

REVIEW AND SYNTHESIS

Stability of pollination services decreases with isolation from natural areas despite honey bee visits

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Abstract

Sustainable agricultural landscapes by definition provide high magnitude and stability of ecosystem services, biodiversity and crop productivity. However, few studies have considered landscape effects on the stability of ecosystem services. We tested whether isolation from florally diverse natural and semi-natural areas reduces the spatial and temporal stability of flower-visitor richness and pollination services in crop fields. We synthesised data from 29 studies with contrasting biomes, crop species and pollinator communities. Stability of flower-visitor richness, visitation rate (all insects except honey bees) and fruit set all decreased with distance from natural areas. At 1 km from adjacent natural areas, spatial stability decreased by 25, 16 and 9% for richness, visitation and fruit set, respectively, while temporal stability decreased by 39% for richness and 13% for visitation. Mean richness, visitation and fruit set also decreased with isolation, by 34, 27 and 16% at 1 km respectively. In contrast, honey bee visitation did not change with isolation and represented > 25% of crop visits in 21 studies. Therefore, wild pollinators are relevant for crop productivity and stability even when honey bees are abundant. Policies to preserve and restore natural areas in agricultural landscapes should enhance levels and reliability of pollination services.

Keywords

Apis mellifera, *Bombus* spp., ecosystem services, flower visitors, landscape management, pollinator services, richness, spatial stability, sustainable agricultural landscapes, temporal stability.

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INTRODUCTION

Agriculture and urban settlements cover almost 40% of Earth's ice-free terrestrial land, with an additional 37% being rangelands and semi-natural habitats that are embedded within agricultural or settled landscapes (Ellis *et al.* 2010). This large footprint of agriculture is a

continuing challenge for sustainability, which involves decisions at the landscape scale to increase agricultural production for a growing human population, while maintaining multiple ecosystem services and biodiversity (Zhang *et al.* 2007; Royal Society of London 2009). The stability of ecosystem functions is a component of sustainability that has received great attention (Balvanera *et al.* 2006; Haddad *et al.* 2011),

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particularly for plant community biomass and productivity (e.g. Doak *et al.* 1998; McCann 2000; Isbell *et al.* 2009); however, empirical evidence for other ecosystem services is scarce (Kremen 2005). Flower-visiting animals, especially insects, provide pollination services by delivery of sufficient quantity and quality of pollen at the appropriate time and place for ovule fertilisation in *c.* 70% of crop species worldwide (Klein *et al.* 2007). Temporal and spatial stability of pollinator diversity and pollination services is important for the conservation of natural plant and animal populations, as well as for maintaining reliable and predictable crop productivity.

Natural or semi-natural areas (hereafter natural areas for brevity) within agricultural landscapes often provide habitat for wild pollinator species, from which they forage on flowering crop and weed plants in agricultural fields (Kremen *et al.* 2007; Ricketts *et al.* 2008; Westphal *et al.* 2008). Although flowering crops themselves often provide important resources for many pollinator species, the short duration of floral availability, low diversity of floral and nesting resources, and pesticide application and tillage often compromise the capacity for these cropped areas, on their own, to support diverse and abundant pollinator communities (Potts *et al.* 2010; Williams *et al.* 2010). Optimal foraging theory predicts that distance (isolation) from natural areas decreases mean levels of pollinator richness, visitation rate and therefore pollination of crop flowers (e.g. Pyke 1984; Cresswell *et al.* 2000). The assumptions underlying these predictions are that a majority of pollinators are central place foragers with fixed nest sites such as in the soil, plant stems, or trees within the natural areas, that there is an energetic cost for flying and that flowers within a crop monoculture do not differ from one another in the reward they provide in terms of diversity of sugars, amino acids, micro-vitamins and minerals (Blüthgen and Klein 2011). These assumptions are realistic for non-parasitic bees (Hymenoptera, Apoidea), the most important pollinators worldwide (Klein *et al.* 2007; Kremen *et al.* 2007). A recent synthesis showed that mean levels of flower-visitor richness and visitation rate in croplands decline with distance from natural areas (Ricketts *et al.* 2008); however, the effects on temporal or spatial stability are not well understood and have seldom been analysed even in individual studies (but see e.g. Kremen *et al.* 2004; Klein 2009).

The stability of flower-visitor richness and visitation rate to crop flowers, here defined as high among-day (temporal) or among-plant (spatial) predictability (i.e. low variability) during crop bloom, are also predicted to change with distance to natural areas. Specifically, higher mean richness closer to natural areas may in itself produce pollinator communities that are more stable over space and time (Ebeling *et al.* 2008) because of complementarity and specialisation among species (Hoehn *et al.* 2008; Blüthgen and Klein 2011), response diversity (Winfree & Kremen 2009), and sampling effects (Tschamtkke *et al.* 2005) among others. Furthermore, agricultural practices such as agrochemical applications can also destabilise plant-pollinator communities because of contrasting conditions in the fields before and after chemical use (Potts *et al.* 2010). If seed and fruit production are pollen limited, low and variable pollination services provided by depauperate pollinator communities far from natural areas can translate into a lower mean and higher variability of crop yield (Klein 2009; Garibaldi *et al.* 2011). This effect should be greater for crop species with higher dependence on biotic pollen deposition and lower capacity for abiotic- or self-pollination (Garibaldi *et al.* 2011). However, to date, empirical evidence linking pollinator richness or visitation rate with crop fruit set as a function of distance from natural

areas is weak (Ricketts *et al.* 2008), and the effects on stability have not yet been explored through a quantitative synthesis.

Differences in pollinator functional types across global regions, such as the prevalence of *Bombus* spp. (bumble bees) in some temperate zones or Meliponini (stingless) bees in the tropics, may greatly influence the response of pollinator communities, and thus pollination services, to landscape structure (Ricketts *et al.* 2008; Williams *et al.* 2010). For example, effects of isolation from natural areas are expected to be lower for pollinators with large flight ranges such as *Bombus* spp. than for smaller species such as Meliponini with shorter flight ranges (Gathmann & Tschamtkke 2002; Steffan-Dewenter *et al.* 2002; Westphal *et al.* 2006; Greenleaf *et al.* 2007; Klein *et al.* 2008). In addition, pollinators that are not central place foragers, such as pollen beetles and syrphid flies, may (Blanche & Cunningham 2005; Meyer *et al.* 2009) or may not (Mayfield 2005; Jauker *et al.* 2009) depend on natural areas for different resources.

Isolation effects should also be less pronounced for *Apis mellifera* L. (honey bee), the most important crop pollinator species worldwide, because of its broad diet, longer foraging ranges compared with most solitary bees, and its ability to locate and utilise discrete patches of resources in the wider landscape efficiently using scouting (Gathmann & Tschamtkke 2002; Steffan-Dewenter *et al.* 2002; Steffan-Dewenter & Kuhn 2003). Furthermore, *A. mellifera* frequently occurs both as domesticated colonies in transportable hives worldwide, but less commonly in lowland tropics (see also Table 1), and as wild native species in Europe and North Africa or as feral populations in all other continents except Antarctica. Managed colonies can be placed in almost any habitat, depending on the demand for commercial pollination or honey production. Therefore, the presence of *A. mellifera* in almost every agricultural landscape in the world may buffer the negative influence that isolation from natural areas may have on crop fruit set.

Using data from 29 crop pollination studies, we explored through hierarchical Bayesian analyses the influence of isolation from natural areas on the temporal and spatial stability and the mean levels of flower-visitor richness, visitation rate to crop flowers, and seed or fruit set. We also assessed whether these effects varied with insect identity (*A. mellifera*, *Bombus* spp., and all insects but *A. mellifera*), degree of crop dependence on pollinator services, and biome (temperate, Mediterranean, and tropical). We found both lower stability and mean levels of pollination services (measured as seed or fruit set) provided by depauperate pollinator communities (measured as richness and visitation rate) with increasing isolation (distance) from natural areas.

MATERIAL AND METHODS

Studies and variables

Our synthesis includes data from 29 studies on a total of 21 crops from 15 countries on five continents. We did not include studies from which visitation rates could not reliably be partitioned into *A. mellifera* and other flower-visitor species, as we expected different responses of *A. mellifera* to landscape structure. In addition, we did not include data from passive sampling techniques such as pan traps as such methods do not exclusively sample the insect species visiting crop flowers (Westphal *et al.* 2008; Table 1). For those studies based on manipulative experimentation, such as control (open) vs. hand-pollinated flowers, or control vs. flower-visitor exclusion (bagged), we always chose the control (open) treatment for comparison across studies.

Table 1 Crop pollination studies used to synthesize the general influence of isolation from natural or semi-natural areas on the temporal and spatial stability and the mean levels of pollination services

Crop and study code	References	Crop species	Key flower-visitors	Managed, <i>A. mellifera</i> feral?†	(semi-) natural areas	Distance range (m)	Location	Spatial CV: no. replicates, sub-replicates§	Temporal CV: no. replicates, sub-replicates§
<i>Tropical and subtropical biomes</i>									
Atromoya	Blanche & Cunningham 2005	<i>Annona squamosa</i> x <i>A. cherimola</i>	Small beetles, especially Nitidulidae	No, yes	0	100–24 000	Australia, Queensland	9, 30–50 trees	No data
Coffee (A) highland	Klein et al. 2003a; Klein 2009	<i>Coffea arabica</i>	<i>Apis</i> spp., <i>Trigona</i> spp., Halictidae, solitary bees	No, no	0	0–1415	Indonesia, Sulawesi	24, 3–4 trees	24, 5
Coffee (B) highland	Ricketts 2004; Ricketts et al. 2004†	<i>Coffea arabica</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	40	3–1392	Costa Rica	20, 5–9 trees	28, 5
Coffee (C) lowland	Klein et al. 2003b	<i>Coffea canephora</i>	<i>Apis</i> spp., <i>Trigona</i> spp., Halictidae, solitary bees	No, no	0	0–1415	Indonesia, Sulawesi	15, 3–4 trees	No data
Grapefruit	Chacoff & Aizen 2006; Chacoff et al. 2008	<i>Citrus paradisi</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	95	0–1000	Argentina, Salta	40, 10 trees	60, 6
Longan	Blanche et al. 2006	<i>Dioscarpus longan</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	49	100–30 000	Australia, Queensland	6, 4 trees	No data
Macadamia	Blanche et al. 2006	<i>Macadamia integrifolia</i>	<i>A. mellifera</i>	No, yes	> 99	10–16 000	Australia, Queensland	5, 4 trees	No data
Mango	Carvalho et al. 2010†	<i>Mangifera indica</i>	Ants, mainly <i>Camponotus</i> spp and <i>Monomorium</i> spp.	Yes, yes	8	100–660	South Africa	No data	6, 2
Oil palm	Mayfield 2005	<i>Elaeis guineensis</i>	<i>Elaeidobius kamerunicus</i>	No, yes	< 1	9–200	Costa Rica	No data	7, 2–4
Passion fruit	Bogdanski 2005; Ricketts et al. 2008†	<i>Passiflora edulis</i>	Carpenter bees (<i>Xylocopa</i> spp.)	No, yes	24	129–617	Brazil, Bahia	No data	16, 3
Sunflower (A)	Carvalho et al. 2011†	<i>Helianthus annuus</i>	<i>A. mellifera</i>	Yes, yes	85	30–1500	South Africa	24, 12 plants	24, 2
<i>Mediterranean biome</i>									
Almond	Klein_unp†	<i>Prunus dulcis</i>	<i>A. mellifera</i> , <i>Andrena cerasifolia</i> , Halictidae, Andrenidae, Syrphidae and other flies	Yes, yes	36	7–2221	USA, California	17, 2 positions (edge vs. interior)	18, 3
Muskmelon	Kremen in Ricketts et al. 2008†	<i>Cucumis melo</i>	<i>A. mellifera</i> , <i>Bombus</i> spp., <i>Halictus</i> spp.	Yes, yes	95	49–3000	USA, California	8, 2 transects	No data
Sunflower (B)	Greenleaf & Kremen 2006b†	<i>Helianthus annuus</i>	<i>A. mellifera</i> , <i>Svastra obliqua expurgata</i> , <i>Anthophora urbana</i> , <i>Diadasia</i> spp., <i>Melissodes</i> spp.	Yes, yes	81	30–9863	USA, California	19, 4 transects	8, 2
Sunflower (C)	Mandelik_unp_A†	<i>Helianthus annuus</i>	<i>A. mellifera</i> , <i>Lasiglossum</i> spp.	Yes, no	96	20–440	Central Israel	4, 2 positions (edge vs. interior)	11, 2
Tomato (cherry)	Greenleaf & Kremen 2006a†	<i>Solanum lycopersicum</i>	<i>Anthophora urbana</i> , <i>Bombus vosnesenskii</i>	Yes, yes	0	30–3939	USA, California	13, 4 transects	16, 3
Watermelon (A)	Kremen et al. 2002, 2004†	<i>Citrullus lanatus</i>	<i>A. mellifera</i> , <i>Bombus</i> spp., <i>Halictus</i> spp.	Yes, yes	68	49–4800	USA, California	46, 3–4 transects	15, 2
Watermelon (B)	Mandelik_unp_B†	<i>Citrullus lanatus</i>	<i>A. mellifera</i> , <i>Lasiglossum</i> spp., <i>Ceratina</i> spp.	Yes, no	85	20–290	Central Israel	8, 2 positions (edge vs. interior)	10, 2

Table 1 (Continued)

Crop and study code	References	Crop species	Key flower-visitors	Managed, feral [†]	<i>A. mellifera</i> visits (%)	(semi-) natural areas	Distance range (m)	Location	Spatial CV: no. replicates, sub-replicates [§]	Temporal CV: no. replicates, sub-replicates [§]
<i>Other temperate biomes</i> [¶]										
Blueberry	Isaacs & Kirk 2010	<i>Vaccinium corymbosum</i> cv Jersey	<i>A. mellifera</i> , andrenid bees, halictid bees, <i>Bombus</i> spp., <i>Xylocopa virginica</i>	Yes, no	85	Woodland	1–218	USA, Michigan	12, 2 positions (edge vs. interior)	12, 2
Buckwheat	Carré <i>et al.</i> 2009 [†]	<i>Fagopyrum esculentum</i>	<i>A. mellifera</i>	Yes, yes	92	Deciduous forest	5–1500	Poland, Lubelszczyzna	10, 10 transects	9, 4
Canola (A)	Arthur <i>et al.</i> 2010*	<i>Brassica napus</i> and <i>juncea</i>	<i>A. mellifera</i> , Syrphidae, native bees	No, yes	33	Dry woodland	50–216	Australia, New South Wales	11, 4–43 transects	No data
Canola (B)	Morandin & Winston 2005*	<i>Brassica napus</i>	Many wild bees, including species of <i>Andrena</i> , <i>Halictus</i> , and <i>Bombus</i>	No, no	< 2	Aspen woodland, grassland, shrubland, wetland	35–210	Canada, Alberta	18, 12 plant pairs	No data
Canola (C)	Winston 2005*	<i>Brassica rapa</i>	<i>Halictus</i> , and <i>Bombus</i>				24–65		8, 12 plant pairs	No data
Cherry	Holzschuh_unp [†]	<i>Prunus avium</i>	<i>A. mellifera</i> , <i>Andrena</i> spp.	Yes, no	67	Calcareous grasslands, orchard meadows	22–182	Germany, Hesse	8, 4 trees	No data
Field bean	Carré <i>et al.</i> 2009	<i>Vicia faba</i>	<i>Bombus</i> spp.	Yes, no	35	Chalk grasslands	100–1875	UK, England	10, 6 transects	10, 4
Kiwi fruit	Ricketts <i>et al.</i> 2006	<i>Actinidia deliciosa</i>	<i>A. mellifera</i>	Yes, yes	91	Mixed evergreen shrubland and forest	7–111	New Zealand	6, 7 vines	20, 3
Spring rape	Carré <i>et al.</i> 2009*	<i>Brassica napus</i>	<i>A. mellifera</i>	Yes, no	82	Semidry pasture	47–337	Sweden	10, 6 transects	No data
Strawberry	Carré <i>et al.</i> 2009*	<i>Fragaria × ananassa</i>	<i>A. mellifera</i>	Yes, no	80	Calcareous grassland, orchard meadows, fallows	147–719	Germany, Lower Saxony	8, 6 transects	8, 4
Watermelon (C)	Winfree <i>et al.</i> 2007, 2008 [†]	<i>Citrullus lanatus</i>	Many wild bee species, <i>A. mellifera</i>	Yes, no	25	Deciduous woodland	17–319	USA, NJ and PA	23, 40 quadrats	23, 2

*Studies for which distance to natural areas was estimated from proportional area of natural areas.

[†]Studies used to model the distance – proportional area relationship, as they measured both variables.

[‡]Are managed or feral (wild for studies in Europe) colonies of *Apis mellifera* (honey bees) present in the study area?

[§]To analyse spatial stability, we used variation among quadrats, transects or plants (sub-replicates) within each site (replicate). To analyse temporal stability, we used variation among days (sub-replicates) within each site (replicate) for all studies.

[¶]Includes all studies located in temperate latitudes (> 23.5° and < 66.5°), except those with Mediterranean climate (warm to hot, dry summers, and mild to cold, wet winters).

Our synthesis adds seven new studies to the previous comprehensive synthesis of pollination services (Ricketts *et al.* 2008). We also include a novel analysis of the spatial and temporal stability of pollination services, as well as for mean levels of *A. mellifera* and *Bombus* spp. as individual species or species groups. We could not use previous synthetic databases (e.g. Ricketts *et al.* 2008) because they did not provide information for spatial or temporal variation within each site and did not include data for sub-replicates within each replicate (Table 1). Therefore, data were provided and checked by authors of each study as they were not available in most associated published articles (see below, Table 1). For fruit set analysis, we omitted two studies (kiwi and passion fruit) included in the synthesis by Ricketts *et al.* (2008), since these studies did not possess temporal or spatial sub-replicates (Table 1). Appendix S1 in Supporting information provides details on the field methods for the four unpublished studies included in our synthesis (see also Tables 1 and S1).

We extracted data on isolation from natural areas, flower-visitor richness in croplands, visitation rate to crop flowers, and seed or fruit set (hereafter fruit set for brevity) when available from each study. Visitation rate to crop flowers was obtained for three main pollinator groups: *A. mellifera*, *Bombus* spp., and all visitors except *A. mellifera*. Our analysis treats *A. mellifera* as a single group because managed or feral colonies cannot be distinguished from one another in field observations of crop flowers (Table 1). Only three of the 29 studies were mainly pollinated by taxa other than bees: *Annona squamosa* L. × *A. cherimola* Mill. hybrids (Atemoya) in Australia pollinated by Nitidulidae (beetle family), *Mangifera indica* L. (Mango) in South Africa by Formicidae, *Elaeis guineensis* Jacq. (Oil palm) in Costa Rica pollinated by *Elaeidobius kamerunicus* Faust (Curculionidae, African oil palm weevil; Table 1).

We chose linear distance to the closest natural areas as our isolation measure because it was reported by the largest number of studies. We followed the decision of the authors of each study regarding what constituted natural areas known to support pollinator populations. Five studies measured isolation only as proportion of natural areas within a circle of a given radius specific to each study. As we needed a single common measure across all studies, we used a model to estimate distance to the closest natural areas for these five studies. Using the 14 studies that measured both variables (Table 1), we developed a predictive model of $\log_{10}(\text{distance} \times \text{radius}^{-1})$ as a linear function of $\log_{10}(\text{proportional area})$, following the approach of Ricketts *et al.* (2008). We parameterized this relationship as a mixed-effects model with the lme function of the nlme package in R (R Development Core Team, 2010), with fixed effect estimates of the slope and intercept, while allowing for study-level random variation in both coefficients. We used restricted maximum-likelihood estimates of the fixed effects to predict linear distance for each study site. To assess model performance, we used the model to estimate distances from proportion of natural area, in the same 14 studies used for parameterisation, then performed a linear regression of observed distances as a function of predicted distances ($n = 275$ sites). Results yielded a slope that was not significantly different from 1 (mean slope = 0.97, 95% confidence interval = 0.89–1.04) with an $r^2 = 0.70$ indicating that the approximation was adequate.

Statistical analyses for different response variables have different sample sizes as not all studies measured all variables. Specifically, 12 studies measured flower-visitor richness (Fig. 1), 27 studies measured visitation rate to crop flowers (Fig. 2) and 15 studies measured fruit set (Fig. 3). Similarly, analyses for temporal and spatial

stability have different sample sizes as not all studies measured both temporal and spatial sub-replicates within each replicate (Table 1). Fruit set data were available for spatial stability, but not for temporal stability, as only one study considered different flowering seasons.

Stability

Following several authors, we defined stability as the inverse of variability (e.g. Lehman & Tilman 2000; McCann 2000; Tilman *et al.* 2006; Griffin *et al.* 2009; Isbell *et al.* 2009; Haddad *et al.* 2011). Specifically, temporal and spatial stability of pollination are defined here as low variation over time (days within the flowering season) and space (within site variation) respectively (Table 1). The inverse of the coefficient of variation ($CV^{-1} = \frac{\text{mean}}{\text{standard deviation}} * 100$) is a convenient measure of stability because it is dimensionless and scale invariant, and accounts for nonlinear dynamics, among other reasons (for further details see Lehman & Tilman 2000; Griffin *et al.* 2009). In our synthesis, we chose CV instead of CV^{-1} so as to permit inclusion of sites that showed standard deviation (SD) equal to zero (3% of total sites); note the impossibility of using zero in the denominator of the CV^{-1} ratio. A large temporal or spatial CV represents low temporal or spatial stability respectively (for the use of CV as a measure of instability, see examples: Doak *et al.* 1998; Kremen *et al.* 2004; Ebeling *et al.* 2008; Klein 2009; Proulx *et al.* 2010; Garibaldi *et al.* 2011). Stability measures have rarely been provided for pollination services to crops, not even by individual studies, as reflected by the fact that only four of the 25 articles listed in Table 1 analysed stability (all four of them calculated CV values). The measure CV accounts for (detrends) among-site co-variation between SD and mean values (for further details see Appendix S2) and is therefore an appropriate metric for considering the relationship between stability and isolation from natural areas.

The temporal CV was estimated separately for each response variable as the ratio between the SD and the mean of repeated measurements through time within each site (Table 1). Specifically, we calculated the variation across days within a particular year, with the time intervals spanning from a week to several months depending on the flower bloom duration of the studied crop species (Tables 1, S1). For spatial CV, we used measurements taken in different positions within each site, such as different plant or transect locations (Table 1). Mean and CV values for each study and each year were z-transformed ($\frac{(\bar{y}_i - \bar{y})}{(SD_i)}$) for comparisons between experiments with contrasting means (\bar{y}) and standard deviations (SD_i). This standardisation was also necessary because not all studies measured the same variable in the same manner (Table 1, Appendix S1). Therefore, we evaluated the relative influence of distance from natural areas on the mean and on the temporal and spatial CV for each variable.

Statistical analyses

We performed hierarchical Bayesian analyses to evaluate the effects of isolation from natural areas across multiple studies (Gelman & Hill 2007). For each response variable (e.g. temporal CV of visitation rate, or spatial CV of flower-visitor richness), we estimated the following linear model that allowed the intercept and the slope to vary among studies: $y_{i\alpha} = \alpha_i + \beta_i D_{i\alpha} + \varepsilon_{i\alpha}$, where α_i and β_i are the intercept and slope of study i respectively, $D_{i\alpha}$ is the distance (in metres) from nearest natural areas of site α in study i , and $\varepsilon_{i\alpha}$ is the residual of site α

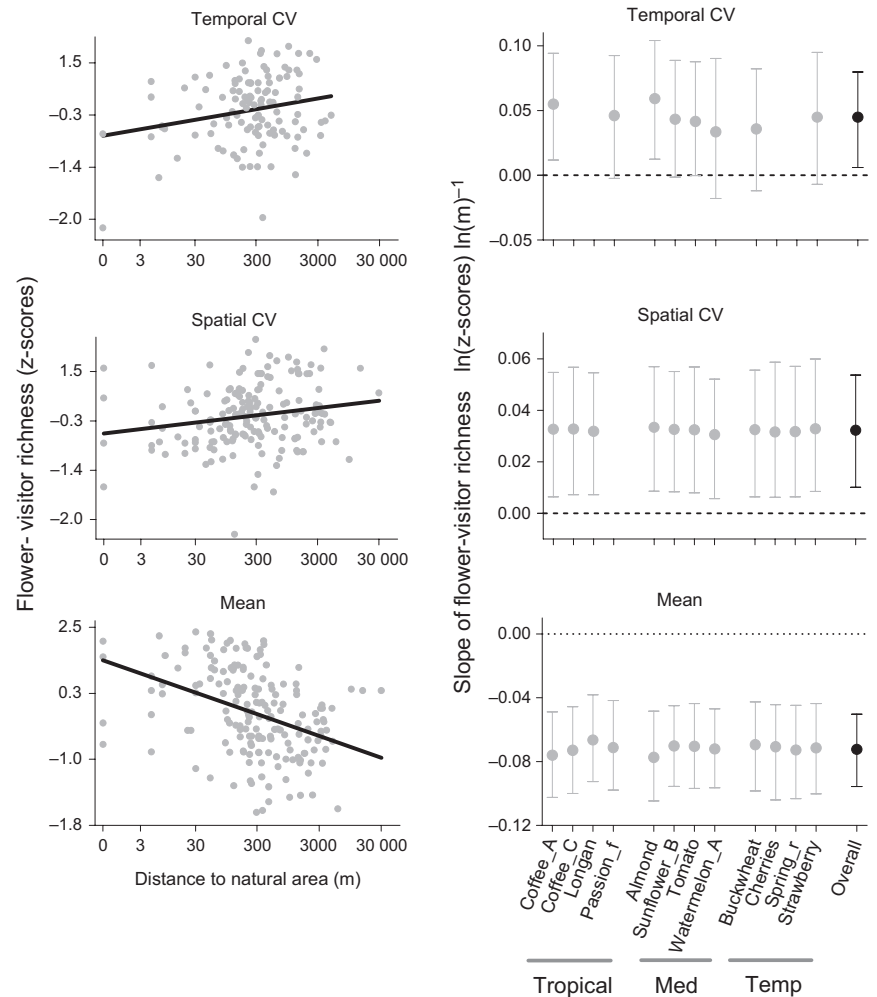


Figure 1 Mean and coefficient of variation (CV) of flower-visitor richness (all insects except *Apis mellifera*) in croplands in relation to distance from natural or semi-natural areas. In the left side panels, each grey point is a site within a study (all studies are shown) and the black line is the overall linear model estimation (note the natural log scale of both axes). Data from different studies were standardised by z-scores prior to analysis. Right panels show slopes (mean and 90% credible interval as circles and lines respectively) for each study (grey) and overall mean (μ_β , black). In the x-axis of the right hand panel, 'tropical' = tropical and subtropical studies, 'med' = mediterranean studies, and 'temp' = temperate studies.

in study i . The α_i and β_i were considered normally distributed with means of μ_α and μ_β , and variances of σ_α^2 and σ_β^2 respectively. Therefore, μ_β describes the overall change across studies (hyperparameter) for a pollination response variable per metre of increase in isolation from natural areas, where the relative influence of each study depends on its sample size and the precision of its local model fit (Gelman & Hill 2007). In addition, we present estimates for the slope of each individual study (β_i), which result from the combination of the overall trend across studies and the local model fit of the study (partial pooling estimates), where the weight of the local model fit increases with sample size and decreases with residual variance (Gelman & Hill 2007).

The association between each response variable and isolation from natural areas was also explored using functional forms other than linear models and with and without z-scores standardisation. All models yielded the same directional trends between each response variable and isolation from natural areas, regardless of the shape assumed for this relationship, or the use of z-scores vs. absolute measurements (data not shown). A linear association between variables on a natural log scale was the best model according to the lower deviance and expected predictive error criteria (data not shown). In addition, the directional patterns described below for any variable was not affected by the exclusion of data taken at extremely long

distances, or by the inclusion into the model of the number of spatial or temporal sub-replicates (Table 1) as a surrogate for differences in sampling effort among studies (Fig. S1).

The posterior probability distribution, which updates the prior distribution using the likelihood model and data, was simulated for each parameter with Markov Chain Monte Carlo (MCMC) using WINBUGS 1.4 (Lunn *et al.* 2000) from R Software (R2WinBUGS package; Gelman & Hill 2007; R Development Core Team 2010). We assigned non-informative priors to all parameters; specifically, normal distributions for μ_α and μ_β (mean = 0 and variance = 10 000 for both parameters), and uniform distributions for σ_α , σ_β (from 0 to 100 for the three variances) and $\rho_{\alpha\beta}$ (from -1 to 1 for the correlation between α and β). For each model, we simulated three MCMC chains for 100 000 iterations (of which the first 50 000 were discarded), thinning the results by a factor of 150 to reduce autocorrelation in the sample. We used the \bar{R} statistics to assess MCMC convergence, which converged in all models, as \bar{R} statistics were approximately equal to 1.0 (Gelman & Hill 2007). For each β_i and μ_β , we report the 90% credible interval (also known as Bayesian confidence interval; Figs 1, 2 and 3), which we calculated as the highest posterior density estimate containing 90% of the posterior distribution of each parameter. In addition, for CV data, the proportion of simulated posterior values that are greater than zero

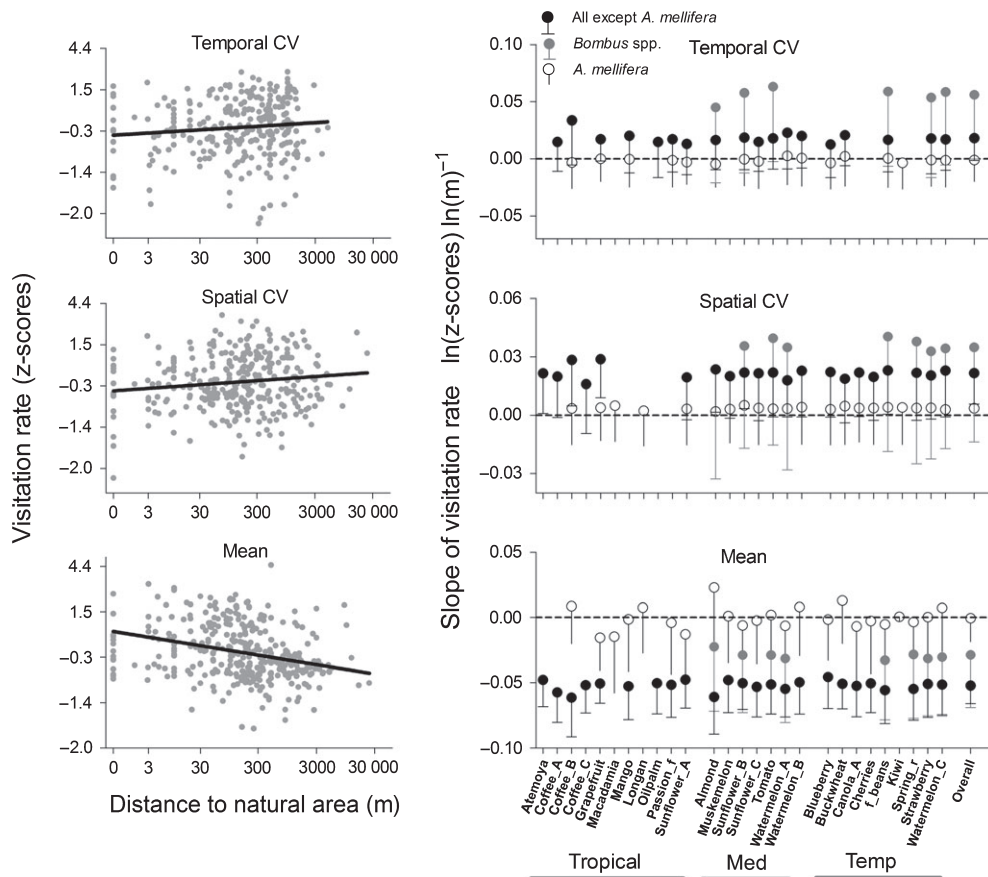


Figure 2 Mean and coefficient of variation (CV) of visitation rate to crop flowers in relation to distance from natural or semi-natural areas. In the left side panels, visitation rate values are only for all insects except *Apis mellifera*, each grey point is a site within a study (all studies are shown), whereas the black line is the overall linear model estimation (note the natural log scale of both axes). Data from different studies were standardised by z-scores prior to analysis. Right panels show individual study (β_i) and overall (μ_β) slopes. Mean and 90% credible interval (only the lower limit is shown for clarity) are depicted as circles and lines respectively. Different analyses were performed for all flower visitors (except *Apis mellifera*, black), *Bombus* spp. (bumble bee, grey) and *A. mellifera* (honey bees, white). In the x-axis, 'tropical' = tropical and subtropical studies, 'med' = Mediterranean studies, and 'temp' = temperate studies.

can be interpreted as the probability that greater isolation is associated with higher CV in a pollination variable, given our priors, data and model. For mean data, the proportion of simulated posterior values that are less than zero can be interpreted as the probability that greater isolation is associated with lower mean values for a pollination variable.

RESULTS

Absolute (non z-scaled) values for within-site spatial variation (spatial CV) were on average ± 1 standard error: 39 ± 3 , 73 ± 12 and $68 \pm 5\%$ for insect flower-visitor richness, visitation rate to crop flowers (all insects but *A. mellifera*) and fruit set respectively (Table S1). Among-day variability within year for a particular site, (temporal CV) was 56 ± 4 and $65 \pm 7\%$ for insect flower-visitor richness and visitation rate to crop flowers (all insects but *A. mellifera*) respectively (Table S1). Spatial and temporal CV for *A. mellifera* visitation to crop flowers was 74 ± 4 and $82 \pm 4\%$, respectively, whereas *Bombus* spp. showed 125 ± 10 and $77 \pm 6\%$ for spatial and temporal CV respectively.

The z-scaled values of both spatial and temporal CV for flower-visitor richness of all insects but *A. mellifera* increased with isolation from natural areas, while mean richness decreased, irrespective of

biome (Fig. 1). At 1 km from natural areas, spatial and temporal CV of flower-visitor richness increased on average by 25 and 39%, respectively, relative to the value at sites bordering natural areas, while mean richness decreased by 34%. Partial pooling estimates (see *Statistical analyses*) for all individual studies were consistent with these patterns, and no study included zero values in the 90% credible intervals from the posterior distribution except for some studies used to analyse temporal CV (Fig. 1).

Spatial and temporal CV of visitation rate to crop flowers by all insects excluding *A. mellifera* increased with distance to natural areas across studies (Fig. 2). Mean visitation rate to crop flowers decreased with isolation (Fig. 2). Spatial and temporal CV of visitation rate increased on average by 16 and 13% at 1 km from natural areas, respectively, whereas mean visitation rate decreased by 27% (Fig. 2). These trends were similar across biomes (Fig. 2). Slopes for all studies showed the same directionality, although individual study estimates for temporal and spatial CV included a small and variable proportion of zero and negative values within the 90% credible intervals (Fig. 2).

Apis mellifera ranged from 0 to 99% of flower visitors, represented 50% of flower visits on average across all studies and provided more than 25% of visits to crop flowers in 21 of the 29 studies (Table 1). Coefficient of variation and mean levels of visitation rate to crop

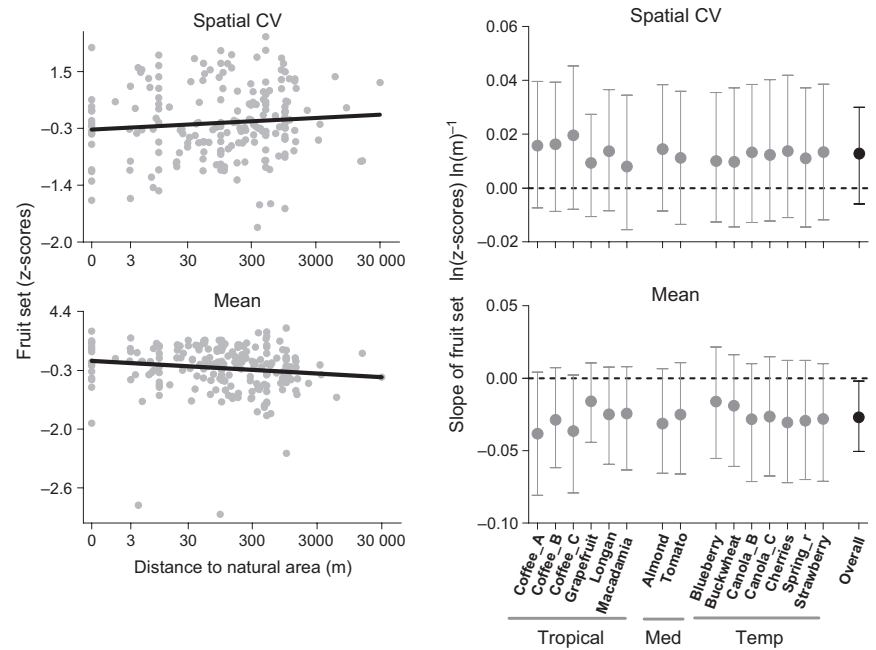


Figure 3 Mean and coefficient of variation (CV) of fruit set in relation to distance from natural or semi-natural areas. In the left side panels, each grey point is a site within a study (all studies are shown) and the black line is the overall linear model estimation (note the natural log scale of both axes). Data from different studies were standardised by z-scores prior to analysis. Right panels show slopes (mean and 90% credible interval as circles and lines respectively) for each study (grey) and overall mean (μ_{β} , black). In the x-axis of the right hand panel, 'tropical' = tropical and subtropical studies, 'med' = Mediterranean studies, and 'temp' = temperate studies.

flowers by *A. mellifera* did not change with isolation (Fig. 2). This was also the case for the few studies in which all *A. mellifera* were known to be either managed or feral (Fig. S2). *Bombus* spp. as a discrete group showed the strongest increase in temporal and spatial CV with isolation from natural areas, although credible intervals were the largest, reflecting lower precision of estimates (Fig. 2). While mean visitation rates to crop flowers decreased with isolation for *Bombus* spp., this decrease occurred at a lower rate than that observed for all insects excluding *A. mellifera* (Fig. 2).

Within-site spatial variation (CV) in fruit set increased with isolation from natural areas, while mean fruit set decreased with isolation (Fig. 3). These results were consistent among individual studies irrespective of biome (Fig. 3), or crop pollinator dependence (Fig. S3), although 90% credible intervals included a variable proportion of values above or below zero for mean and CV respectively (Fig. 3). Overall, spatial CV of fruit set increased by 9% at 1 km from natural areas, while mean fruit set decreased by 16%.

The increase in CV with isolation from natural areas was highest for the response variable of flower-visitor richness (all but *A. mellifera*), as μ_{β} yielded 0.045 and 0.032 for temporal and spatial CV respectively (Fig. 1). Visitation rate (all insects but *A. mellifera*) showed an intermediate rate of change, as μ_{β} yielded 0.018 and 0.022 for temporal and spatial CV respectively (Fig. 2). Fruit set showed the lowest rate of change, as μ_{β} yielded 0.013 for within site CV (Fig. 3). Similarly, the magnitude of the negative association of isolation from natural areas on the means of response variables was highest for richness of flower-visitors (all but *A. mellifera*) as $\mu_{\beta} = -0.072$ (Fig. 1), intermediate for visitation rate to crop flowers by insects (all but *A. mellifera*) as $\mu_{\beta} = -0.052$ (Fig. 2) and lowest for fruit set as $\mu_{\beta} = -0.027$ (Fig. 3). Across all studied response variables, the mean values showed a stronger change with isolation than stability, i.e. absolute values of μ_{β} were higher for means than for stability. Moreover, in all cases, SD decreased less steeply than mean levels with distance to natural habitats, thus relative variation (CV) increased with isolation (Appendix S2). We found no correlation between mean and SD among sites for fruit set, while the opposite was true for visitation rates (Appendix S2).

DISCUSSION

Many studies have shown that pollinator communities lose species as natural and semi-natural habitats are removed from agricultural landscapes (Westphal *et al.* 2008; Winfree *et al.* 2009; Bommarco *et al.* 2010; Potts *et al.* 2010; Williams *et al.* 2010). Ecological theory predicts that depauperate communities will deliver ecosystem services at lower and less stable rates over both time and space (Doak *et al.* 1998; Ghazoul 2006; Kremen *et al.* 2007; Ebeling *et al.* 2008; Hoehn *et al.* 2008), but this has rarely been tested empirically. Our findings were consistent with the prediction that isolation from diverse natural and semi-natural areas reduces both the stability and the mean levels of flower-visitor richness, visitation rate and fruit set in crop areas.

Results from contrasting biomes, crops and landscapes were remarkably consistent, as reflected by our partial pooling estimates (Figs 1, 2 and 3). The standardised relative scale with z-scores used here may show less differences among studies with contrasting mean and stability than when absolute values of slopes are used. For example, the overall 34% decrease in mean flower-visitor richness at 1 km from natural areas implies a greater decrease in absolute values of number of species for highly diverse tropical pollinator communities than for less diverse temperate ones, a pattern consistent with a recent synthesis (Ricketts *et al.* 2008). In addition, the similarity across studies and in response variables of the negative effect of isolation from natural areas suggests that habitat loss is a major and consistent cause for the decline in richness and abundance of pollinating insects across the globe (see also Winfree *et al.* 2009; Potts *et al.* 2010; Williams *et al.* 2010), and their associated services to agriculture.

Species richness of flower-visitors showed the greatest decrease with distance to natural areas, visitation rates showed an intermediate rate of change and fruit set showed the smallest decrease with isolation. Visitation rates may decrease less steeply than species richness because not all flower-visiting insect species are negatively affected by distance to natural areas due to response diversity (Winfree & Kremen 2009), e.g. ants visiting mango flowers (Carvalho *et al.*

2010). The weaker signal for fruit set patterns may have occurred because, first, most of the crops in our study are able to self-pollinate to a certain extent or have a degree of parthenocarpy (Klein *et al.* 2007). Second, *A. mellifera* showed no trend with isolation and in most of the studies, crops probably benefit from *A. mellifera* pollination (Table 1). Third, other factors that limit fruit set, for instance, pests and limitation of water or nutrients, were not standardised in all studies. Finally, even if lower pollen supply occurred due to isolation, it might still be sufficient for ovule fertilisation, as the functional form between pollen supply and fruit set is positive, but asymptotic (Aizen & Harder 2007; Garibaldi *et al.* 2011).

When seed or fruit crop production are pollen limited, however, lower spatial and temporal stability of flower-visitor richness or visitation rate with isolation may decrease both the mean and stability of fruit set (Klein 2009; Garibaldi *et al.* 2011). For example, among-plant spatial variation in pollination may result in failed fertilisation for some flowers in particular locations, whereas greater temporal variation in pollination would produce differences in ovule fertilisation for flowers blooming at different periods. Additionally, lower mean levels of richness or visitation rate are known to reduce both the mean and stability of fruit set (e.g. Hoehn *et al.* 2008; Carvalheiro *et al.* 2010).

Importantly, we provide novel evidence of a negative relationship between isolation from natural areas and both spatial stability and mean level of crop fruit set. Our synthesis adds to a previous one that found no significant overall trend in mean fruit set with isolation from natural areas (Ricketts *et al.* 2008), and provides the first information on the effects of spatial stability on crop production and temporal stability on proxies of pollination services (pollinator richness, visitation rate). Differences in overall mean trends between this study and the previous Ricketts *et al.* (2008) synthesis may have occurred because we standardised data across studies (*z*-scores) and included six new crops (almond, blueberry, buckwheat, cherry, spring rape, and strawberry) all measuring seed or fruit set at (or very close to) harvest. More studies are needed to enhance precision of our parameter estimates (Fig. 3), as well as to detect whether isolation effects vary among crops with different degrees of pollinator dependence (Fig. S3). Our results suggest that pollen limitation of seed or fruit production is frequent for entomophilous crops in agricultural fields isolated from natural habitats. This is in agreement with a recent study reporting that crops with greater pollinator dependence had lower mean and stability in relative yield and yield growth, despite global yield increases for most crops (Garibaldi *et al.* 2011). Pollen limitation has also been found to be common within natural areas (Knight *et al.* 2005), and habitat fragmentation has been found to negatively affect pollination and reproduction of wild plants (Aguilar *et al.* 2006).

Given that a negative association between isolation and crop fruit set was detected in the absence of a trend for *A. mellifera* visitation with distance to natural areas, our data suggest that pollination services provided by other (wild) insects are important even in the presence of *A. mellifera*. Wild insects may increase fruit set through enhanced amount and quality of pollen deposition, especially in crops that are not efficiently pollinated by *A. mellifera* such as tomato (Greenleaf & Kremen 2006a), for example, by complementarity among species in pollen placement (Chagnon *et al.* 1993; Hoehn *et al.* 2008) or by enhancing foraging behaviour of *A. mellifera* (Greenleaf & Kremen 2006b; Carvalheiro *et al.* 2011). Overall, our analyses suggest that improved management of farmland for pollination services should increase both the amount and spatial within-site stability of production for entomophilous crops.

Bees were the most important pollinators in all but three studies (Table 1; Blanche & Cunningham 2005; Mayfield 2005; Carvalheiro *et al.* 2010). This is not surprising because bees are known to be the most important group of crop pollinators worldwide (Klein *et al.* 2007; Kremen *et al.* 2007; Potts *et al.* 2010). However, there is a need for more studies directly examining responses to natural habitat isolation of other non-bee pollinators, such as beetles (Blanche & Cunningham 2005; Mayfield 2005), syrphid flies (Meyer *et al.* 2009), ants (Carvalheiro *et al.* 2010), midges and moths.

Flower-visitor identity had a major influence on the relationship between visitation rate and distance to natural areas. As expected, mean visitation rates to crop flowers by *Bombus* spp. decreased with isolation from natural areas, and this decline was weaker than that observed for flower-visitation by all insects (excluding *A. mellifera*), which include species of smaller size and flight capacity (Gathmann & Tschardt 2002; Greenleaf *et al.* 2007; Klein *et al.* 2008). Moreover, this weaker effect is also expected because some *Bombus* spp. nest in disturbed areas such as gardens, hedgerows and fence lines (Osborne *et al.* 2008).

Apis mellifera visitation, however, showed no change with isolation, which is in agreement with a recent meta-analysis of the effects of anthropogenic disturbance on the abundance of feral or managed *A. mellifera* (Winfree *et al.* 2009). This species may be less affected by landscape composition because it has larger foraging ranges than many solitary bees (Gathmann & Tschardt 2002; Steffan-Dewenter & Kuhn 2003) and also because hives of *A. mellifera* are frequently placed in farmland without reference to the distance from natural areas (Table 1; Winfree *et al.* 2009; Carvalheiro *et al.* 2011). Only 7% of the sampled sites included in our study were located farther than 2 km from natural areas (Table 1). At this distance, negative effects of isolation on visitation rate by feral *A. mellifera* may become evident, as indicated by mean levels of visitation to macadamia flowers (Fig. S2). Thus, greater distances from natural areas than those commonly observed in our synthesis may affect feral *A. mellifera* as well as other wild pollinators and produce greater decreases in both stability and mean of fruit set.

Biological diversity may enhance ecosystem services provisioning by increasing the mean level of delivery, as well as by providing services more stably over time and space (Doak *et al.* 1998; McCann 2000; Kremen 2005; Isbell *et al.* 2009; Proulx *et al.* 2010; Haddad *et al.* 2011). Several mechanisms have been proposed to explain why richer pollinator communities might have enhanced function or stability, including species response diversity, functional redundancy, functional complementarity and sampling effects (Tschardt *et al.* 2005; Hoehn *et al.* 2008; Winfree & Kremen 2009; Blüthgen and Klein 2011). Our analyses suggest common directional effects of the expansion of low-diversity crop land in place of more diverse natural areas on ecosystem services provided by mobile organisms such as pollinating insects, even for contrasting crops and biomes around the world. Hence, we expect policies that promote natural areas nearby crops in agricultural landscapes will increase the stability and quantity of pollinator diversity and pollination services, leading to enhanced and stabilised productivity of entomophilous crop species.

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AUTHOR CONTRIBUTIONS

LAG and AMK designed the study, prepared the data, analysed the data and wrote the paper; ISD, CK, RB and SAC designed the study, prepared the data and wrote the paper; JMM analysed the data and wrote the paper; LGC, NPC, JHD, SSG, AH, RI, KK, YM, MMM, LAM, SGP, THR, HS, BFV, CW and RW prepared the data and wrote the paper.

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SUPPORTING INFORMATION

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

Appendix S1 Methodology of four studies included in our synthesis that are currently unpublished.

Appendix S2 Decomposition of coefficient of variation (CV) into mean and standard deviation (SD): implications for understanding the effects of isolation from natural habitats.

Figure S1 Slopes for mean and coefficient of variation (CV) of visitation rate to crop flowers (all insects but *Apis mellifera*) as a function of the number of sub-replicates.

Figure S2 Visitation rate to crop flowers by feral or managed *Apis mellifera* (honey bees) with increasing distance from natural or semi-natural areas.

Figure S3 Slopes for mean and coefficient of variation (CV) of fruit set as a function of crops' pollinator dependence.

Table S1 Extension of Table 1 showing for each study the distance among sampling points, the length of the flowering period, the duration of sampling events, and the spatial and temporal coefficient of variation (CV) for visitation rate.

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