

# **Is there a relationship between distance to natural habitat and pollination services in tropical smallholder farms? A systematic review and meta-analysis**

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1 **ABSTRACT**

2 Proximity to natural habitat is known to enhance pollination services in agricultural landscapes,  
3 particularly in large-scale industrialised farms. However, it remains unclear whether these  
4 patterns hold in tropical smallholder farms – ecologically complex landscapes that sustain  
5 millions of the world’s most food-insecure communities and depend heavily on biodiversity-  
6 derived ecosystem services. Here, we present a systematic review and meta-analysis of 32  
7 studies assessing the relationship between distance from natural habitat and pollinator  
8 abundance, species richness, and crop fruit set in tropical smallholder farms. We found no  
9 consistent effect of distance on pollinator abundance and crop fruit set. While pollinator species  
10 richness declined with increasing distance to natural habitat, especially when excluding  
11 managed honeybees, this relationship was highly variable across studies, constraining the  
12 generalisability of observed trends. Our results thus indicate that diverse smallholder  
13 landscapes may buffer against negative effects of distance to natural habitat on pollination  
14 services. Yet, variability in study methodologies and spatial scales – ranging from a few  
15 hundred meters to several kilometres – limits the ability to determine clear patterns. More  
16 standardised, open-access research is needed to clarify the nuanced pollination dynamics in  
17 tropical smallholder farms and inform conservation strategies that support both biodiversity  
18 and rural livelihoods.

19 **KEYWORDS**

20 Pollination, pollinator diversity, honeybee, ecosystem services, landscape ecology, tropical  
21 agriculture, agroecosystems, sustainable agricultural landscapes, synthesis, biodiversity  
22 conservation

## 23 1 INTRODUCTION

24 Pollination plays a key role in supporting biodiversity and food production in agricultural  
25 landscapes (IPBES 2016), with an estimated 30% of the global food crop production volume  
26 depending on pollinators (Klein et al. 2007). Pollination services, recognised as a key Nature’s  
27 Contribution to People (IPBES 2019), underpin the availability of diverse and nutritionally-  
28 balanced diets (Eilers et al. 2011, Smith et al. 2015, Gazzea et al. 2023), with many pollinator-  
29 dependent crops relying on both managed and wild pollinators to boost yields (Osterman et al.  
30 2021, Siopa et al. 2024). This is particularly important in tropical smallholder farms (TSFs)  
31 which account for 84% of the 570 million farms worldwide (Lowder et al. 2021) and constitute  
32 the primary means of livelihood for many of the world's most food insecure communities  
33 (Laborde Debucquet et al. 2020, World Bank 2022). TSFs are typically defined as family-  
34 managed farms that produce crops or livestock on small plots of land (although definitions vary  
35 by region and context; FAO 2017) and have been found to support higher crop and non-crop  
36 diversity compared to larger farms (Ricciardi et al. 2021). By depending more on natural  
37 ecosystem services than industrial inputs (Timberlake et al. 2022), TSFs rely on pollination  
38 services for crop yields and nutrition, with pollinator-dependent crops providing essential  
39 micronutrients that prevent malnutrition (Chaplin-Kramer et al. 2014, Tibesigwa et al. 2019,  
40 Mulungu et al. 2023). Maintaining and enhancing pollinator populations and diversity in TSFs  
41 is thus a conservation and food security priority (United Nations 2015), especially in the face  
42 of ongoing land-use change and habitat fragmentation, increasing pesticide application,  
43 environmental pollution, and decreasing resource diversity (Potts et al. 2010, Dicks et al. 2021).

44 One way of sustaining pollination services in TSFs is through pollinator-friendly  
45 management and design strategies (IPBES 2016, Potts et al. 2016). In particular, maintaining  
46 semi-natural and natural habitat (hereafter ‘natural habitat’) in close proximity to TSFs could

47 be effective since these habitats provide essential resources for pollinators, such as food and  
48 nesting sites (Ricketts et al. 2008, Garibaldi et al. 2011, Cole et al. 2017, Tscharntke et al.  
49 2021). Evidence from previous meta-analyses supports this notion, demonstrating that  
50 increasing distance from natural habitat negatively affects pollination services (Ricketts et al.  
51 2008, Garibaldi et al. 2011). However, these meta-analyses included primarily data from  
52 studies on larger-scale, more industrialised farms rather than TSFs which typically exhibit high  
53 agrobiodiversity and landscape heterogeneity (Ricciardi et al. 2021, Tscharntke et al. 2022).  
54 Furthermore, these meta-analyses are now over a decade old, and were not underpinned by a  
55 systematic review, meaning that relevant studies (old and new) may have been missed, and  
56 meta-analytical results were not presented within the important context of quality appraisal of  
57 the included studies. Indeed, recent studies on effects of isolation from natural habitat on  
58 pollination services in TSFs present a diverse array of findings, ranging from declines (e.g.  
59 Silva et al. 2019, Obregon et al. 2021, Severiano-Galeana et al. 2024) to no or even positive  
60 relationships (e.g. Bravo-Monroy et al. 2015, Buchori et al. 2019, Toledo-Hernandez et al.  
61 2021). This raises the questions of how consistently these patterns are reported in TSFs, and  
62 what might explain the variability in findings across different studies.

63 Here, we tested for the presence of a consistent negative relationship between distance  
64 from natural habitat and three proxies for pollination services - pollinator abundance, species  
65 richness, and fruit set. We further explored whether the presence of managed honeybees (*Apis*  
66 *mellifera* and *Apis cerana*) masked negative relationships between distance from natural habitat  
67 and other pollinator species. Managed honeybees have been found to respond less strongly to  
68 increasing distance from natural habitat compared to wild pollinators (Garibaldi et al. 2011),  
69 probably due to their larger foraging ranges, generalist feeding habits, and capacity to colonise  
70 various habitats (Gathmann and Tscharntke 2002, Steffan-Dewenter et al. 2002, Steffan-  
71 Dewenter and Kuhn 2003, Scott Schneider et al. 2004, Osterman et al. 2021). We also

72 hypothesised that decay relationships would be stronger in relatively high agricultural intensity  
73 TSFs, since extensive use of pesticides and other agrochemicals is strongly associated with  
74 pollinator declines (Millard et al. 2021), possibly making proximity to natural habitat more  
75 critical for maintaining pollination services. In contrast, low and intermediate levels of  
76 agricultural intensity can support diverse pollinator communities (Millard et al. 2021), and  
77 might thus sustain populations even at greater distances from natural habitat. Furthermore, we  
78 hypothesised that crops with higher pollinator dependence would experience stronger negative  
79 effects on fruit set with increasing distance to forest. We expect this because a decline in  
80 pollination services, for instance due to isolation from natural habitats, might lead to stronger  
81 declines in fruit or seed production for crops that rely heavily on biotic pollination and have  
82 limited capacity for abiotic- or self- pollination (Klein et al. 2007).

83 We investigated these hypotheses through a systematic review and meta-analysis of  
84 ecological studies on the effects of isolation from natural habitat on pollination services in  
85 TSFs. This synthesis advances previous meta-analyses (Ricketts et al. 2008, Garibaldi et al.  
86 2011) as our more defined scope enables us to underpin our meta-analysis with a full systematic  
87 review, conducted to current standards. This includes systematic searches for all relevant  
88 literature, quality appraisal of the included studies, and more comprehensive and up-to-date  
89 meta-analytical methods for the primary, subgroup and sensitivity analyses. These key features  
90 of a systematic review are designed to help reconcile the conflicting evidence for pollination  
91 distance-decay relationships in TSFs, and thus inform more effective conservation and  
92 agricultural management strategies in these vital components of global food security and  
93 biodiversity.

## 94 **2 METHODS**

### 95 **2.1 Pre-registration, guidelines and reporting**

96 The original systematic review and meta-analysis plan was preregistered on the Open Science  
97 Framework in November 2022 (Bosshard et al. 2022). While the core hypotheses and overall  
98 methodological approach remain consistent with the preregistration, we since implemented  
99 specific updates – particularly to the search strategy and statistical analysis – to align the  
100 systematic review with current best practices in evidence synthesis. All deviations from the  
101 original plan are reported in Table S3 following the standardised schema of Willroth and  
102 Atherton (2024). The systematic review and meta-analysis was conducted and reported  
103 according to PRISMA (Page et al. 2021) and Cochrane Handbook guidelines (Higgins et al.  
104 2024), to the extent possible for ecological studies.

### 105 **2.2 Eligibility criteria**

106 Studies were considered eligible for inclusion based on the PECO-type systematic review  
107 criteria, which define the Population, Exposure/Comparator and Outcome of interest (Morgan  
108 et al. 2018). Firstly, our Population criterion was that studies focused on insect pollinators  
109 and/or insect-pollinated crops in TSFs. Farms were considered tropical if they were located  
110 between the Tropics of Cancer (23°27) and Capricorn (23°27), and ‘smallholder’ if the study  
111 described them as ‘smallholder’, ‘small-scale’ or ‘subsistence’ farms; or farm size was  
112 quantified as <2ha. As there is no universal definition of smallholder farms, and size can vary  
113 across regions (FAO 2017), farms <15ha were also considered as TSFs if the description in the  
114 original publication mentioned a) low agricultural intensity, b) high crop diversity within the  
115 farm, and/or c) produce use mainly intended for household and local markets, (Fig. S1), or if  
116 corresponding authors provided this information.

117 Secondly, our Exposure/Comparator criterion was that studies compared pollination  
118 variables in TSFs with varying degrees of isolation from natural habitat. We followed the  
119 definition of ‘natural habitat’ based on the classification used in the original studies, without  
120 imposing a standardised definition. What constituted natural habitat thus varied depending on  
121 how it was defined by the respective study authors (e.g., forests, shrublands, or other semi-  
122 natural areas). We included studies with different measures of isolation from natural habitat,  
123 including the proportion of natural habitat within a specific radius around the farm and  
124 categorical classifications such as ‘near’ and ‘far’, provided we were able to standardise these  
125 measures to distance to the nearest natural habitat (see data collection and data items section).

126 Thirdly, our Outcome criterion was that studies assessed at least one of three proxies  
127 associated with insect pollination in smallholder farms; pollinator abundance (count of number  
128 of individual pollinators), pollinator species richness (count of pollinator species), or fruit/seed  
129 set of pollinator crops (proportion of flowers that successfully developed into fruits or seeds).

130 Additionally, studies had to be empirical field studies, published in English, and report  
131 or make available upon request sufficient data to permit our meta-analysis. A more detailed  
132 overview of our eligibility criteria is provided in Table S1.

### 133 **2.3 Information sources and search strategy,**

134 We identified relevant studies primarily by conducting systematic searches of three  
135 bibliographic databases: the Web of Science Core Collection, Scopus, and CAB Abstracts.  
136 These databases were selected to identify peer-reviewed reports of scientific studies (i.e.  
137 scientific papers) in ecology and agriculture. Web of Science and Scopus are widely recognised  
138 as core databases for ecological research (Foo et al. 2021), whilst CAB Abstracts is a dedicated  
139 database for agriculture and applied life sciences.

140 We searched the databases on 22 December 2024 using search terms related to 1)  
141 pollination services, particularly pollinator abundance, species richness, and/or fruit set; 2)  
142 agriculture and smallholder farms; 3) distance or isolation from natural habitat; and 4) the  
143 tropical biogeographic region. Boolean operators were used to combine terms, and the search  
144 strings were translated across information sources using PolyGlot (Clark et al. 2020). The  
145 complete search strategy is provided in Table S2.

146 In addition to the database searches, we screened all reports cited in three previously  
147 published meta-analysis on this topic (i.e., Ricketts et al. 2008, Garibaldi et al. 2011, Moreaux  
148 et al. 2022), as well as studies and unpublished datasets that were recommended to us by  
149 colleagues and included those that met the above outlined eligibility criteria.

#### 150 **2.4 Selection process**

151 We conducted the study screening using Rayyan, a web-based platform designed to facilitate  
152 systematic review screening (Ouzzani et al. 2016). Duplicate records were first removed using  
153 Rayyan's automated deduplication function. We then screened titles and abstracts to assess the  
154 relevance of the studies based on our eligibility criteria. We employed partial double-blind  
155 screening during the title and abstract review stage, where the primary reviewer (EB) screened  
156 all titles and abstracts, and two additional reviewers (MLJ and MEH) independently screened  
157 a subset of 20% of the titles and abstracts without knowledge of the other reviewers'  
158 assessments. Discrepancies between reviewers were discussed and resolved through  
159 consensus. All studies that passed the initial abstract screening stage were subjected to full-text  
160 review to confirm their eligibility based on the predefined eligibility criteria.

## 161 **2.5 Data collection process and data items**

162 We extracted data from all studies that met our eligibility criteria, focusing on distance to the  
163 nearest natural habitat (explanatory variable) in relation to pollinator abundance, species  
164 richness, and/or fruit set (response variables). Where possible, we accessed studies' raw data  
165 from open-access repositories or directly from authors upon request, following an individual  
166 participant data style approach for the first stage of our meta-analysis (Tierney et al. 2024).  
167 This allowed us to reduce the variability associated with differing model specifications and co-  
168 variates used to generate distance slopes (the effect size of interest) between studies. If raw  
169 data were not accessible, we extracted data from figures using the online graphical extraction  
170 tool 'plotdigitizer' where possible (Aydin and Yassikaya 2022). We also included relevant raw  
171 data from the online database compiled by Ricketts et al. (2008), who made their meta-analysis  
172 data publicly available (NCEAS 2008). Studies for which we could not obtain at least one of  
173 the three response variables in relation to distance from natural habitat were excluded from the  
174 meta-analysis, following our eligibility criteria. An overview of the variables and data  
175 extraction criteria is provided in the following sections. Outcomes regarding the inclusion and  
176 exclusion of studies are illustrated in the PRISMA diagram and detailed in the results section,  
177 alongside an overview of the characteristics of the included studies.

### 178 **2.5.1 Study metadata**

179 We extracted metadata for each study on the location, number of sampling sites, crop species  
180 and/or flowering plant community observed, and the description of the natural habitat  
181 following the definition in the original studies. We also recorded the focal pollinator taxa for  
182 each study, distinguishing between studies that considered all insect pollinators and those that  
183 focused on specific taxonomic groups (e.g., bees, Diptera, or Arthropods). Taxonomic  
184 classifications were recorded as provided in the original studies, using the highest level of  
185 specificity reported.

### 186 2.5.2 *Pollination variables*

187 For each study, we extracted raw data relating to at least one of the three response variables:  
188 pollinator abundance, species richness, and/or fruit set (or seed set; collectively termed ‘fruit  
189 set’ herein). For the pollinator abundance and richness, we compiled count data of the number  
190 of individual pollinators (abundance) and pollinator species (richness) sampled within a  
191 specified time frame and area. We included studies that sampled pollinator abundance and  
192 richness with both active (such as timed observations of flower visitors either in plots or along  
193 transects, often by sweep netting) and passive methods (such as pan traps, sticky traps, and  
194 glue traps). Where possible, we also extracted separate data for wild pollinator abundance and  
195 richness, excluding the honeybees *Apis mellifera* and *Apis cerana* in areas where these were  
196 reported to be managed. We followed the definition of ‘pollinators’ provided in each primary  
197 study without further standardisation, but accounted for inconsistencies or lack of clear  
198 definitions in our risk of bias assessment (see risk of bias section).

199 The term ‘fruit set’ in our synthesis refers to the proportion of crop flowers that  
200 successfully develop into fruits or seeds. This is the most direct proxy for pollination services  
201 among the three response variables as it captures the actual outcome of pollination, namely the  
202 successful fertilisation leading to fruit or seed production. Yet, it is also less frequently reported  
203 in the literature (e.g., Ricketts et al. 2008), and does not necessarily capture any insights on  
204 pollinator populations or diversity, as pollination services might be provided by a small  
205 minority of dominant species (Kleijn et al. 2015). Moreover, crop species vary widely in their  
206 levels of self-compatibility and dependence on pollinators (Klein et al. 2007, Siopa et al. 2024),  
207 and fruit set can be influenced by various other factors such as soil nutrients, water availability,  
208 and climate conditions (Bos et al. 2007). To ensure consistency across studies, we included  
209 only data on naturally occurring (open) fruit set, meaning fruit set measured under natural  
210 pollination conditions without experimental manipulation such as hand pollination or pollinator

211 exclusions. We included both early-stage and final fruit set data, depending on what was  
212 reported in each study, without distinguishing between the two.

### 213 **2.5.3 Distance measures**

214 We focused on the distance to the nearest natural habitat (in meters) as the explanatory variable  
215 for all three response variables. Some studies directly reported the distance of each sampling  
216 site from the nearest natural habitat, whereas others measured the proportion of natural habitat  
217 within the surrounding landscape in a specific radius or used distance categories such as ‘near’  
218 and ‘far’ from natural habitat. Where possible, these indirect measures were converted to  
219 distance in meters using GPS locations provided by the corresponding authors to derive the  
220 distances from satellite imagery using the historical view in Google Earth Pro, estimated as  
221 close to the time of the study as possible (detailed description in Appendix 4 and Table S5).  
222 Otherwise, they were excluded from the systematic review and meta-analysis as per the  
223 eligibility criteria because we could not derive the required data for the quantitative synthesis  
224 (Table S6).

### 225 **2.5.4 Other potential moderator variables**

226 To inform subgroup analyses (see below), we also extracted data related to three variables  
227 hypothesised to be key moderators of the distance relationship: exclusion of managed  
228 honeybees in the pollinator counts, relative agricultural intensity, and crop-pollinator  
229 dependency for the fruit set response variable. Where managed honeybees (*Apis mellifera* and  
230 in some cases *Apis cerana*) were present in the study areas, we extracted separate data for the  
231 pollinator abundance and species richness variables with and without these species if this  
232 information was accessible from the published data or corresponding authors. Agricultural  
233 intensity was coded as three categories: ‘high’ for studies on farms using synthetic pesticides  
234 and/or growing crops in monocultures; ‘low’ for study farms with no or very little agrochemical  
235 application and diverse crops; and ‘both’ where the study included sites with both relatively

236 'high' and 'low' agricultural intensity. Where primary studies did not report sufficient  
237 information to categorise the agricultural intensity of the farm sites, additional information was  
238 requested from the corresponding authors to confirm the categorisation. Crop-pollinator  
239 dependency levels for each crop within a study were assigned based on predefined quantitative  
240 values from a worldwide assessment of available pollination experiments (Siopa et al. 2024).  
241 We classified the continuous values ranging from 0-1 (zero representing lack of pollinator  
242 dependency and one representing the highest level) to the previously established following six  
243 levels of pollinator dependency by Klein et al. (2007): 'essential' (crop production reduction  
244 without pollinators  $\geq 90\%$ ); 'high' (40- $<90\%$  reduction); 'modest' (10- $<40\%$  reduction); 'little'  
245 ( $>0$  and  $<10\%$  reduction); 'none' (0% reduction) and 'unknown' (no empirical studies  
246 available).

## 247 **2.6 Study risk of bias assessment**

248 In systematic review, a risk of bias assessment (a type of critical appraisal) is used to evaluate  
249 the quality and reliability of included studies by identifying potential sources of methodological  
250 bias that could influence the overall findings (Moher et al. 2009, Stanhope and Weinstein  
251 2023). We conducted study-level risk of bias assessments using the Collaboration for  
252 Environmental Evidence's Critical Appraisal Tool (CEECAT) Version 0.3, a prototype that is  
253 currently one of the only available tools for environmental management research (Konno et al.  
254 2021). The tool consists of six risks of bias criteria for observational studies: 1) confounding  
255 bias; 2) exposure selection bias; 3) misclassified comparison bias; 4) detection bias; 5) outcome  
256 reporting bias; 6) outcome assessment bias. More details on the risk of bias assessment are  
257 provided in Appendix 6.

## 2.7 Effect measures (non meta-analytical models)

All effect measures for the meta-analysis were calculated in R version 4.2.2 (R Core Team 2022). We estimated the slopes of distance to nearest natural habitat against each of the three pollination proxies (pollinator abundance, pollinator richness, and fruit set) as the effect measures of our meta-analyses. These effect measures estimate the expected change in pollination variables as distance to natural habitat increases. Slopes can be used directly as effect measures for meta-analyses provided the slope in every study is measured in the same units (Rosenberg et al. 2013). This raw data approach allowed us to ensure standardised units across slopes for each of the three response variables, namely the count of pollinators (abundance), count of pollinator species (richness), and/or proportion of crop flowers setting fruit/seed (fruit set) per meter of increasing distance.

Following the approach of Garibaldi et al. (2011) and Ricketts et al. (2008), we estimated the exponential relationship via GLMs according to the following equation for each study individually in the first stage:

$$\gamma[iz] = \alpha[i] + \beta[i]D[iz] + \varepsilon[iz]$$

where  $\alpha[i]$  and  $\beta[i]$  are the intercept and slope of study  $i$  respectively,  $D[iz]$  is the distance of site  $z$  in study  $i$  to the nearest natural habitat in meters, and  $\varepsilon[iz]$  is the residual of site  $z$  in study  $i$ . We used a negative binomial error distribution (with a log link function) for pollinator abundance and richness data as most studies showed overdispersion (Lindén and Mäntyniemi 2011), and a binomial error distribution for fruit set data, which aligned with the most frequent approach used in the primary studies. We used the ‘glm’ and ‘glm.nb’ functions from the MASS package for the regression models (Venables and Ripley 2002). As the explanatory variable (distance to the nearest natural habitat) was recorded at varying scales across the primary studies, we transformed the scales using the logarithm of the distance ( $\log + 1$ ) when

282 fitting the GLMs. The model fits were evaluated based on the diagnostic plots and deviance  
283 residuals. We then extracted the estimated slopes and its standard error for each primary study  
284 for the meta-analysis (Rosenberg et al. 2013), before quantitative synthesis via meta-analysis.

## 285 **2.8 Meta-analytical synthesis methods**

### 286 **2.8.1 Primary analyses**

287 To estimate the overall effects across studies we fitted separate meta-analytical models for each  
288 of the three response variables, using the ‘rma’ function from the *metafor* package in R  
289 (Viechtbauer 2010). Effect sizes were represented by the estimated slopes from individual  
290 studies (see section 2.7), with corresponding variances used as weights. A random-effects  
291 model with restricted maximum likelihood (REML) estimation was applied to account for  
292 variation among studies, assuming that the true effect size differs across studies rather than  
293 being a single fixed value. We assessed the presence and strength of an effect using 95%  
294 confidence intervals (CIs) and p-values, but did not rely solely on p-value significance (e.g.,  $p$   
295  $< 0.05$ ) and interpreted effect sizes also in the context of their uncertainty, with narrower CIs  
296 indicating more precise estimates (Schünemann et al. 2023). Heterogeneity among the studies  
297 was assessed using the Q statistic and  $I^2$  outputted from the ‘rma’ function. We used the  
298 following established rules of thumb when interpreting  $I^2$  heterogeneity estimates: low,  
299 moderate, and high for  $I^2$  values of 25%, 50%, and 75% respectively (Higgins et al. 2003). We  
300 also used the meta-analytic effect size estimates to model the predicted decay and associated  
301 95% confidence interval for all three pollination proxies with increasing distance from natural  
302 habitat, applying an exponential decay function based on the natural log of distance.

### 303 **2.8.2 Subgroup analyses**

304 To explore possible reasons for statistical heterogeneity, we conducted three subgroup analyses  
305 related to key hypotheses in the field. To test our hypothesis that the presence of managed  
306 honeybees may mask negative effects of distance from natural habitats on other pollinator

307 species, we re-ran our models after excluding the honeybees *A. mellifera* as well as *A. cerana*  
308 in studies where the Asian honeybee was reported to be domesticated (Krishnan et al. 2012,  
309 Motzke et al. 2016, Schrader et al. 2018). The ‘fruit set’ model was not rerun because it did not  
310 include a direct measure relating to pollinators. The results of subgroup models were then  
311 compared to those of the primary models in terms of the effect size estimate, statistical  
312 significance (p-value), and direction of the distance relationship.

313 In addition, we performed meta-regressions to investigate whether agricultural intensity  
314 and crop pollinator-dependency could moderate the effects of increasing distance to natural  
315 habitat on pollination variables. To test this, we extended the meta-analytic models by adding  
316 single categorical moderators for agricultural intensity and crop pollinator dependency (more  
317 details on data items in section 2.5.4) (Thompson and Higgins 2002).

### 318 **2.8.3 Sensitivity analyses**

319 We performed several sensitivity analyses to explore the robustness of our meta-analytical  
320 results. To test whether the presence of outliers and influential cases may affect the validity  
321 and robustness of our meta-analyses (Viechtbauer and Cheung 2010), we repeatedly fitted the  
322 model leaving out one study at a time using the ‘leave1out’ function provided in the *metafor*  
323 package (Viechtbauer 2010). We considered the results robust if excluding any individual study  
324 did not change the direction of the effect or shift the p-value across the 0.05 threshold. We  
325 further conducted multiple sensitivity analyses to test for the potential effects of: i) risk of bias;  
326 ii) method of sampling pollinators (active vs passive sampling methods); iii) method of  
327 measuring distance to nearest natural habitat (reported vs estimated); and iv) spatial scale of  
328 maximum distances considered in each study (categorised as small <750m, medium 750 –  
329 3,000m, and large >3,000m). Each moderator was included separately in the models to test its  
330 influence on effect size estimates for the meta-analyses. More details on these sensitivity  
331 analyses are provided in Appendix 8 in the Supporting Information.

## 332 **2.9 Publication bias assessment**

333 We tested for publication bias (Egger et al. 1997), which can occur in meta-analyses when  
334 certain research findings, such as non-significant results, are less likely to be published, leading  
335 to a skewed representation of the available evidence (Nakagawa et al. 2022). We first generated  
336 funnel plots of the individual study effect sizes against their corresponding standard errors, and  
337 evaluated the funnel plot asymmetry visually as an informal assessment of small study  
338 publication bias (Egger et al. 1997). However, as visual interpretation alone is subjective (Tang  
339 and Liu 2000), we also used the more formal method of Egger’s regression, where a non-  
340 significant result suggests no strong evidence of publication bias (Egger et al. 1997).

## 341 **2.10 Certainty assessment**

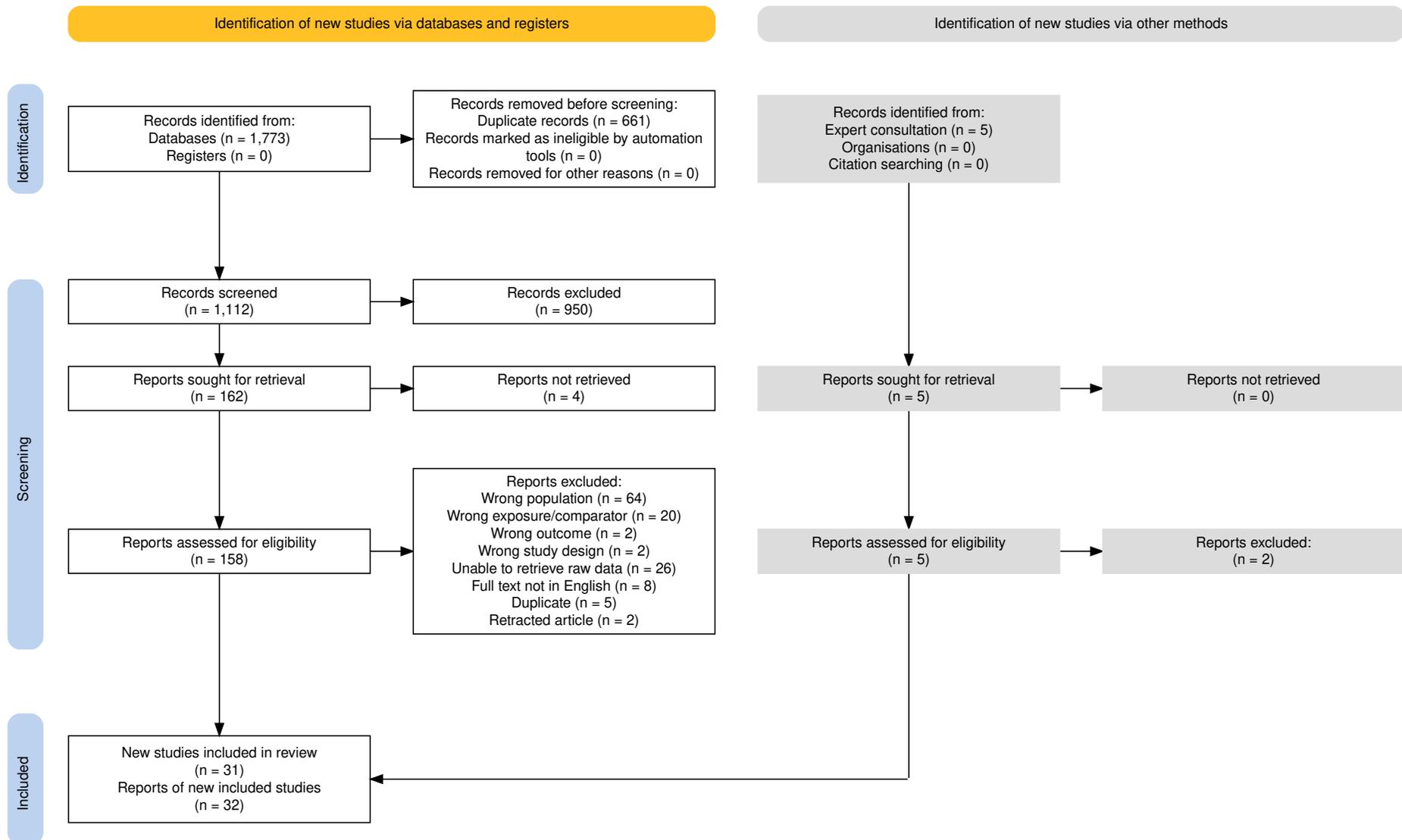
342 Finally, we conducted a certainty assessment, which is a standardised way to bring together the  
343 results of a systematic review and meta-analysis by evaluating the strength of the available  
344 evidence, considering factors that may influence confidence in the results (Schünemann et al.  
345 2023). We used the GRADE (Grading of Recommendations, Assessment, Development, and  
346 Evaluations) approach, following the Cochrane guidelines as far as possible in the context of  
347 our ecology-focused meta-analysis (Schünemann et al. 2023). Certainty was categorised as  
348 high, moderate, low, or very low, based on five domains for potential downgrading: i) risk of  
349 bias, assessed using CEECAT to evaluate the potential for bias in individual studies; ii)  
350 inconsistency, assessed via visual inspection of heterogeneity in the forest plots and via the  $I^2$   
351 statistic; iii) indirectness, considering whether the available evidence directly answers our  
352 research question or if there are differences in study populations, exposure measures (distance  
353 from natural habitat), and pollination response variables that make the evidence less applicable;  
354 iv) imprecision, based on confidence interval width and sample size adequacy; and v)  
355 publication bias, assessed using funnel plots and Egger’s regression test. As our systematic

356 review and meta-analysis focused on observational studies, the initial certainty of evidence was  
357 set as low. Each of the five domains could further downgrade or, in some cases, upgrade the  
358 certainty by one or more levels (Schünemann et al. 2023). Final certainty ratings were  
359 summarised in a ‘Summary of Findings’ table, following GRADEpro GDT recommendations.

## 360 **3 RESULTS**

### 361 **3.1 Study selection**

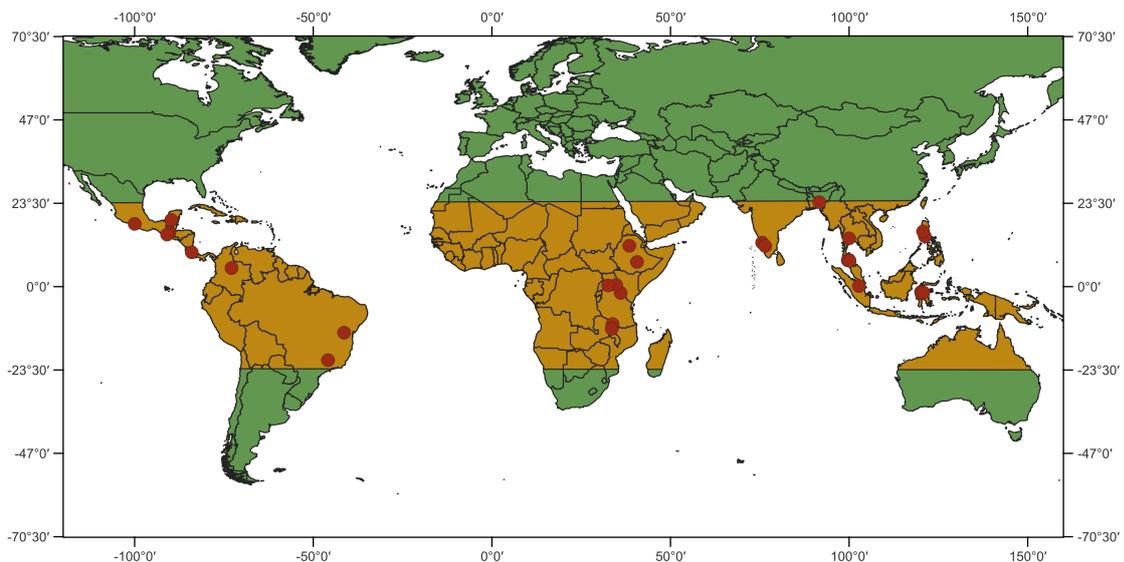
362 Our database searches returned a total of 1,773 records, which were reduced to 1,112 unique  
363 records after removing 661 duplicates. During title and abstract screening, 950 records were  
364 excluded based on our eligibility criteria, leaving 162 records for which we sought full-text  
365 reports and subsequently 158 records for which we were able to obtain full texts. We excluded  
366 129 of these based on our eligibility criteria (Table S5) and thus were able to obtain data of 29  
367 reports identified through the systematic literature review. Corresponding authors from whom  
368 we requested data also directed us towards other potentially relevant datasets, resulting in the  
369 inclusion of three additional reports. The final dataset therefore included raw data from 32  
370 reports (i.e. journal articles and unpublished manuscripts). The full selection process is  
371 summarised in the PRISMA flow diagram (Fig. 1).



**Figure 1.** PRISMA flow diagram, created using the PRISMA flow diagram tool (Haddaway et al. 2022) .

372 **3.2 Study characteristics**

373 The 32 datasets included in the meta-analysis covered over 500 farms across 13 tropical  
374 countries, with 28 studies reporting pollinator abundance, 27 studies species richness, and 16  
375 studies reporting fruit set in relation to isolation from natural habitat (Fig. 2, Table 1). Half of  
376 the studies were from Asia (16 studies; 50%), followed by the Americas (9; 28%) and Africa  
377 (7; 22%). Of the 32 studies, 22 directly reported distances to the nearest natural habitat, whilst  
378 distance had to be calculated using satellite imagery for the remaining 10 studies. In total,  
379 distances of 21 studies (66%) were measured to the nearest natural forest, while distances for  
380 11 studies (34%) focused on other types of natural habitat such as agroforests and shrublands.  
381 The studies covered a broad range of spatial scales, with maximum distances considered in  
382 studies ranging from 60m to 10,000m (median = 550m, mean = 1,980m). A total of 14 studies  
383 were carried out on low-intensity farms that used very little or no agrochemicals and employed  
384 diverse cropping systems, twelve on relatively high-intensity farms with chemical pesticide use  
385 or monocultures, four spanned both intensities, and two lacked sufficient data to classify.



**Figure 2.** Map showing the geographic distribution of the 32 studies included in the meta-analysis, represented by red dots. Note that there is spatial overlap of studies conducted in the same or nearby regions. The tropics are indicated in orange. Map was created in QGIS.

**Table 1.** Characteristics of the 32 reports on pollination variables in TSFs included in our analysis, with information on study location, number of study sites, crop species and pollinator dependency, focal pollinator taxa, agricultural intensity, a description of the semi-natural habitat (SNH), reported distance measure, spatial scales, and estimated slopes for the three pollination variables: a = pollinator abundance, r = pollinator richness, f = fruit set.

Authors and year	Country	Study sites	Crop species	Pollinator dependence <sup>1</sup>	Focal pollinator taxa	Agri. intensity <sup>2</sup>	SNH <sup>3</sup>	Distacne measure <sup>4</sup>	Spatial scale	Estimated slopes		
										a	r	f
Banks et al. (2013)	Costa Rica	12	 coffee (arabica)	0.31	Hymenoptera	high	Forest, min. 0.5ha size	estimated	0-300m	-0.13	0.02	-
Banks et al. (2014)	Costa Rica	12	 coffee (arabica)	0.31	Hymenoptera	high	Forest, min. 0.5ha size	estimated	0-300m	-0.05	-	-
Basu et al. (2016)	India	12	 general community	NA	Bees	both	Fallow	reported	4-500m	-0.07	0.02	-
Enriquez et al. (2015)	Guatemala	10	 squash	1	Bees	low	Secondary vegetation	reported	12-240m	-0.32	-0.02	0.47
Escobedo-Kenefic et al. (2024)	Guatemala	22	 <i>Brassica rapa</i>	0.39	Insecta	both	Humid montane and low-montane forest	reported	3-700m	0.11	-	-0.03
Deepthi et al. (2019)	India	10	 coffee (canephora)	0.63	Bees	high	Riparian forest	reported	10-60m	0.06	0.03	-
Geeraert et al. (2020)	Ethiopia	18	 coffee (arabica)	0.31	Bees	low	Coffee production forest	estimated	40-400m	-0.04	-0.20	-0.07
Gemmill-Herren and Ochieng (2008)	Kenya	NA	 Eggplant	0.83	Bees	high	forest	reported	0-150m	-0.17	-0.00	-
Hansen et al. (2020)	Thailand	6	 guava	0.08	Insecta	high	Evergreen forest	reported	200-1,700m	-0.30	-0.34	0.33
Hass et al. (2018)	Philippines	16	 rice	NA	Bees	high	Agroforests	reported	0-2,55m	0.03	-0.14	-
Kasina et al. (2009)	Kenya	28	 dry common bean	0.19	Bees	low	Rainforest	reported	0-8,000m	0.08	-0.00	-
Klein et al. (2003a)	Indonesia	24	 coffee (arabica)	0.31	Bees	low	Rainforest	reported	0-2,500m	-0.03	-0.10	-0.11

<sup>1</sup>Crop pollinator dependence levels from Siopa et al. (2024) <sup>2</sup>Agricultural intensity of the study sites was categorised into ‘high’, ‘low’ or ‘both’ if the study contained both sites with high and low agricultural intensity; <sup>3</sup>SNH = semi-natural habitat as described in the original study; <sup>4</sup>The distance measure of primary studies was classified as either 'reported' (distances directly provided in the original research) or 'estimated' (distances derived from satellite imagery). More details on these variables can be found in the methods section (data items).

Table 1 continued

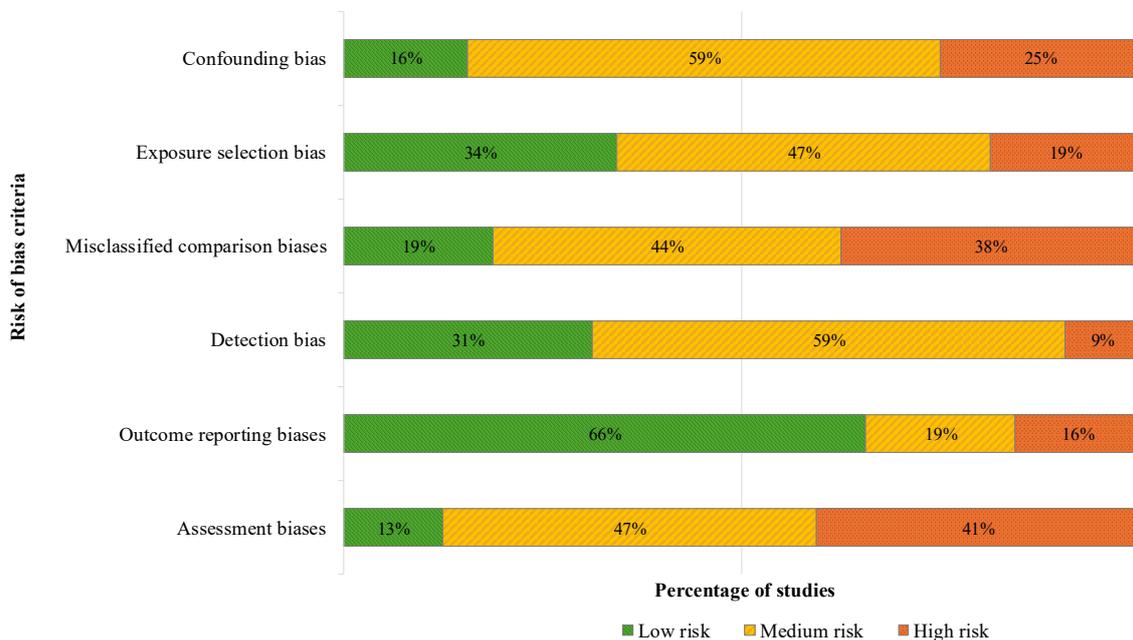
Authors and year	Country	Study sites	Crop species	Pollinator dependence <sup>1</sup>	Focal pollinator taxa	Agri. Intensity <sup>2</sup>	SNH <sup>3</sup>	Distance measure <sup>4</sup>	Spatial scale	Estimated slopes		
										a	r	f
Klein et al. (2003b)	Indonesia	15	 coffee (canephora)	0.63	Bees	low	Rainforest	reported	0-1,500m	-0.03	-0.05	-0.17
Klein et al. (2009)	Indonesia	24	 general community	NA	Bees	low	Rainforest	reported	0-1,415m	-0.17	-0.14	-
Krishnan et al. (2012)	India	35	 Coffee (canephora)	0.63	Bees	NA	Forest fragments (0.3 – 20ha)	reported	0-500m	0.04	-0.02	0.01
Landaverde-Gonzalez et al. (2017)	Mexico	37	 chilli	0.48	Bees	high	Forest, woody vegetation, pastures	estimated	0-600m	0.04	-0.04	-0.14
Latini et al. (2020)	Brazil	8	 Coffee (arabica)	0.31	NA	both	Atlantic Forest Remnants	reported	0-120m	-	-	-0.07
Li et al. (2022)	Indonesia	1	 oil palm	0.81	Arthropods	high	dipterocarp forest	reported	0-100m	0.37	0.01	-0.21
Lucas-García and Rosas-Guerrero (unpublished)	Mexico	18	 mango	0.71	Insecta	high	Forest	reported	50-1100m	-0.41	-0.14	-0.38
Motzke et al. (2016)	Indonesia	13	 cucumber	0.56	Bees	NA	Rainforest	reported	1-2300m	0.08	-	-
Munyuli (2012)	Uganda	17	 Coffee (canephora)	0.63	Bees	low	Forest, wetland	reported	5-7000m	-	-	-0.33
Obregon et al. (2021)	Colombia	10	 'lulo' (or 'naranjilla')	1	Bees	high	Primary/secondary forest	estimated	0-90m	-0.07	-0.02	0.06
Schrader et al. (2018)	Philippines	18	 general community	NA	Bees	low	Woody habitat	estimated	0-90m	-0.20	-0.13	-
Severiano-Galeana et al. (2024)	Mexico	24	 mango	0.71	Insecta	high	Tropical dry forest patches	reported	50-200m	-0.46	-0.20	-0.27
Sitotaw et al. (2022)	Ethiopia	72	 mango, coffee (arabica), horse bean and field pea	0.71; 0.31; 0.05; NA	Insecta	low	Sacred church forest	reported	1-5000m	-	-0.23	-

Table 1 continued

Authors and year	Country	Study sites	Crop species	Pollinator dependenc <sup>1</sup>	Focal pollinator taxa	Agri. Intensity <sup>2</sup>	SNH <sup>3</sup>	Distance measure <sup>4</sup>	Spatial scale	Estimated slopes		
										a	r	f
Sritongchuay et al. (2019)	Thailand	20	 general community	NA	Insecta	low	Rainforest (360 - 65,000 ha)	estimated	500-8,000m	-0.06	0.26	-
Tangtorwongsakul et al. (2018)	Thailand	24	 mango	0.71	Bees	high	Mangrove forest, wetlands	estimated	100-5,500m	0.18	0.08	-
Toledo-Hernandez et al. (2021)	Indonesia	18	 cocoa	1	Diptera	low	Secondary forest patches and cocoa agroforests	reported	100-3,200m	0.31	0.17	-
Viswanathan et al. (2020)	India	7	 general community	NA	Insecta	both	Forest reserve	reported	100-2,200m	-	-0.31	-
Vogel et al. (2021)	Malawi	10	 pigeon pea	0.17	Bees	low	Shrubland and forest	estimated	10-250m	-0.32	0.15	0.27
Vogel et al. (2023)	Malawi	24	 pumpkin	1	Insecta	low	shrubland	estimated	5-200m	0.30	-0.02	-0.19
Wayo et al. (2020)	Thailand	30	 general community	NA	Stingless bees	low	Rainforests and fragmented patches	reported	0-10,000m	-0.67	-0.28	-

386 **3.3 Risk of bias assessment**

387 As expected in observational field studies, all studies included in the systematic review and  
388 meta-analysis exhibited a medium to high risk in at least one of the six domains assessed,  
389 particularly concerning risk of confounding bias, misclassified comparison bias and outcome  
390 assessment bias (Fig. 3; Appendix 6 in the Supporting Information). Most studies did not  
391 account for all key confounding factors such as the influence of agrochemical application or  
392 the size and quality of natural habitat. Further, several studies lacked explicit justifications for  
393 spatial scales used to define isolation from natural habitat and minimum distances between  
394 study sites, making it difficult to assess potential non-independence. Additionally, many  
395 studies had small sample sizes, which contributed to underpowered analyses and increased the  
396 risk of outcome assessment bias.



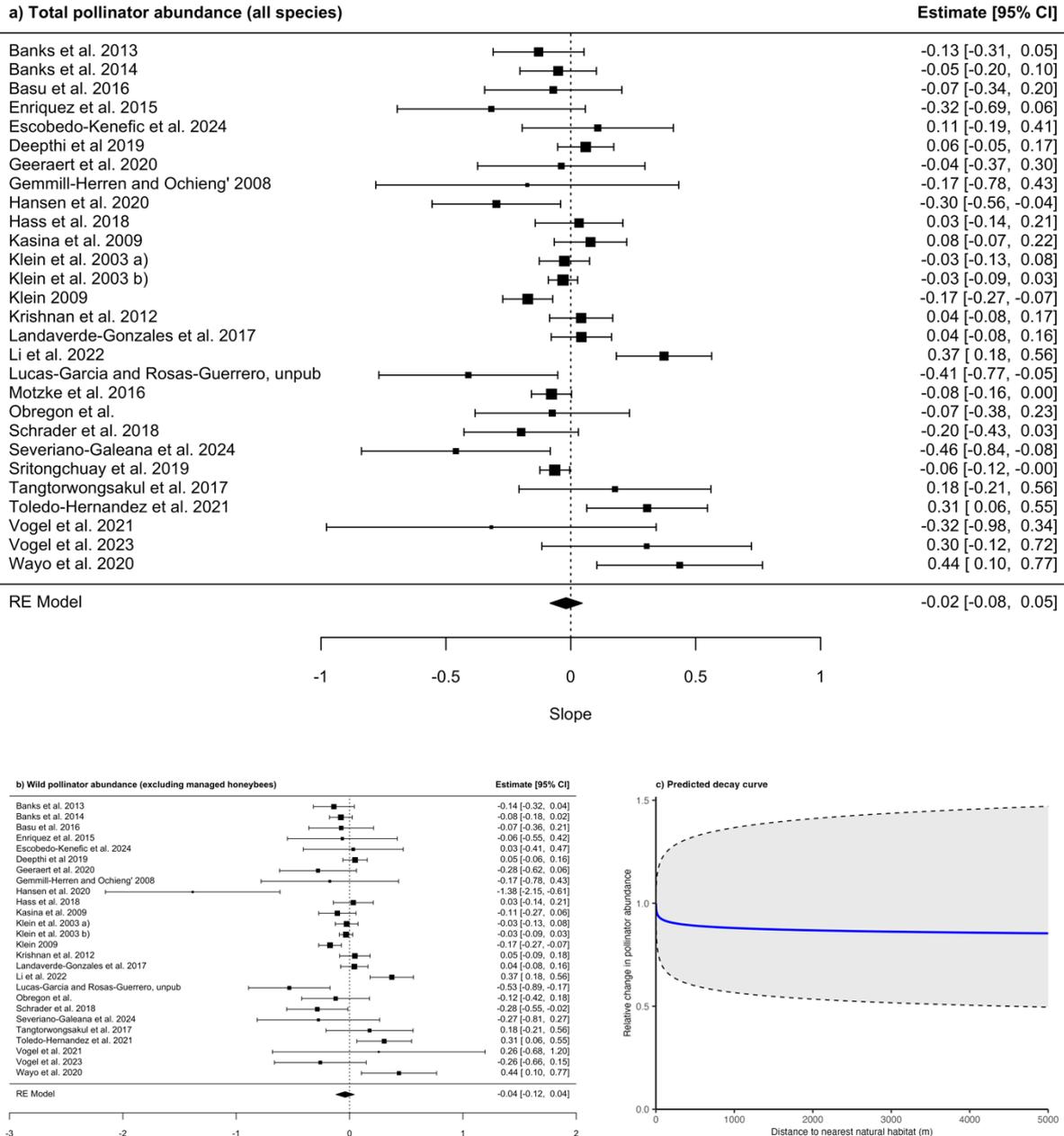
**Figure 3.** Outcome of the risk of bias assessment across the studies included in the meta- analysis (N = 32).

### 397 3.4 Effects of distance on pollinator abundance

398 Effect measures representing the relationship between distance to the nearest natural habitat  
399 and pollinator abundance were calculable for 28 studies. The maximum distance to the nearest  
400 natural habitat varied across studies, ranging from 60m to 9,937m, with a mean of 2,157m and  
401 a median of 551m. An overview of the individual data and model fits for the relationship  
402 between pollinator abundance and linear distance to the nearest natural habitat of each study  
403 can be found in Fig. S3, and the study-level effect sizes are presented in Table S7. When meta-  
404 analytically aggregating the effect sizes from these models, there was no evidence for a  
405 consistent relationship between distance and pollinator abundance (slope: -0.02, 95% CI: -0.08  
406 to 0.05  $p = 0.57$ ; Fig. 4a, Table S8). Based on the slope of the meta-analysis, the predicted  
407 decline in abundance at 1km distance from natural habitat was 12%. Many studies had effect  
408 sizes close to zero, and high heterogeneity was observed between the studies ( $I^2 = 75.68\%$ ,  $\tau^2$   
409  $= 0.02$ ,  $\tau = 0.13$ ,  $Q(df = 27) = 74.73$ ,  $p < 0.0001$ ; Table S9).

410 A subgroup analysis of the 26 studies for which we were able to restrict pollinator  
411 abundance to wild pollinators (i.e. exclude managed honeybees; study-level effect sizes in  
412 Table S10) did not detect an effect either (slope: -0.04, 95% CI: -0.12 to 0.04,  $p = 0.34$ ; Fig.  
413 4b). Similarly, we did not detect significant moderation of the effect by relative agricultural  
414 intensity ( $QM(df = 3) = 0.48$ ,  $p = 0.92$ ). Residual heterogeneity remained high ( $I^2 = 80.74\%$ ,  $\tau^2$   
415  $= 0.03$ ,  $\tau = 0.16$ ,  $QE(df = 23) = 69.70$ ,  $p < 0.001$ ), suggesting substantial unaccounted variability  
416 across studies.

417



**Figure 4.** Relationship between pollinator abundance and distance to the nearest natural habitat: **a)** forest plots showing the slopes (effect sizes) and 95% confidence intervals (CI) of pollinator abundance for all species ( $N = 28$  studies); and **b)** a subgroup analysis of the abundance of only wild pollinators (excluding managed honeybees;  $N = 26$  studies). The size of each square is proportional to the weight of the study in the meta-analysis, which is based on the inverse variance of its estimate. The dotted line represents a null effect (slope = 0); studies whose confidence intervals do not overlap this line indicate a statistically significant relationship between pollinator abundance and distance to the nearest natural habitat. **c)** the decay curve showing the expected relative change in pollinator abundance (all species) with increasing distance from natural habitat, based on the estimated slope (-0.02) and 95% CIs (-0.08 to 0.05) from the meta-analysis. The solid blue line represents the mean predicted abundance, while the shaded region and dashed lines indicate the 95% CI.

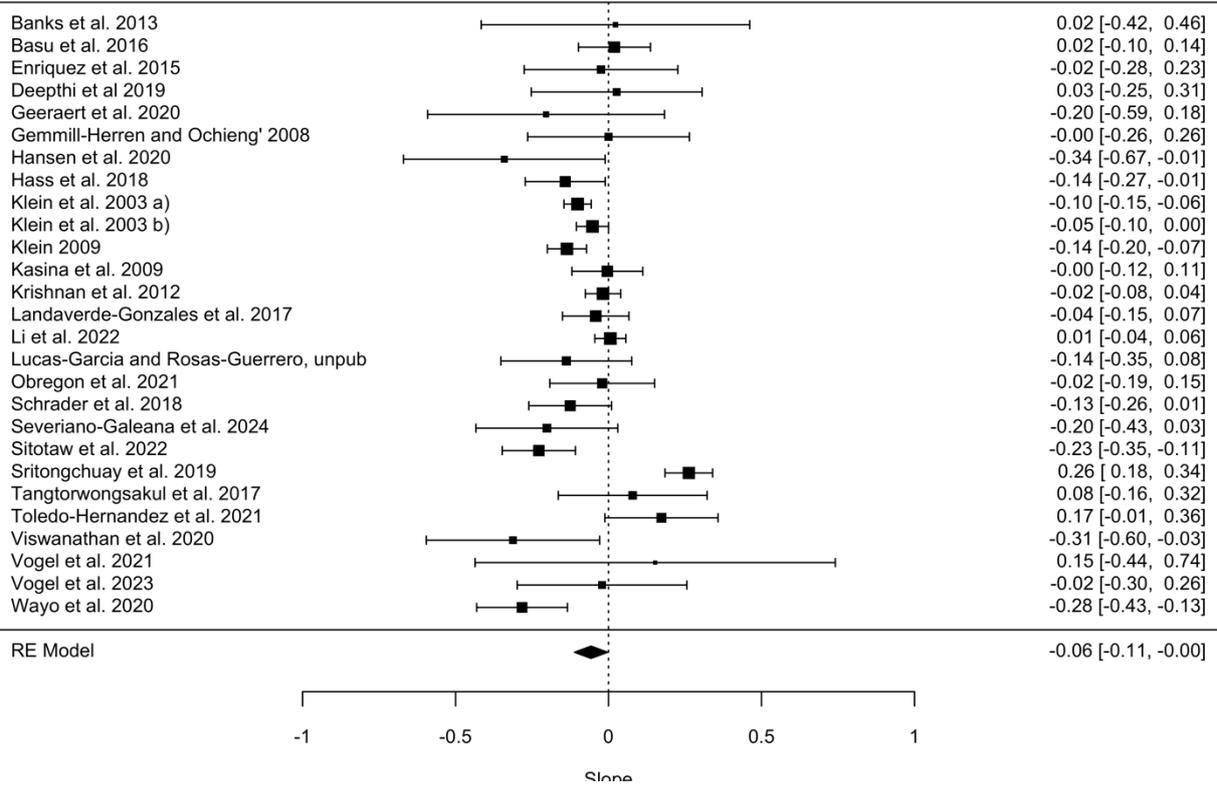
### 418 3.5 Effects of distance on pollinator species richness

419 Effect measures representing the relationship between distance to the nearest natural habitat  
420 and pollinator richness were calculable for 27 studies (see Fig. S4 and Table S11). Variation in  
421 the maximum distance to natural habitat across studies ranged from 60m to 9,937m, with a  
422 mean of 2,254m and a median of 602m. When meta-analytically aggregating the effect  
423 measures from these models, we detected a significant negative relationship between distance  
424 to the nearest natural habitat was associated with and pollinator richness (slope: -0.06, 95% CI:  
425 -0.11 to -0.00,  $p = 0.04$ ; Fig. 5a, Table S12). The predicted decline in species richness at 1km  
426 distance from natural habitat was 33%. Similar as for abundance, there was high heterogeneity  
427 in slope estimates between studies ( $I^2 = 81.22\%$ ,  $\tau^2 = 0.01$ ,  $\tau = 0.12$ ,  $Q(df = 26) = 119.56$ ,  $p <$   
428  $0.0001$ ; Table S13).

429 The subgroup analysis of the 21 studies for which we were able to restrict the pollinator  
430 richness to wild pollinators (Table S14) identified a stronger negative effect of distance on wild  
431 pollinator richness (slope: -0.08, 95% CI: -0.13 to -0.03,  $p = 0.001$ ; Fig. 5b). However, we did  
432 not detect moderation of the effect by relative agricultural intensity ( $QM(df = 3) = 4.04$ ,  $p =$   
433  $0.26$ ) and residual heterogeneity remained high ( $I^2 = 81.27\%$ ,  $\tau^2 = 0.02$ ,  $\tau = 0.13$ ,  $QE(df = 23)$   
434  $= 116.82$ ,  $p < 0.001$ ).

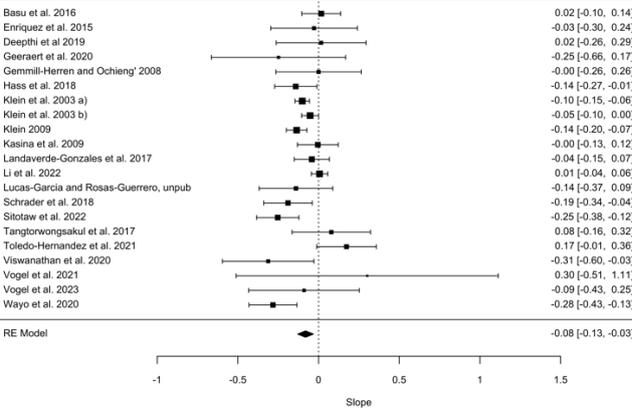
**a) Total pollinator richness (all species)**

Estimate [95% CI]

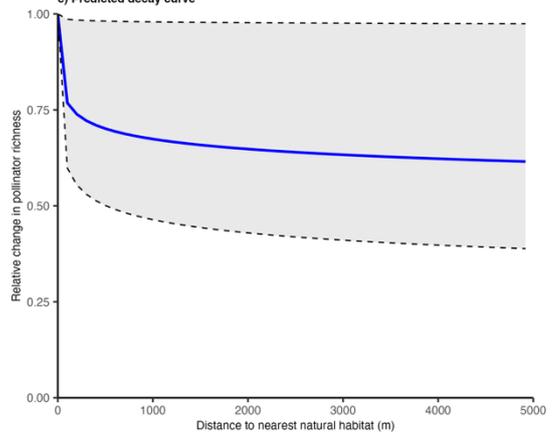


**b) Wild pollinator richness (excluding managed honeybees)**

Estimate [95% CI]



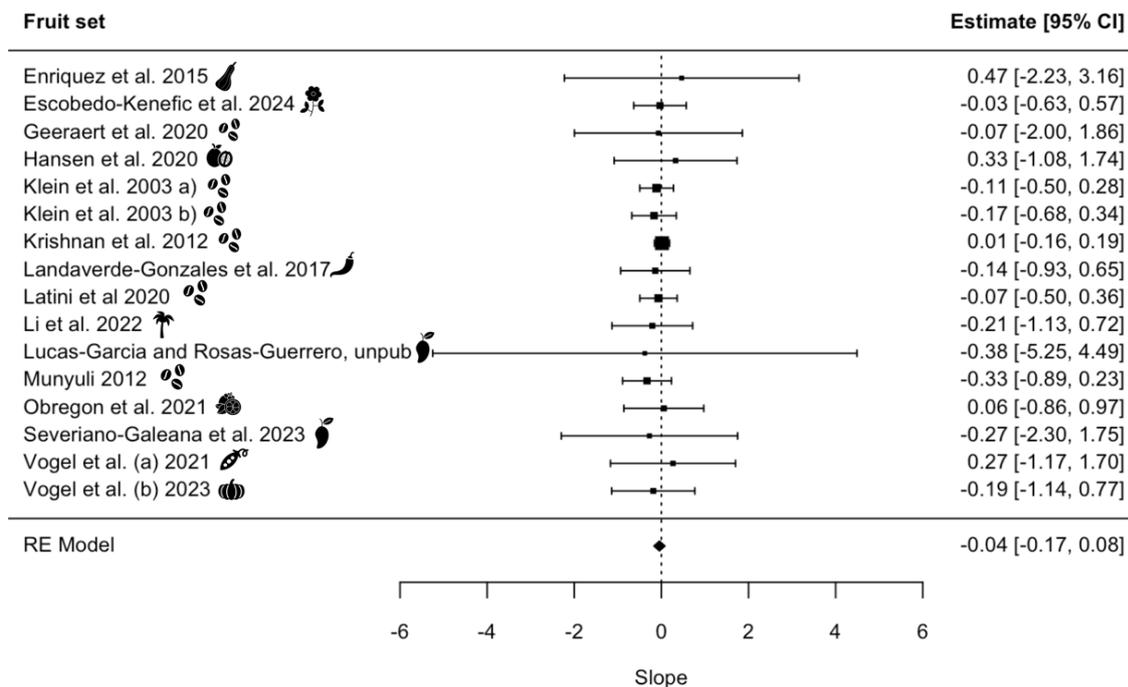
**c) Predicted decay curve**

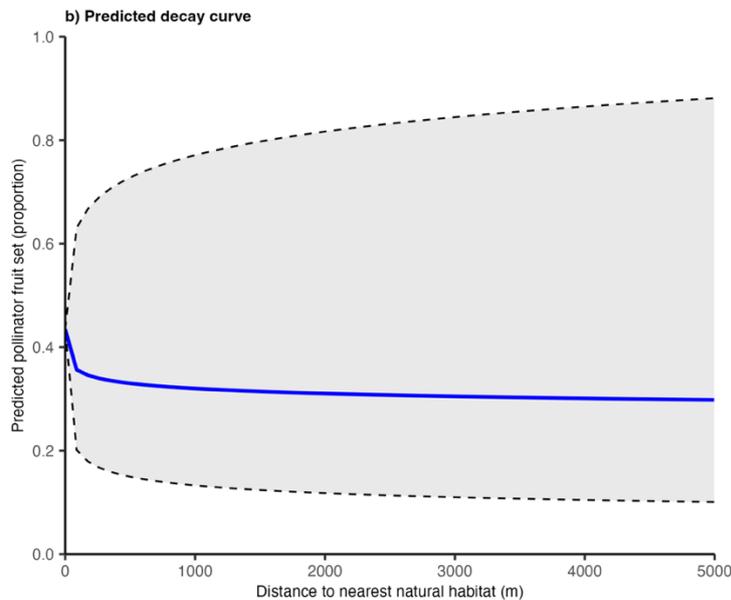


**Figure 5.** Relationship between pollinator species richness and distance to the nearest natural habitat: **a)** forest plots showing the slopes (effect sizes) and 95 confidence intervals (CI) for the total pollinator species richness (N = 27 studies); and **b)** a subgroup analysis of studies that provided data for wild pollinator richness (excluding managed honeybees; N = 21 studies). The size of each square is proportional to the weight of the study in the meta-analysis, which is based on the inverse variance of its estimate. The dotted line represents a null effect (slope = 0); studies whose confidence intervals do not overlap this line indicate a statistically significant relationship between pollinator abundance and distance to the nearest natural habitat; and **c)** the decay curve of the predicted pollinator richness (all species) with increasing distance from natural habitat, based on the estimated slope (-0.06) and 95% CIs (-0.11 to -0.00) from the meta-analysis. The solid blue line represents the mean predicted species richness, while the shaded region and dashed lines indicate the 95% CI.

435 **3.6 Effects of distance to natural habitat on fruit set**

436 Effect measures representing the relationship between distance to the nearest natural habitat  
 437 and fruit set were calculable for 16 studies (see Fig. S5 and Table S15). Across the studies, the  
 438 maximum distances to natural habitat ranged from 90m to 8,676m, with a mean of 1,600m and  
 439 a median of 445m. When meta-analytically aggregating the effect measures from these models,  
 440 we detected no effect of distance to natural habitat (slope: -0.04, 95% CI: -0.17, 0.08,  $p = 0.50$ ;  
 441 Fig. 6, Table S16), and these findings appeared relatively consistent across all studies ( $I^2 = 0\%$ ,  
 442  $\tau^2 = 0$ ,  $\tau = 0$ ,  $Q(df = 15) = 2.74$ ,  $p = 0.99$ , Table S17). Based on the slope from the meta-analysis,  
 443 the predicted decline in fruit set at 1km distance from natural habitat was 26%. In subgroup  
 444 analyses, we did not detect any moderation of the effect by the agricultural intensity ( $QM(df =$   
 445  $3) = 1.65$ ,  $p = 0.65$ ) or level of pollinator-dependency of the target crop species ( $QM(df = 4) =$   
 446  $0.51$ ,  $p = 0.97$ ).





**Figure 6.** Relationship between fruit set and distance to the nearest natural habitat: **a)** forest plot showing the slopes (effect sizes;  $N = 16$  studies). An icon representing the crop for each study is shown, as the pollinator-dependency of crops was included as a moderator analysis for the fruit set model only. For the crop names relating to symbols, please see Table 1. The size of each square is proportional to the weight of the study in the meta-analysis, which is based on the inverse variance of its estimate. The dotted line represents a null effect (slope = 0); studies whose confidence intervals do not overlap this line indicate a statistically significant relationship between pollinator abundance and distance to the nearest natural habitat. **b)** the decay curve of fruit set with increasing distance from natural habitat based on estimated effect size, CIs, and proportion of fruit set at 0m (slope = -0.04, CI = -0.17 to 0.08). The solid blue line represents the mean predicted abundance, while the shaded region and dashed lines indicate the 95% CI.

### 447 3.7 Sensitivity analyses

448 The sensitivity analyses revealed one influential study for the pollinator abundance, richness,  
 449 and fruit set models each (a different study in each respective model; Figs. S6, S8, and S10).  
 450 Re-running the meta-analysis using leave-one-out analysis confirmed that excluding the outlier  
 451 did not change the direction or strength of evidence in any of the three meta-analyses (Tables  
 452 S18, S19, and S20). For all three response variables (pollinator abundance, species richness,  
 453 and fruit set), the Egger's regression test indicated no significant asymmetry (abundance:  $p =$   
 454 0.60; richness:  $p = 0.56$ ; fruit set:  $p = 0.73$ ), and none of the funnel plots indicated clear  
 455 asymmetry (Figs. S7, S9, and S11). Thus, we found no evidence of publication bias.

456 Additional sensitivity analyses showed that excluding studies with a high risk of bias did  
457 not change the model results for abundance (slope: 0.03, CI: -0.09 to 0.15,  $p = 0.63$ ; see Table  
458 S8 for all abundance model outputs), richness (slope: 0.04, CI: -0.07 to 0.14,  $p = 0.48$ ; Table  
459 S12 for all richness model outputs), or fruit set (slope: -0.01, CI: -0.16 to 0.14,  $p = 0.91$ ; Table  
460 S16 for all fruit set model outputs). However, moderator analyses examining the effects of  
461 pollinator sampling methods ('active', 'passive', and 'combined') showed that the active  
462 sampling method significantly influenced the effect sizes for the richness model (slope: -0.08,  
463 CI: -0.14 to -0.02,  $p = 0.01$ ), but not for the abundance model (slope: -0.05, CI: -0.12 to 0.02,  $p$   
464  $= 0.14$ ). No significant effect was found for the passive or combined methods. Further  
465 moderator analyses exploring the potential influence of distance determination methods  
466 ('reported' vs. 'estimated') showed that effect measures based on reported distances were more  
467 strongly related to richness than those based estimated distances; slope: -0.09, CI: -0.15 to -  
468 0.03,  $p = 0.005$ ), but were not more strongly related to abundance (slope: -0.01, CI: -0.09 to  
469 0.07,  $p = 0.84$ ) or fruit set (slope: -0.04, CI: -0.18 to -0.09,  $p = 0.52$ ). We also found a stronger  
470 negative effect for studies with a maximum distance between 750m – 3,000m (medium spatial  
471 scales) for pollinator abundance (slope: -0.13, CI: -0.25 to -0.01,  $p = 0.04$ ) and pollinator  
472 richness (slope: -0.14, CI: -0.023 to -0.06,  $p = 0.001$ ), but not for fruit set (slope: -0.14, CI: -  
473 0.44 to 0.17,  $p = 0.38$ ).

### 474 **3.8 Certainty assessment**

475 The certainty of evidence was rated as very low for all three response variables, primarily due  
476 to concerns with study risk of bias, high heterogeneity among studies, indirectness of  
477 pollination proxies, and imprecision from small sample sizes in the fruit set meta-analysis.  
478 Table 2 summarises the key results alongside their certainty ratings and plain language  
479 interpretations (see Table S21 for a more detailed description of the GRADE assessment).

**Table 2.** Summary of findings on the relationship between distance to natural habitat and pollination in TSFs, following Cochrane recommendations (Schünemann et al. 2023). The four symbols represent levels of certainty (very low, low, moderate, and high), with a ‘⊕’ indicating retained certainty and a ‘⊖’ indicating a downgrade in certainty level.

<b>Response variables</b>	<b>No of studies</b>	<b>Relative effect (95% CI)</b> (distance to natural habitat)	<b>Certainty of the evidence</b> (GRADE)	<b>Plain language interpretation</b>
<b>Pollinator abundance</b> (count of pollinators)	Based on 836 data points from 28 studies	Slope: -0.02 (-0.08 to 0.05) p = 0.57 distance range 0 – 9,937 m (maximum distance median = 551m, mean = 2,157m)	⊕⊖⊖⊖ <b>very low</b> <sup>1, 2, 3, 4</sup>	Increasing distance to natural habitat may not affect pollinator abundance in TSF
<b>Pollinator richness</b> (count of unique pollinator species)	Based on 804 data points from 27 studies	Slope: -0.06 (-0.11 to -0.00) p = 0.04 distance range 0 – 9,937 m (maximum distance median = 602m, mean = 2,254m)	⊕⊖⊖⊖ <b>very low</b> <sup>1, 2, 3</sup>	Increasing distance to natural habitat may reduce pollinator species diversity in TSF
<b>Fruit set</b> (proportion of flowers developed into fruits)	Based on 398 data points from 16 studies	Slope: -0.04 (-0.17 to 0.08) p = 0.50 Distance 0 – 8,676m (maximum distance median = 445m, mean = 1,600m)	⊕⊖⊖⊖ <b>very low</b> <sup>1, 3, 4</sup>	Increasing distance to natural habitat may not influence fruit set of pollinator-dependent crops in TSF

<sup>1</sup> concerns with medium and high risk of bias in studies; <sup>2</sup> high heterogeneity among studies; <sup>3</sup> indirectness concerns due to variability in pollinator taxa (for pollinator abundance and richness) and spatial scales of distance to natural habitat. <sup>4</sup> imprecision concerns due to wide confidence intervals

## 480 **4 DISCUSSION**

481 Tropical smallholder farms make up 84% of all farms worldwide (Lowder et al. 2021) and are  
482 a key priority for reducing poverty and hunger while sustainably managing natural resources  
483 (United Nations 2015). These farms rely heavily on biodiversity-derived ecosystem services  
484 such as pollination for nutrition and food security (Tibesigwa et al. 2019, Timberlake et al.  
485 2022, Mulungu et al. 2023). Understanding how to support pollination services provided by  
486 wild insects in TSF landscapes is therefore important, both for informing landscape  
487 conservation management strategies and for supporting farmers to sustain their livelihoods. We  
488 conducted a systematic review and meta-analysis of 32 studies, and found no consistent decline  
489 in pollinator abundance (28 studies) or fruit set (16 studies) with increasing distance of TSFs  
490 to natural habitat, and only weak evidence that suggests a negative effect of natural habitat  
491 proximity on pollinator species richness (27 studies). The latter relationship was particularly  
492 marked in wild pollinators (excluding managed honeybees), yet high heterogeneity in effect  
493 sizes across studies suggests strong context dependency.

494 Our findings contrast with previous global syntheses that have shown consistent declines in  
495 pollinators and pollination services, particularly in the tropics (Ricketts et al. 2008, Garibaldi  
496 et al. 2011). Two possible explanations for these contrasting results emerge from our synthesis:  
497 firstly, TSF landscapes may provide resilience to and buffer against negative effects of  
498 increasing distance to natural habitat on pollination services; and secondly, the complexities  
499 and methodological variation across studies may limit our ability to detect consistent patterns.

### 500 **4.1 Could TSF landscapes buffer negative effects of distance to natural habitat?**

501 The lack of a consistent decline in pollination services with distance from natural habitat in  
502 TSF landscapes may reflect the stark differences between tropical smallholder farming systems  
503 and more industrial agricultural landscapes. While previous syntheses reported clear declines

504 in pollination services with increasing distance to natural habitat (Ricketts et al. 2008, Garibaldi  
505 et al. 2011), many of their underlying studies provided data from larger-scale, commercially  
506 managed farms. In contrast, TSFs are characterised by small field sizes, relatively high crop  
507 diversity, and flower-rich herbaceous semi-natural habitat patches, creating a high degree of  
508 landscape heterogeneity (Perfecto and Vandermeer 2010, Tscharntke et al. 2012). Specifically,  
509 TSFs provide a pollinator-friendly mosaic of vegetation and habitat types with diverse nesting  
510 sites, staggered floral resources across time, and sheltering areas (e.g., Tamburini et al. 2020,  
511 von Königslöw et al. 2021, Astegiano et al. 2024, Marrero et al. 2024, Fijen et al. 2025).  
512 Furthermore, agroforestry practices that integrate trees and shrubs alongside crops are  
513 widespread in TSF landscapes (Nair et al. 2021), offering a variety of additional floral  
514 resources and specialised nesting sites that can support wild pollinators and enhance pollination  
515 services (Anders et al. 2023, Kingazi et al. 2024). These landscapes may thus buffer effects of  
516 habitat loss, making distance to natural habitat a less significant factor than in more simplified  
517 landscapes.

518 We found no decline in the total number of pollinators with increasing distance to natural  
519 habitat, but a decline pollinator species richness, suggesting that human-modified TSF  
520 landscapes may favour fewer highly abundant species whereas rarer, potentially more  
521 specialised wild pollinators decline with increasing distance to natural habitat. The decline in  
522 pollinator species richness was stronger when we excluded managed honeybees (*Apis mellifera*  
523 and *Apis cerana*), further supporting existing evidence that wild pollinators are more sensitive  
524 to landscape change compared to honeybees (e.g. Garibaldi et al. 2011). Functional redundancy  
525 among pollinators may help explain the lack of an effect on crop fruit set, assuming that fruit  
526 set of many tropical crops is pollination limited. In some cases, dominant pollinator species  
527 can partially compensate for those pollinators that decline, maintaining pollination services to  
528 a certain extent (Yachi and Loreau 1999, Memmott et al. 2004). For example, crops in tropical

529 Asia, South America and Africa increasingly rely on managed and feral Africanised honeybee  
530 colonies for pollination (Calfee et al. 2020, Phiri et al. 2022). Using honeybees for crop  
531 pollination comes with a suite of drawbacks, however, including high colony mortality,  
532 negative impacts on native, non-managed pollinators (Aizen et al. 2020, Osterman et al. 2021),  
533 reduced pollination effectiveness (Klein et al. 2003a, Garibaldi et al. 2013), and lower  
534 resilience against environmental fluctuations compared to species-rich wild pollinator  
535 communities (Dainese et al. 2019, Woodcock et al. 2019).

#### 536 **4.2 Could methodological limitations prevent the detection of effects of distance to** 537 **natural habitats on TSF pollination services?**

538 Whilst there may be a biological explanation for the weak effects observed, (sometimes  
539 unavoidable) methodological limitations of the included studies could be an alternative or  
540 complementary explanation. We assessed the certainty of the evidence to be very low for all  
541 three pollination outcomes in this systematic review and meta-analysis (Table 2). In particular,  
542 our risk of bias assessment highlights systemic challenges in observational pollination field  
543 studies – including difficulties in controlling for major confounding factors, standardising  
544 spatial scales, and ensuring large sample sizes, all of which can contribute to variability in  
545 effect sizes. These issues are likely compounded by the fact that smallholder farming  
546 landscapes across the tropics are, by definition, highly diverse environments (FAO 2017). The  
547 studies included in our meta-analysis span a wide range of different biomes, natural habitat  
548 types, spatial scales, focal pollinator taxa, and temporal variation in pollinator composition, all  
549 of which can influence pollination variables. As a result, detecting landscape-scale patterns in  
550 pollination dynamics is methodologically more complex in TSF landscapes compared to larger,  
551 more homogenised farming systems (Steward et al. 2014). This could explain the high  
552 heterogeneity in effect sizes in our pollinator abundance and richness analyses in particular.

553 Theoretically, our subgroup analyses should have helped us identify such drivers of  
554 heterogeneity. However, we lacked data resolution to conduct meaningful subgroup analyses,  
555 for example to explore effects for different taxonomic groups beyond excluding managed  
556 honeybees. Studies also varied widely in the maximum distances to the nearest natural habitat  
557 assessed. Given that resource requirements and dependence on natural habitat vary widely  
558 across different pollinator guilds due to functional traits such as body size, foraging range and  
559 sociality (Gathmann and Tschamntke 2002, Steffan-Dewenter et al. 2002, Steffan-Dewenter and  
560 Kuhn 2003), the spatial scales at which distance to natural habitat is measured also need to  
561 align with the biology and functional traits of the focal pollinator groups (e.g. Basu et al. 2016,  
562 Hass et al. 2018). Variation in the maximum distances assessed across studies may therefore  
563 contribute to unexplained heterogeneity in our results.

564 Furthermore, to explore effects of distance from natural habitat, we relied on primary studies'  
565 definitions of semi-natural habitat. These varied considerably across studies, with over half of  
566 the studies measuring distance to the nearest natural forest or forest fragments, and others  
567 focusing on shrublands, wetlands, agroforests, and other semi-natural habitats. Therefore,  
568 resources provided to pollinators, such as nesting sites, nectar, and pollen sources, vary  
569 considerably between 'natural habitats' (Eraerts and Isaacs 2023, Ulyshen et al. 2023),. The  
570 lack of detailed definitions of the natural habitats across all studies and overall small number  
571 of studies included in the meta-analysis precluded subgroup analysis. Such ecological and  
572 methodological limitations highlight the importance of recording more detailed metrics for  
573 quantifying habitat isolation, type, and size in future research.

574 An additional set of potential confounding variables may contribute to the difficulty in  
575 detecting a consistent effect of distance to natural habitat in TSF landscapes. While several  
576 studies explored covariates such as pesticide use (Basu et al. 2016, Obregon et al. 2021),  
577 seasonality (Banks et al. 2013), functional groups (Basu et al. 2016, Motzke et al. 2016, Hass

578 et al. 2018), or local floral abundance (Schrader et al. 2018, Wayo et al. 2020), only a limited  
579 subset of studies reported each specific covariate and resolution of the data varied across  
580 studies. For example, our coarse distinction between high and low farming intensity may mask  
581 potentially pollinator-relevant differences, such as the type, intensity, and frequency of  
582 pesticides applied, as well as the historical land-use and deforestation context (Yang et al.  
583 2024), which may explain the lack of effect in our agricultural intensity subgroup analysis.

#### 584 **4.3 Future research directions**

585 Our systematic review and meta-analysis found no consistent relationship between distance to  
586 natural habitat and pollination variables in TSFs. This could be due to high heterogeneity and  
587 agrobiodiversity in TSF landscapes, indicating that these agroecosystems may buffer negative  
588 effects of distance from natural habitat. We also found a decline in pollinator species richness  
589 with increasing distance to natural habitat, especially for wild pollinators – highlighting the  
590 importance of natural habitats in agricultural landscapes for supporting pollinators. However,  
591 limitations such as variation in study methodologies, focal pollinator taxa, and spatial scales  
592 weaken our evidence and highlight key areas for future research. Systematic evidence  
593 syntheses, including meta-analyses, are iterative rather than static endeavours (Gurevitch et al.  
594 2018), and our study highlights the need for greater data accessibility, transparency, and  
595 standardisation in pollination research, including more detailed data on, for example, pollinator  
596 traits and habitat variables as the data reported in the original papers. Given the complexity and  
597 variability of smallholder farming landscapes across the tropics, accounting for key potential  
598 confounding variables such as pesticide use, local floral resources, and temporal dynamics will  
599 be essential for advancing our understanding of pollinator dynamics in these highly  
600 heterogeneous landscapes. As the proportion of natural habitat within the landscapes has been  
601 shown to influence pollination (Fahrig 2013, Sirami et al. 2019), future research could benefit  
602 from incorporating proportional measures of habitat or other landscape heterogeneity metrics,

603 for example using remote sensing data (Eeraerts and Isaacs 2023, Ulyshen et al. 2023).  
604 Furthermore, ensuring that spatial scales are biologically meaningful for focal pollinator  
605 groups, and providing more detailed descriptions of natural habitat across studies would also  
606 improve comparison and strengthen ecological interpretations.

607 To gain a better understanding of the temporal and spatial dynamics of pollinators and  
608 their resources in TSFs, more community-level studies are needed, especially in under-  
609 represented areas, that report detailed, standardised methodologies and make data openly  
610 available. Establishing these standards will improve the reliability of future syntheses and  
611 strengthen evidence-based conservation and agricultural policies supporting pollination  
612 services in TSFs. A globally coordinated synthesis comparing TSFs with large-scale  
613 commercial farms could provide further evidence on the role of TSFs for food security and  
614 pollinator conservation. Such insights would be valuable for informing landscape management  
615 strategies and priorities that balance agricultural productivity with biodiversity conservation.

## 616 **5 ACKNOWLEDGEMENTS**

617 We thank Information Specialist Alison Bethel for her generous insights into the (re)design of  
618 the searches, even though she did not have capacity at the time for more involvement in  
619 designing, running and processing them as a co-author. We also thank Taylor Ricketts for  
620 generously sharing access to the raw data underlying their 2008 meta-analysis. Furthermore,  
621 we acknowledge that this research was supported by a doctoral scholarship to Ennia Bosshard  
622 funded by the Bakala Foundation and the One CGIAR Nature+ initiative.

## 623 **6 CONFLICT OF INTEREST**

624 The authors have no conflicts of interest to declare.

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651 Review and Editing, Supervision. **Chris Kaiser-Bunbury:** Conceptualisation, Methodology,  
652 Funding acquisition, Writing - Review and Editing, Supervision.

## 653 **8 DATA AVAILABILITY STATEMENT**

654 Raw data and R code for conducting the meta-analysis are available via GitHub  
655 ([https://github.com/enniabosshard/pollinatorhabitatTSF\\_SRMA/](https://github.com/enniabosshard/pollinatorhabitatTSF_SRMA/)), and the version used for  
656 this manuscript will be permanently archived at Zenodo  
657 (<https://doi.org/10.5281/zenodo.15088749>).

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