0.517	-0.001	0.001	0.507
m(Visit)*pp	-0.001	0.001	0.167	-0.001	0.001	0.148
m(FS)*lat*S(sp)	-0.453	0.084	< <b>0.001</b>	-0.400	0.084	< <b>0.001</b>
m(RAD)*lat*S(sp)	-0.164	0.069	<b>0.017</b>	-0.118	0.068	0.085

m(Visit)*lat*S(sp)	-0.247	0.063	< <b>0.001</b>	-0.194	0.062	<b>0.002</b>
m(FS)*tmp*S(sp)	-1.149	0.187	< <b>0.001</b>	-0.984	0.187	< <b>0.001</b>
m(RAD)*tmp*S(sp)	-0.791	0.193	< <b>0.001</b>	-0.635	0.192	< <b>0.001</b>
m(Visit)*tmp*S(sp)	-0.609	0.142	< <b>0.001</b>	-0.451	0.142	<b>0.001</b>

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