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The global contribution of wild insect and honeybee visitation to crop pollination success is asymptotic

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Data and Code Availability Statement

The data and code of this study are available athttps://figshare.com/articles/dataset/The_global_contribution_of_wild_insect_and_honeybee_visitation_to_crop_pollination_success_is_asymptotic/27118575.

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Conflict of interest disclosure

The authors have no conflict of interest to declare.

Abstract

Background

Animal-mediated pollination plays a crucial role in the reproductive success of flowering plants, and insect pollination in particular for crops. Pollination biology suggests that the effect of pollen deposition from animal visitation on pollination success is asymptotic. Initially, increased insect visitation increases pollination success in decreasing increments, eventually reaching a saturation threshold where additional visits do not further increase pollination success. However, most crop pollination research considers linear relations between insect visitation and pollination success, which overlooks the fact that pollination success is necessarily limited by an asymptotic relation.

Asymptotic models improve predictions for global data

Utilizing the CropPol database, we tested whether non-linear models (asymptotic and hump-shaped) improve the fit of the relation between honeybee and wild insect visitation and crop pollination success compared to linear models. Our results indicate that the relation is best described by asymptotic models.

Synthesis and management implications

We argue that incorporating asymptotic models to crop pollination research can advance our understanding of the pollination contributions of honeybees and wild insects and inform pollinator management to maximize food production. From a management viewpoint, asymptotic models imply that insect visitation can be optimized to maximize crop pollination and yield. Moreover, declines in pollinator populations and their effects on crop pollination may go unnoticed until pollinator visitation falls below the saturation threshold. In sum, these findings can guide development of evidence-based and cost-effective pollination management strategies.

Keywords

Agriculture, *Apis mellifera*, asymptotic model, bees, biodiversity, crop yield, wild pollinators

Key findings of crop pollination research

Insect pollinators are critical for food security, as they contribute to the pollination of most of the world's food crops, thereby increasing fruit and seed production (Klein et al. 2007; Siopa et al. 2024). A diversity of wild insects, including bees, flies and moths, play a significant role in crop production (Garibaldi et al. 2013; Rader et al. 2016). Additionally, farmers rely on managed insects to ensure pollination services, with the Western honeybee (*Apis mellifera* Linnaeus) being the most common used species (Osterman et al. 2021). The contribution of wild insects and honeybees often depends on certain features of the farming system, including crop species, flower morphology and mating system, cultivar, landscape structure and farming intensity (Gaines-Day and Gratton 2016; Dainese et al. 2019; Reilly et al. 2020; Ohlnuud et al. 2022; Eeraerts et al. 2023, 2024). Over the last 30-40 years, the global area dedicated to pollinator-dependent crops has increased faster (+137%) than the area of all crops (+41%; Aizen et al. 2019), leading to a growing reliance on insect pollinators in agriculture. Declines in wild insect populations over recent decades, coupled with increasing pressure on honeybee health, have raised concerns about the maintenance and reliance of their pollination service (Biesmeijer et al. 2006; Goulson et al. 2015; Osterman et al. 2021; Requier et al. 2024). If pollination services are to be sustainably managed to maintain food production in the face of increasing agricultural demand and continued pollinator decline, it is essential to identify evidence-based guidelines to safeguard pollinator populations.

In recent decades, crop pollination research has received increasing attention (Allen-Perkins et al. 2022). This has resulted in multiple syntheses aimed at disentangling the effects of flower visitation frequency by honeybees and wild insects (hereafter "honeybee and wild insect visitation") on crop pollination success and yield. The distinction between honeybees and wild insect pollinators is pertinent because both require different management strategies, with a focus on hive application for honeybees and a focus on maintaining and creating high-quality landscapes for wild pollinators (Isaacs et al. 2017; DeVetter et al. 2022). These syntheses, which include multiple crops, mainly detect clear, positive effects of insect visitation on crop pollination success, but with lower overall effect sizes for honeybee visitation compared to wild insect visitation (Garibaldi et al. 2013; Rader et al. 2016; Dainese et al. 2019). Crop-specific synthesis of pollination research in oilseed rape, coffee and highbush blueberry detect similar effects (Woodcock et al. 2019; Moreaux et al. 2022; Eeraerts et al. 2023). Additionally, a recent multi-crop synthesis presented an impressive assessment of the contributions of pollinator visitation to crop pollination, concluding that honeybee and wild insect visitation contribute equally and positively to crop pollination, and that this contribution of both honeybees and wild insects is crop-dependent (Reilly et al. 2024).

Asymptotic relation between insect visitation and pollination success

The relation between flower visit frequency by pollinators and fruit and seed set can be understood through two biological mechanisms. First, the number of pollen grains deposited per stigma typically increases asymptotically with the number of insect pollinator visits per flower (Wilson 1995a, 1995b; Chacoff et al. 2008; Morris et al. 2010; MacInnis and Forrest 2019; Kendall et al. 2022). This might be due to the limiting surface area of the stigma, which can hold a finite amount of pollen (e.g., 200-300 pollen tetrads per stigma for highbush blueberry; Parrie and Lang 1992). Second, the relation between stigma pollen receipt and fruit and seed set is also asymptotic (mathematically formalized by Aizen and Harder 2007; for empirical examples see: Falque et al. 1995; Cane and Schiffhauer 2003; Broussard et al. 2021). This is explained by the limited number of ovules available per flower, the limited amount of maternal resources available to develop ovaries and embryos into mature fruits and seeds (Harder and Routley 2006; Aizen and Harder 2007; Harder and Aizen 2010), or by the limited amount of resources available within the style that enable the pollen tubes to grow up to the ovary, implying a maximum load of pollen tubes that can reach the base of the style (Harder et al. 2016a, 2016b). These two mechanisms imply an asymptotic relation between the insect pollinator visitation and the resulting fruit and seed set, which aligns with empirical findings observed in several studies (Chagnon et al. 1993; Aras et al. 1996; Richards et al. 2009; Morris et al. 2010; Alonso et al. 2011; Andrikopoulos and Cane 2018; Nicholson and Ricketts 2019; Reilly et al. 2020; Eeraerts et al. 2024; Turo et al. 2024). In addition, modelling and cage studies have also suggested that pollination success can decrease in case of very high rates of pollen deposition or insect pollinator visitation, suggesting over-visitation or over-pollination (Morris et al. 2010; Brittain et al. 2013; Sáez et al. 2018; Rollin and Garibaldi 2019). More recently this negative relation or hump-shaped relation has also been detected in studies performed in realistic field setups (Sáez et al. 2014; Miñarro et al. 2023; Ramírez-Meíja et al. 2024).

To infer the relation between insect visitation and crop pollination success, we propose four possible relations: (i) no relation (intercept-only model) if the maximum crop pollination success is reached (i.e., all the ovules of all flowers are fertilized) across the entire gradient of insect visitation (**Fig. 1A**), (ii) a positive, linear relation if the maximum crop pollination success is not reached along the gradient of insect visitation (**Fig. 1B**), (iii) an asymptotic relation, where pollination success increases with insect visitation but at diminishing rates, eventually reaching a saturation threshold beyond which additional visits do not further enhance pollination success (**Fig. 1C**), and (iv) a hump-shaped relation, in which pollination success increases with insect visitation until reaching a saturation level, with additional visits reducing pollination success (**Fig. 1D**). However, asymptotic and hump-shaped models have not yet been considered in crop pollination syntheses across multiple crops (Garibaldi et al. 2013; Rader et al. 2016; Dainese et al. 2019; Reilly et al. 2024; but see Turo et al. 2024), nor in crop-specific syntheses (Woodcock et al. 2019; Moreaux et al. 2022; Eeraerts et al. 2023), as these syntheses have only used linear models.

Analyses of global dataset confirm asymptotic relation

The most recent synthesis of global crop pollination research by Reilly *et al.* (2024) investigated the relative importance of different insect pollinators to crop pollination, highlighting that wild insects and honeybees contribute equally to pollination of crops worldwide. As is conventional, pollination syntheses have mainly considered linear models to assess the relative contributions of wild insects and honeybees to crop pollination success (Garibaldi et al. 2013; Woodcock et al. 2019; Eeraerts et al. 2023; Reilly et al. 2024). However, predicting pollination service contribution using an asymptotic or hump-shaped models may increase the accuracy and biological relevance of the model predictions (**Fig. 1**). Therefore, we investigated the extent to which asymptotic and hump-shaped models may better describe the relation between insect visitation and crop pollination success than linear models. To ensure our estimates are comparable with previous research we generally follow the methods of Reilly *et al.* (2024).

We used the CropPol database version 2.0.0 (Allen-Perkins et al. 2022), an open, global database of crop pollination research, that compiles data from 137 studies across 49 crops to analyse the relation between crop pollination success and flower visit frequency by two main groups of insect pollinators, honeybees and wild insects. We modelled the relation between insect visitation and crop pollination success using a series of linear mixed-effects models (R function *lmer*, R package *lme4*; Bates et al. 2015). Specifically, we compared models in which both honeybee and wild insect visitation were modelled as a linear model ($y = a + b \cdot x$), as a negative exponential model for the asymptotic relation ($y = a + b \cdot e^{-x}$), and as a quadratic model for the hump-shaped relation ($y = a + b \cdot x + c \cdot x^2$). For linear, asymptotic and hump-shaped relations, we constructed five models: a null model, a model with only honeybee visitation, one with only wild insect visitation, one with both honeybees and wild insects without their interaction, and one with both honeybees and wild insects including their interaction (see **Table S1** and supplementary methods for detailed model description). Additionally, we considered three more models, one linear, one asymptotic and one hump-shaped where total insect visitation was used as a fixed variable (i.e., the sum of honeybee and wild insect visitation; **Table S1**). All models included both random intercepts and random slope for the study system. The most parsimonious model was determined based on the corrected Akaike Information Criteria (ΔAIC_C).

Before analyses, the data from the different studies were standardized by means of z-scores to allow comparison of data originating from different studies. More comprehensive details on the methods can be found in supplementary material. All analyses were computed with the *R* software, version 4.2.0 (R Development Core Team, 2022).

Our analyses indicate that the asymptotic model, which includes both honeybee and wild insect visitation, best explains crop pollination success (**Table 1**, **S1**; **Figure 2A**, **2B**). Moreover, the best model identified by our analyses was more informative compared to all other models (**Table 1**, **S1**; ΔAIC_C = 8.07 compared to the model with the second lowest AIC_C). In the asymptotic model, the effect size of honeybees on crop pollination success (-0.091 ± 0.040, estimate ± SE; **Table 1**) was equivalent to the effect size of wild insects (-0.088 ± 0.037). This finding aligns with Reilly et al. (2024), also reporting similar effect sizes for honeybees and wild insects (0.069 ± 0.034 and 0.061 ± 0.031, respectively; **Table 1; Figure 2C**, **2D**) in their best (linear) model. Additional analyses that excluded outlier datapoints for the response variable gave consistent results (**Table S2**, **S3**; **Figure S1**).

Implications of asymptotic relation for pollination research

Our analyses indicate that asymptotic models provide a better fit of the relation between pollinator visitation and crop pollination success in a global analysis compared to linear models. This highlights the importance of considering the underlying mechanisms of pollination biology when modelling crop pollination success.

Given the widespread use of linear models in pollination research, our findings stress the need to consider asymptotic models in future research. The asymptotic models highlight equivalent contributions for the two pollinator groups (see Reilly et al. 2024). However, it is important to note how the predictions differ: an asymptotic relationship suggests that the potential gain from higher visitation of honeybees and wild insects will depend on the current state of pollination within the crop system. Overlooking asymptotic models may explain, at least in part, the frequently reported non-significant effects of honeybee visitation on crop pollination success observed in various case studies and syntheses (e.g., fruit set increased significantly with honeybee visitations in only 14% of the crop systems synthesized in Garibaldi *et al*. (2013)). Hence, given the theoretical relation between pollen deposition and yield, our analysis suggest that asymptotic relations need to be considered, and their performance compared to that of linear models in future research (for possible additional non-linear modelling approaches such as logarithmic or segmented regressions, see Bolker 2008; Reilly et al. 2020; Osterman et al. 2023; Turo et al. 2024).

Our analyses also did not provide evidence for the hump-shaped relation observed in other studies (Morris et al. 2010; Rollin and Garibaldi 2019; Ramírez-Meíja et al. 2024), neither for a negative relation between pollinator visitation and pollination success (Sáez et al. 2014; Miñarro et al. 2023; Li et al. 2025). Hence, we conclude that, globally, there is no evidence of over-visitation or over-pollination in crops (Sáez et al. 2014; Rollin and Garibaldi 2019; Ramírez-Meíja et al. 2024). Still, given the current evidence for these negative or hump-shaped patterns, we also recommend incorporating these types models to study possible over-visitation or over-pollination in pollination research as it can further advance our understanding of the pollination contributions of honeybees and wild pollinators.

The composition of pollinator communities can also influence the pollination success, given both the variability of species-specific functional traits and the potential effects of interspecific interactions on the pollination contribution of pollinator species (Blüthgen and Klein 2011). A range of morphological, behavioural and phenological traits can influence pollination efficiency of pollinator species, being pollinator communities with non-overlapping functional traits hypothesized to provide a higher overall pollination service (Blüthgen and Klein 2011; Woodcock et al. 2019). Yet, evidence for this complementarity hypothesis in crops pollination is limited (but see Woodcock et al. 2019; Greenop et al. 2023). In general, pollination efficiency varies among pollinator species, with wild bees often showing a higher pollination efficiency on a per flower visit basis compared to honeybees (e.g., MacInnis and Forrest 2019; Page et al. 2021; Kendall et al. 2022). Moreover, the pollination performance of honeybees can be positively influenced by the presence of wild insect pollinators (e.g., Brittain et al. 2013; Osterman et al. 2023). Future research should improve our understanding of how the pollinator community composition impacts the slopes of the asymptotic relation and the associated optimum pollinator visitation rates associated with the asymptote.

Implications for pollination management and conservation

There is growing evidence that pollination deficits are limiting crop production across crops, cultivars and production regions (Reilly et al. 2020; Garratt et al. 2021; Ohlnuud et al. 2022; Eeraerts et al. 2023; Osterman et al. 2024; Siopa et al. 2024; Turo et al. 2024). Hence, pollinator management is increasingly recognized as a critical agricultural input which could benefit from optimalisation (Tamburini et al. 2019; Garibaldi et al. 2020). Research based solely on linear models can lead to the guideline "more pollinators are better". In contrast, the guideline developed from asymptotic models is that optimum pollinator visitation rates can be determined to maximize crop pollination success (e.g., Garibaldi et al 2016; Garibaldi et al. 2020). This information can then be used to inform policy and management, as it provides more meaningful and concrete information compared to linear models, potentially leading to economic gains if existing pollination levels are suboptimal (Garratt et al. 2021; Ohlnuud et al. 2022; Eeraerts et al. 2023; Turo et al. 2024).

Another key conclusion of these analyses is that honeybees and wild insect pollinators contribute equally to global crop pollination. This is in line with earlier syntheses, confirming the positive contribution of wild insects (Garibaldi et al. 2013; Rader et al. 2016; Dainese et al. 2019; Woodcock et al. 2019; Eeraerts et al. 2023; Reilly et al. 2024) and it adds to the findings of more recent studies that highlight the positive contribution of honeybees to crop pollination success (Sáez et al. 2022; Eeraerts et al. 2023; Reilly et al. 2024). From other research we conclude that some wild insects are more effective pollinators compared to the honeybee, e.g., higher pollen deposition load or greater capacity for foraging in suboptimal weather conditions (Vicens and Bosch 2000; Hung et al. 2018; MacInnis and Forrest 2019; Page et al. 2021; Kendall et al. 2022). However, not all wild pollinating insects are per se more efficient compared to honeybees (Hung et al. 2018; Page et al. 2021), and especially in self-compatible crops honeybees can be effective pollinators (Rader et al. 2009; Sáez et al. 2022; Eeraerts et al 2023). The large database that was used here captures considerable variation across studies in multiple crops of visitation rates of honeybees and wild insects (see Reilly et al. 2024), yet on average their visitation rates are nearly equal (mean proportion of visits for honeybees and wild insects is 52.2% and 47.8%, respectively). In sum, the equal, overall contributions of honeybees and wild insects that we observed can therefore be attributed to the fact that within this large database some highly efficient wild insect species compensate for the variation in pollination efficiency between wild insect species. Following the crop-focused synthesis in Reilly *et al*. (2024), future synthesis should focus on how the contribution of honeybees and wild insect pollinators varies across crops (see also Bartomeus et al. 2014; Geslin et al. 2017), as well as pollination metrix considered (e.g., seed set, seed weight, kg per plant; Garratt et al. 2021; Eeraerts et al. 2024).

Additionally, the declines and pressures observed on populations of wild insect pollinators raise concerns for future pollination services and crop production (Biesmeijer et al. 2006; Goulson et al. 2015). The asymptotic relation observed in our study between flower visitation rates by wild insect pollinators and pollination success has implications on how pollinator declines can impact food production. Specifically, an asymptotic relation suggests a threshold around which the asymptote is reached, and below which a small decrease in pollinator populations would disproportionally reduce crop pollination success and conversely a small increase would disproportionally enhance it (Jensen's inequality; see Richards et al. 2009; Garibaldi et al. 2011, 2016). In contrast, pollinator declines resulting in reduced visitation rates close to the asymptote might show little to no consequences on yield and might remain undetected. Therefore, improving our understanding of the pollination requirements of crops and how to manage crop pollination is crucial to ensure that practices related to wild insect pollinator management contribute to efficient crop production.

In conclusion, our findings underscore benefits of pollinator management will be context dependent with the greatest benefits in crop systems where pollinator abundances are impoverished. In addition, our findings underscore that both wild insects and honeybees contribute to crop pollination success, suggesting that different pollinator management strategies can be employed to enhance and optimize pollination. For instance, management of honeybees and other alternative managed bees entails renting honeybee hives or purchasing commercial nests of alternative bees and introducing these managed bees during crop flowering (Gaines-Day and Gratton 2016; Eeraerts et al. 2022; Osterman et al. 2021, 2023). While on the other hand, wild pollinator populations in and around farms can be enhanced by conserving or creating on-farm and off-farm pollinator friendly habitats (Eeraerts 2023; Tscharntke et al. 2024) and by adopting pollinator-friendly practices that reduce the impact of pesticides, diseases and parasites or that promote flower and nesting resources continuity (Stanley et al. 2015; Isaacs et al. 2017).

Data and Code Availability Statement

The data and code of this study are available at 10.6084/m9.figshare.27118575.

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Figures and tables

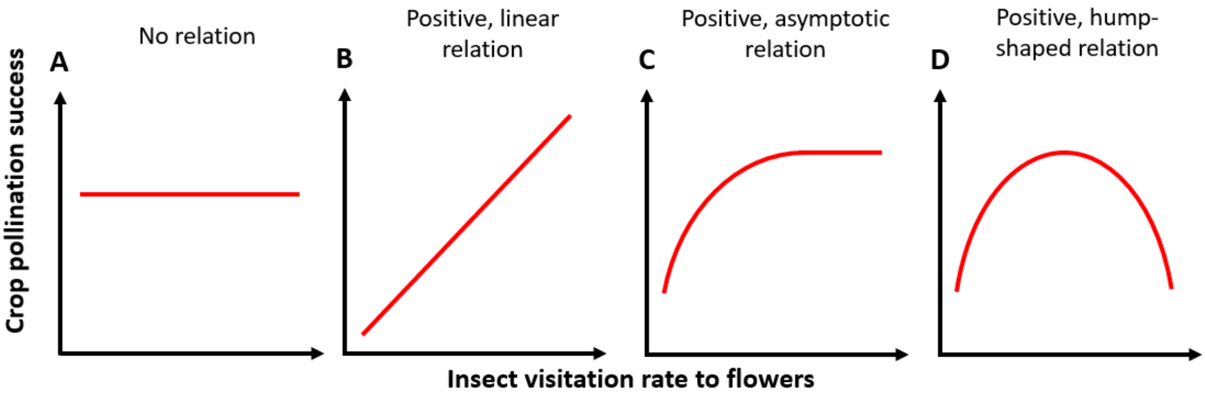

Figure 1: Conceptual figure illustrating the possible relations between insect visitation and crop pollination success. Pollination success can be expected to (A) be unaffected by insect visitation, concluding no relation, (B) increase linearly with insect visitation without reaching the maximum pollination success, (C) increase non-linearly and reaching a maximum pollination success along the gradient of insect visitation, resulting in an asymptotic relation, or (D) increase non-linearly, reaching a saturation level beyond which it decreases with increasing insect visitation, resulting in a hump-shaped relation.

Table 1: Linear mixed-effect models assessing the effect of honeybee (HB) and wild insect (WI) visitation on crop pollination success. The best model of our analyses and the best model identified by Reilly *et al*. (2024) are reported with their ΔAIC_c, marginal R^2 (R^2_m), model estimates, standard errors (SE), *t*-statistics and *P*-values. ΔAIC_c is the difference between (a) the AIC_c of the model with the lowest AIC_c and the AIC_c of the model with the second lowest AIC_c, and (b) the AIC_c of the model with the lowest AIC_c and the AIC_c of the best model identified by Reilly *et al*. (2024).

Model	ΔAIC_c	R^2_m	Parameters	Estimate	SE	*t*	*P*
$e^{-HB} + e^{-WI}$	8.07 (a)	0.0135	intercept	0.242	0.075	3.25	0.002
			e^{-HB}	-0.091	0.040	-2.31	0.024
			e^{-WI}	-0.088	0.037	-2.40	0.019
HB + WI	17.08 (b)	0.0092	intercept	1.907e-17	0.020	0.00	1.000
			HB	0.069	0.034	2.00	0.049
			WI	0.061	0.031	1.98	0.053

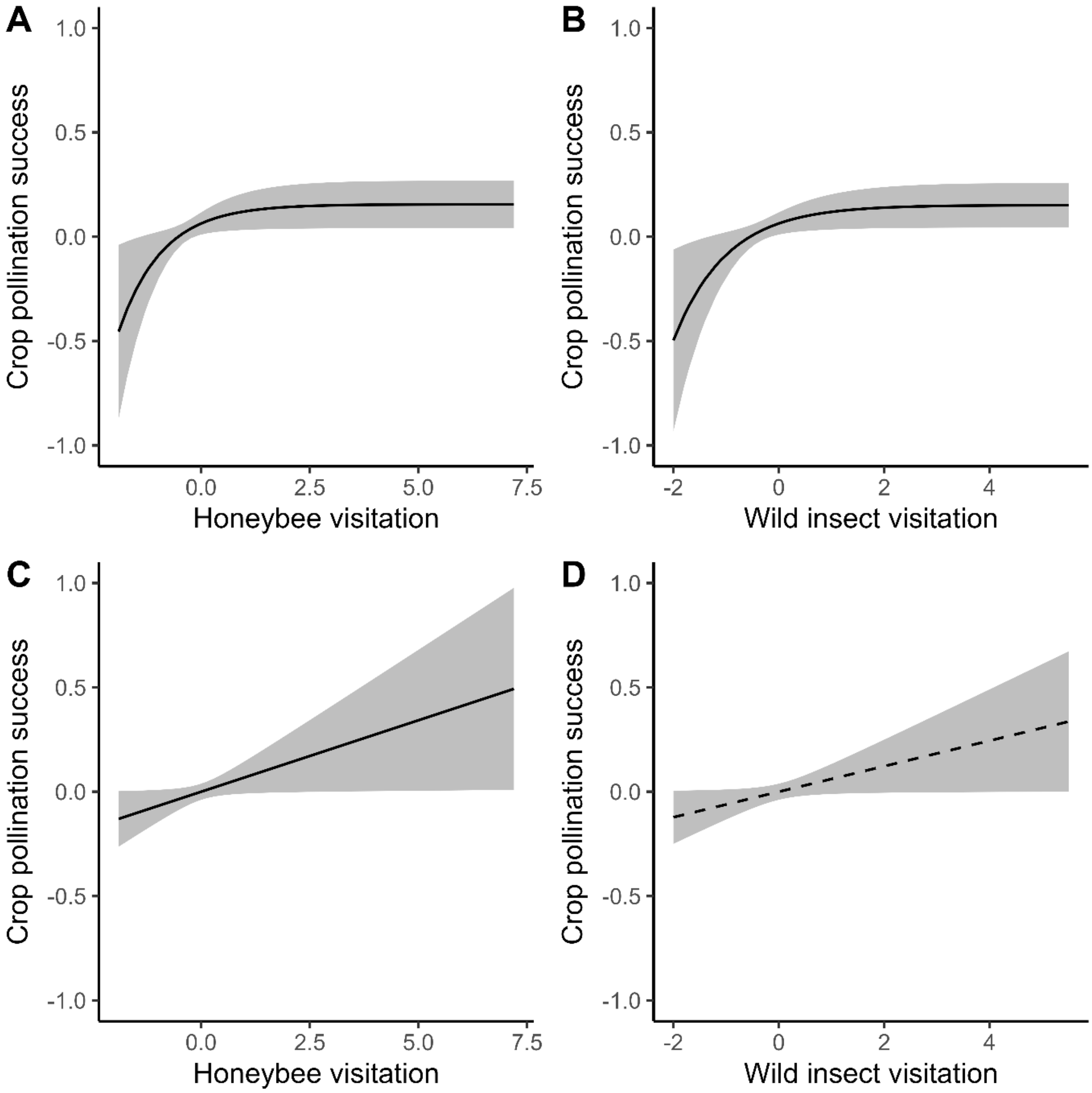

Figure 2: Relation between crop pollination success and honeybee (A) and wild insect (B) visitation as modelled asymptotically (most parsimonious model identified in our analyses). Relation between crop pollination success and honeybee (C) and wild insect (D) visitation as modelled linearly (most parsimonious model identified by Reilly *et al.* (2024)). Data of both fixed and response variables are expressed as z-scores. The solid lines show relations with P < 0.05, the dashed line shows a relation with P ≥ 0.05, and the grey shaded areas show the 95% confidence interval around the mean predictions.

Supplementary file content

Supplementary methods for analyses

Model ranking table

Model ranking table without outliers

Model results table without outliers

Model result figure without outliers