

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

Short running title: **Habitat isolation and pollination stability**

Lucas A. Garibaldi<sup>1,2,\*</sup>, Ingolf Steffan-Dewenter<sup>3</sup>, Claire Kremen<sup>4</sup>, Juan M. Morales<sup>1</sup>, Riccardo Bommarco<sup>5</sup>, Saul A. Cunningham<sup>6</sup>, Luísa G. Carvalheiro<sup>7,8,9,10,†</sup>, Natacha P. Chacoff<sup>11</sup>, Jan H. Dudenhöffer<sup>12</sup>, Sarah S. Greenleaf<sup>4</sup>, Andrea Holzschuh<sup>3,12</sup>, Rufus Isaacs<sup>13</sup>, Kristin Krewenka<sup>12</sup>, Yael Mandelik<sup>14</sup>, Margaret M. Mayfield<sup>15</sup>, Lora A. Morandin<sup>4</sup>, Simon G. Potts<sup>16</sup>, Taylor H. Ricketts<sup>17</sup>, Hajnalka Szentgyörgyi<sup>18</sup>, Blandina F. Viana<sup>19</sup>, Catrin Westphal<sup>12</sup>, Rachael Winfree<sup>20</sup>, Alexandra M. Klein<sup>21</sup>

<sup>1</sup>Laboratorio de Ecotono, INIBIOMA-CONICET and CRUB-UNCOMA, Quintral 1250, 8400 Bariloche, Río Negro, Argentina.

<sup>2</sup>Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, 1417 Buenos Aires, Argentina.

<sup>3</sup>Department of Animal Ecology and Tropical Biology, Biozentrum, University of Würzburg, Am Hubland, 97074 Würzburg, Germany.

<sup>4</sup>Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720-3114, USA.

<sup>5</sup>Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, 75007 Uppsala, Sweden.

<sup>6</sup>CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia.

<sup>7</sup>South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735, South Africa.

<sup>8</sup>Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

<sup>9</sup>Institute of Integrative and Comparative Biology, University of Leeds, Leeds LS2 9JT, UK.

<sup>10</sup>NCB-Naturalis, postbus 9517, 2300 RA, Leiden, The Netherlands.

<sup>11</sup>Instituto de Argentino de Investigaciones de las Zonas Aridas, CCT CONICET Mendoza, CC 507, 5500 Mendoza, Argentina.

<sup>12</sup>Agroecology, Georg August University Göttingen, Grisebachstr. 6, D-37077 Göttingen, Germany.

<sup>13</sup>Department of Entomology, Michigan State University, East Lansing, MI 48824, USA.

<sup>14</sup>Department of Entomology, The Hebrew University of Jerusalem, P.O. Box 12, Rehovot 76100, Israel.

<sup>15</sup>The University of Queensland, School of Biological Sciences, Goddard Building, St Lucia Campus, Brisbane 4072 Queensland Australia.

<sup>16</sup>Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading, RG6 6AR, UK.

<sup>17</sup>Conservation Science Program, WWF, Washington D.C., USA.

<sup>18</sup>Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 7, 30-387, Kraków, Poland.

<sup>19</sup>Instituto de Biologia, Universidade Federal da Bahia, 40170-210, Ondina, Salvador, Bahia

<sup>20</sup>Department of Entomology, Rutgers University, New Brunswick, NJ 08901. USA.

<sup>21</sup>Institute of Ecology, Section Ecosystem Functions, Leuphana University of Lüneburg, Scharnhorststraße 1, 21335 Lüneburg, Germany.

\*Corresponding author's e-mail: [garibald@agro.uba.ar](mailto:garibald@agro.uba.ar)

**Author contributions:** L.A.G. and A.M.K designed the study, prepared the data, analysed the data, and wrote the paper; I.S.D., C.K., R.B., and S.A.C. designed the study, prepared the data, and wrote the paper; J.M.M. analysed the data and wrote the paper; L.G.C., N.P.C., J.H.D., S.S.G., A.H., R.I., K.K., Y.M., M.M.M., L.A.M., S.G.P., T.H.R., H.S., B.F.V., C.W., and R.W. prepared the data and wrote the paper.

†Between Luísa Carvalheiro and Rachael Winfree we choose an alphabetical order of authors, as they contributed equally to this synthesis.

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

**Type of article:** Reviews and Syntheses

**Abstract:** 197 words

**Manuscript:** 7758 words

**Main Text:** 5236 words

**References:** 70

**Figures and tables:** 5

## **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 synthesized 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.

## 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), particularly for plant community biomass and productivity (e.g. Doak *et al.* 1998; Isbell *et al.* 2009; McCann 2000); 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 fertilization in ~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 each other in the reward they provide in terms of diversity of sugars, amino acids, micro-vitamins and minerals (Blüthgen & 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 analyzed even in individual studies (but see for example, 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 & Klein 2011), response diversity (Winfree & Kremen 2009), and sampling effects (Tschardtke *et al.* 2005) among others. Furthermore, agricultural practices such as agrochemical applications can also destabilize 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 & Tschardtke 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 to most solitary bees, and its ability to locate and utilise discrete patches of resources in the wider landscape efficiently using scouting (Gathmann & Tschardtke 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 a 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 since 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 enclosure (bagged), we always chose the control (open) treatment for comparison across studies. Our synthesis adds 7 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 since 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 Table 1, 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 out of the 29 studies were mainly pollinated by taxa other than bees: *Annona squamosa* L. x *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. Because 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 parameterization, 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 to 1.04) with an  $r^2=0.70$  indicating that the approximation was adequate.

Statistical analyses for different response variables have different sample sizes since 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 but not temporal stability since 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 ( $\frac{y_i - \bar{y}}{SD_y}$ ) for comparisons between experiments with contrasting means ( $\bar{y}$ ) and standard deviations ( $SD_y$ ). This standardization 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:  $y_{iz} = \alpha_i + \beta_i D_{iz} + \epsilon_{iz}$ , where  $\alpha_i$  and  $\beta_i$  are the intercept and slope of study  $i$  respectively,  $D_{iz}$  is the distance (in metres) from nearest natural areas of site  $z$  in study  $i$ , and  $\epsilon_{iz}$  is the residual of site  $z$  in study  $i$ . The  $\alpha_i$  and  $\beta_i$  were considered to be normally distributed with means of  $\mu_\alpha$  and  $\mu_\beta$ , and variances of  $\sigma^2_\alpha$  and  $\sigma^2_\beta$ , respectively. Therefore,  $\mu_\beta$  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 ( $\beta_i$ ), 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 standardization. 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  $\mu_\alpha$  and  $\mu_\beta$  (mean=0 and variance=10,000 for both parameters), and uniform distributions for  $\sigma_y$ ,  $\sigma_\alpha$ ,  $\sigma_\beta$  (from 0 to 100 for the three variances) and  $\rho_{\alpha\beta}$  (from -1 to 1 for the correlation between  $\alpha$  and  $\beta$ ). 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  $\beta_i$  and  $\mu_\beta$  we report the 90% credible interval (also known as Bayesian confidence interval; Figs. 1, 2, 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 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  $\pm 1$  standard error:  $39 \pm 3\%$ ,  $73 \pm 12\%$ , 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  $56 \pm 4\%$  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  $74 \pm 4\%$  and  $82 \pm 4\%$ , respectively, whereas *Bombus* spp. showed  $125 \pm 10\%$  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 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  $\mu_\beta$  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  $\mu_\beta$  yielded 0.018 and 0.022 for temporal and spatial CV, respectively (Fig. 2). Fruit set showed the lowest rate of change, as  $\mu_\beta$  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  $\mu_\beta$  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. Focussing on pollination services, 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, 3). The standardized relative scale with z-scores used here may show lesser 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 1km 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 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 standardized in all studies. Finally, even if lower pollen supply occurred due to isolation, it might still be sufficient for ovule fertilization, since 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 fertilization for some flowers in particular locations, while greater temporal variation in pollination would produce differences in ovule fertilization 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; Carvalho *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 standardized 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 (Carvalho *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 & Tscharrntke 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 solitary bees (Gathmann & Tscharrntke 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; Carvalho *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; Bluethgen & 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 stabilized productivity of entomophilous crop species.

## Acknowledgments

LAG was supported by the German Academic Exchange Programme (DAAD) and AMK by the German Science Foundation (KL 1849/4-1). This work is part of the working group Restoring Pollination Services led by CK and NM Williams at the National Center for Ecological Analysis and Synthesis (NCEAS NSF grant no. DEB-00-72909). The study is part of the STEP- (Status and Trends of European Pollinators, grant no. 244090 – STEP – CP – FP) and ALARM-projects (Assessing Large scale Risks for biodiversity with tested Methods, grant no. GOCE-CT-2003-506675) funded by the European Commission in the 6<sup>th</sup> and 7<sup>th</sup> Framework Programmes for Research and Technological Development. Three anonymous reviewers provided encouraging and constructive comments.

## References

- Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006). Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.*, 9, 968-80.
- Aizen, M.A. & Harder, L.D. (2007). Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *Ecology*, 88, 271-281.

- Arthur, A.D., Li, J., Henry, S. & Cunningham, S.A. (2010). Influence of woody vegetation on pollinator densities in oilseed *Brassica* fields in an Australian temperate landscape. *Basic Appl. Ecol.*, 11, 406-414.
- Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D. & Schmid B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.*, 9, 1146-1156.
- Blanche, R. & Cunningham, S.A. (2005). Rain forest provides pollinating beetles for atemoya crops. *J. Econ. Entomol.*, 98, 1193-1201.
- Blanche, K.R., Ludwig, J.A. & Cunningham, S.A. (2006). Proximity to rainforest enhances pollination and fruit set in orchards. *J. Appl. Ecol.*, 43, 1182-1187.
- Blüthgen, N. & Klein, A.M. (2011). Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.*, in press. (online first available).
- Bogdanski, A. (2005). The influence of landscape context on flower visitation and pollination of *Passiflora edulis* Sims f. *flavicarpa* Degener in central Bahia, Brazil. Department of Animal Ecology and Tropical Biology, University of Würzburg, Würzburg.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., *et al.* (2010). Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. Lond. B, Biol. Sci.*, 277, 2075-82.
- Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., *et al.* (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agricult. Ecosys. Environ.*, 133, 40-47.
- Carvalho, L.G., Seymour, C.L., Veldtman, R. & Nicolson, S.W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J. Appl. Ecol.*, 47, 810-820.
- Carvalho, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S. & Nicolson, S.W. (2011). Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.*, 14, 251-259.
- Chacoff, N.P. & Aizen, M.A. (2006). Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.*, 43, 18-27.
- Chacoff, N.P., Aizen, M.A. & Aschero, V. (2008). Proximity to forest edge does not affect crop production despite pollen limitation. *Proc. R. Soc. Lond. B, Biol. Sci.*, 275, 907-913.
- Chagnon, M., Gingras, J. & De Oliveira, D. (1993). Complementary aspects of strawberry pollination by honey and indigenous bees (Hymenoptera). *J. Econ. Entomol.*, 86, 416-420.
- Cresswell, J.E., Osborne, J.L. & Goulson, D. (2000). An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecol. Entomol.*, 25, 249-255.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998). The statistical inevitability of stability-diversity relationships in community ecology. *Am. Nat.*, 151, 264-276.

- Ebeling, A., Klein, A.M., Schumacher, J., Weisser, W.W. & Tschardtke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117, 1808-1815.
- Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecol. Biogeogr.*, 19, 589-606.
- Garibaldi, L.A., Aizen, M.A., Klein, A.M., Cunningham, S.A. & Harder, L.D. (2011). Global growth and stability in agricultural yield decrease with dependence on pollinator services. *Proc. Natl. Acad. Sci. USA*, 108, 5909-5914.
- Gathmann, A. & Tschardtke, T. (2002). Foraging ranges of solitary bees. *J. Anim. Ecol.*, 71, 757-764.
- Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *J. Ecol.*, 94, 295-304.
- Greenleaf, S.S. & Kremen, C. (2006a). Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biol. Conserv.*, 133, 81-87.
- Greenleaf, S.S. & Kremen, C. (2006b). Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci. USA*, 103, 13890-13895.
- Greenleaf, S.S., Williams, N.M., Winfree, R. & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, 153, 589-596.
- Griffin, J.N., O'Gorman, E.J., Emmerson, M.C., Jenkins, S.R., Klein, A.M., Loreau, M. & Symstad, A. (2009). Biodiversity and the stability of ecosystem functioning. In: *Biodiversity, ecosystem functioning, and human wellbeing - an ecological and economic perspective* (eds. Naeem S., Bunker, D.E., Hector, A., Loreau, M. & Perrings, C.) Oxford University Press, pp. 78-93.
- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J. & Tilman, D. (2011). Plant diversity and the stability of foodwebs. *Ecol. Lett.*, 14, 42-46.
- Hoehn, P., Tschardtke, T., Tylianakis, J.M. & Steffan-Dewenter, I. (2008). Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. Lond. B, Biol. Sci.*, 275, 2283-2291.
- Isaacs, R. & Kirk, A.K. (2010). Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J. Appl. Ecol.*, 47, 841-849.
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009). Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecol. Lett.*, 12, 443-51.
- Jauker, F., Diekötter, T., Schwarzbach, F. & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecol.*, 24, 547-555.
- Klein, A.M. (2009). Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecol. Manag.*, 258, 1838-1845.

- Klein, A.M., Steffan-Dewenter, I. & Tscharntke, T. (2003a). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. Lond. B, Biol. Sci.*, 270, 955-961.
- Klein, A.M., Steffan-Dewenter, T. & Tscharntke, T. (2003b). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.*, 90, 837-845.
- Klein, A.M., Cunningham, S.A., Bos, M. & Steffan-Dewenter, I. (2008). Advances in pollination ecology from tropical plantation crops. *Ecology*, 89, 935-43.
- Klein, A.M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. B, Biol. Sci.*, 274, 303-313.
- Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., *et al.* (2005). Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Syst.*, 36, 467-497.
- Kremen, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecol. Lett.*, 8, 468-479.
- Kremen, C., Williams, N.M. & Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA*, 99, 16812-16816.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, 7, 1109-1119.
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., *et al.* (2007). Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecol. Lett.*, 10, 299-314.
- Lehman, C.L. & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *Am. Nat.*, 156, 534-552.
- Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000). WinBUGS - A Bayesian modelling framework: Concepts, structure, and extensibility. *Stat. Comput.*, 10, 325-337.
- Mayfield, M.M. (2005). The importance of nearby forest to known and potential pollinators of oil palm (*Elaeis guineënsis* Jacq.; Areceaceae) in southern Costa Rica. *Econ. Bot.*, 59, 190-196.
- McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228-233.
- Meyer, B., Jauker, F. & Steffan-Dewenter, I. (2009). Contrasting resource-dependent responses of hoverfly richness and density to landscape structure. *Basic Appl. Ecol.*, 10, 178-186.
- Morandin, L.A. & Winston, M.L. (2005). Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications*, 15, 871-881.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., *et al.* (2008). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *J. Appl. Ecol.*, 45, 784-792.

- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.*, 25, 345-353.
- Proulx, R., Wirth, C., Voigt, W., Weigelt, A., Roscher, C., Attinger, S., *et al.* (2010). Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. *PLoS ONE*, 5, e13382.
- Pyke, G.H. (1984). Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Syst.*, 15, 523-575.
- R Development Core Team (2010). R: A language and environment for statistical computing. Available at: <http://www.r-project.org/>.
- Ricketts, T.H. (2004). Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.*, 18, 1262-1271.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Michener, C.D. (2004). Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. USA*, 101, 12579-12582.
- Ricketts, T.H., Williams, N.M. & Mayfield, M.M. (2006). Connectivity and ecosystem services: crop pollination in agricultural landscapes. In: Connectivity for Conservation (eds Sanjayan M. & Crooks K.). Cambridge University Press, Cambridge, UK, pp. 255–289.
- Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., *et al.* (2008). Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.*, 11, 499-515.
- Royal Society of London (2009). *Reaping the benefits: science and the sustainable intensification of global agriculture*. The Royal Society, London, UK.
- Steffan-Dewenter, I. & Kuhn, A. (2003). Honeybee foraging in differentially structured landscapes. *Proc. R. Soc. Lond. B, Biol. Sci.*, 270, 569-575.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421-1432.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629-632.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.*, 8, 857-874.
- Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. (2006). Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia*, 149, 289-300.
- Westphal, C., Bommarco, R., Carré, G., Lamborin, E., Morison, N., Petanidou, T., *et al.* (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.*, 78, 653-671.
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L. & Potts, S.G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol. Conserv.*, 143, 2280-2291.

- Winfree, R., Williams, N.M., Dushoff, J. & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.*, 10, 1105-1113.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. (2008). Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.*, 45, 793-802.
- Winfree, R. & Kremen, C. (2009). Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. Lond. B, Biol. Sci.*, 276, 229-237.
- Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G. & Aizen, M.A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, 90, 2068-2076.
- Zhang, W., Ricketts, T., Kremen, C., Carney, K. & Swinton, S. (2007). Ecosystem services and dis-services to agriculture. *Ecol. Econ.*, 64, 253-260.

## Supporting information

The following Supporting Information is available for 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.



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

Please note: Blackwell Publishing is not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

## Figure legends

**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 standardized 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 ( $\mu_{\beta}$ , black). In the x-axis of the right hand panel, “tropical” = tropical and subtropical studies, “med” = Mediterranean studies, and “temp” = temperate studies.

**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 standardized by z – scores prior to analysis. Right panels show individual study ( $\beta_i$ ) and overall ( $\mu_{\beta}$ ) 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.

**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 standardized 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 ( $\mu_{\beta}$ , black). In the x-axis of the right hand panel, “tropical” = tropical and subtropical studies, “med” = Mediterranean studies, and “temp” = temperate studies.

Fig. 1

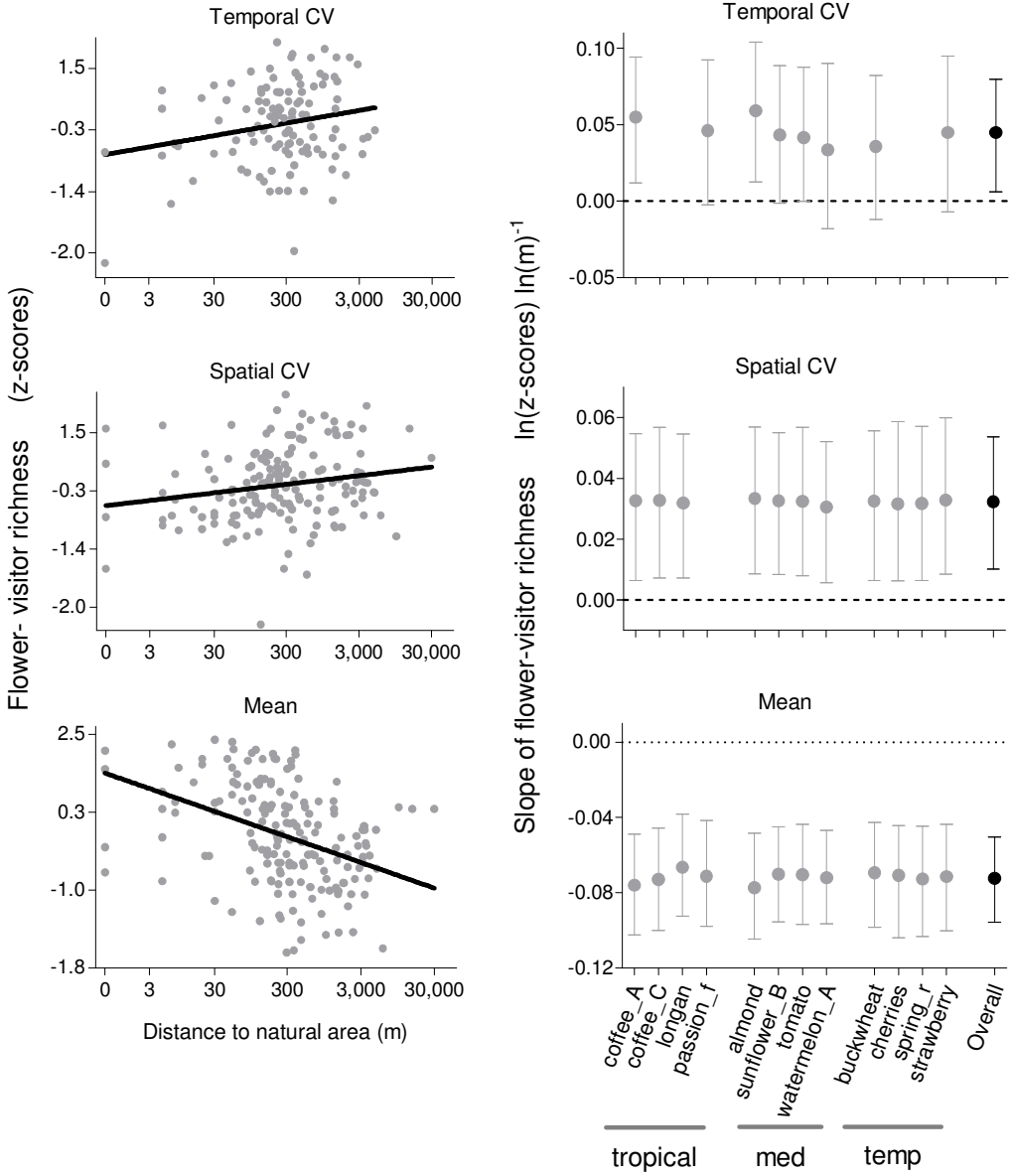


Fig. 2

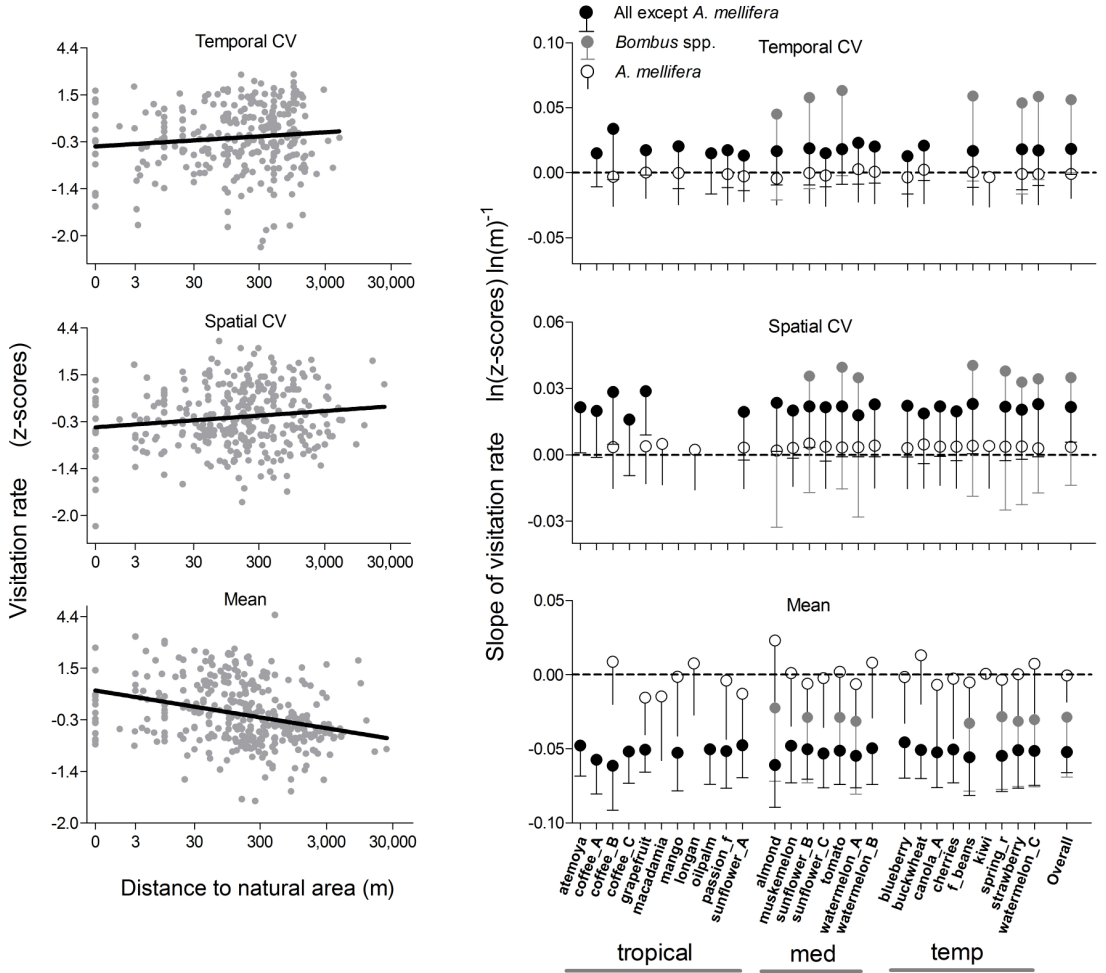
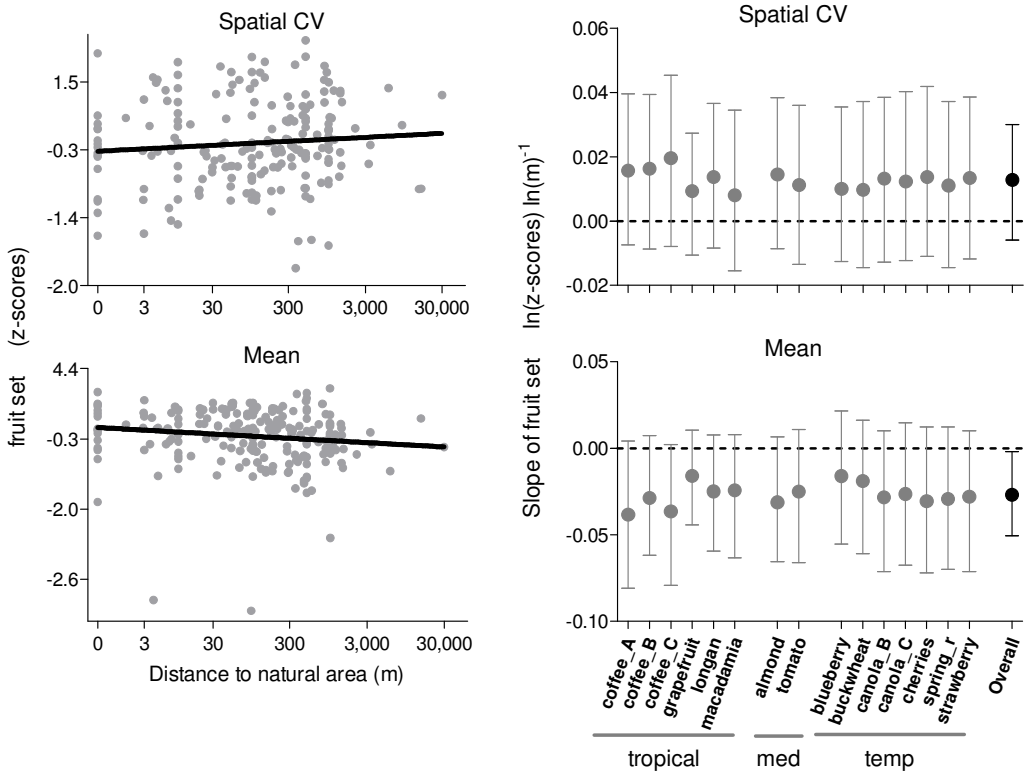


Fig. 3



**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	Reference	Crop species	Key flower-visitors	Managed, feral? <sup>‡</sup>	<i>A. mellifera</i> visits	(semi-) natural areas	Distance range (m)	Location	Spatial CV: no. replicates, sub-replicates <sup>§</sup>	Temporal CV: no. replicates, sub-replicates <sup>§</sup>
<b>Tropical and subtropical biomes</b>										
Atemoya	Blanche & Cunningham 2005	<i>Annona squamosa</i> x <i>A. cherimola</i>	Small beetles, especially Nitidulidae	No, yes	0%	Tropical rain forest	100 – 24,000	Australia, Queensland	9, 30-50 trees	No data
Coffee (A) highland	Klein <i>et al.</i> 2003a; Klein 2009	<i>Coffea arabica</i>	<i>Apis</i> spp., <i>Trigona</i> spp., Halictidae, solitary bees	No, no	0%	Tropical rain forest	0 – 1,415	Indonesia, Sulawesi	24, 3-4 trees	24, 5
Coffee (B) highland	Ricketts 2004; Ricketts <i>et al.</i> 2004 <sup>†</sup>	<i>Coffea arabica</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	40%	Tropical, premontane moist forest	3 – 1,392	Costa Rica	20, 5-9 trees	28, 5
Coffee (C) lowland	Klein <i>et al.</i> 2003b	<i>Coffea canephora</i>	<i>Apis</i> spp., <i>Trigona</i> spp., Halictidae, solitary bees	No, no	0%	Tropical rain forest	0 – 1,415	Indonesia, Sulawesi	15, 3-4 trees	No data
Grapefruit	Chacoff & Aizen 2006; Chacoff <i>et al.</i> 2008	<i>Citrus paradisi</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	95%	Subtropical, premontane forest	0 – 1,000	Argentina, Salta	40, 10 trees	60, 6
Longan	Blanche <i>et al.</i> 2006	<i>Dimocarpus longan</i>	<i>A. mellifera</i> , stingless bees (Meliponini)	No, yes	49%	Tropical rain forest and savannah	100 – 30,000	Australia, Queensland	6, 4 trees	No data
Macadamia	Blanche <i>et al.</i> 2006	<i>Macadamia integrifolia</i>	<i>A. mellifera</i>	No, yes	>99%	Tropical rain forest and savannah	10 – 16,000	Australia, Queensland	5, 4 trees	No data
Mango	Carvalho <i>et al.</i> 2010 <sup>†</sup>	<i>Mangifera indica</i>	Ants, mainly <i>Camponotus</i> spp	Yes, yes	8%	Semi-dry savannah	100 - 660	South Africa	No data	6, 2

and *Monomorium* spp.

Oil palm	Mayfield 2005	<i>Elaeis guineensis</i>	<i>Elaeidobius kamerunicus</i>	No, yes	<1%	Tropical forest	9 - 200	Costa Rica	No data	7, 2-4
Passion fruit	Bogdanski 2005; Ricketts <i>et al.</i> 2008 <sup>†</sup>	<i>Passiflora edulis</i>	Carpenter bees ( <i>Xylocopa</i> spp.)	No, yes	24%	Dry shrubland forest	129 - 617	Brazil, Bahia	No data	16, 3
Sunflower (A)	Carvalho <i>et al.</i> 2011 <sup>†</sup>	<i>Helianthus annuus</i>	<i>A. mellifera</i>	Yes, yes	85%	Semi-dry savannah	30 – 1,500	South Africa	24, 12 plants	24, 2
<b>Mediterranean biome</b>										
Almond	Klein_unp <sup>†</sup>	<i>Prunus dulcis</i>	<i>A. mellifera</i> , <i>Andrena cerasifolii</i> , Halictidae, Andrenidae, Syrphidae and other flies	Yes, yes	36%	Chaparral scrub, oak savannah, riparian woodland	7 - 2,221	USA, California	17, 2 positions (edge vs. interior)	18, 3
Muskmelon	Kremen in Ricketts <i>et al.</i> 2008 <sup>†</sup>	<i>Cucumis melo</i>	<i>A. mellifera</i> , <i>Bombus</i> spp., <i>Halictus</i> spp.	Yes, yes	95%	Chaparral scrub, oak savannah, riparian woodland	49 – 3,000	USA, California	8, 2 transects	No data
Sunflower (B)	Greenleaf & Kremen 2006b <sup>†</sup>	<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%	Chaparral scrub, oak savannah, riparian woodland	30 – 9,863	USA, California	19, 4 transects	8, 2
Sunflower (C)	Mandelik_unp_A <sup>†</sup>	<i>Helianthus annuus</i>	<i>A. mellifera</i> , <i>Lasioglossum</i> spp.	Yes, no	96%	Shrubland, dwarf	20 - 440	Central Israel	4, 2 positions (edge vs.	11, 2

Tomato (cherry)	Greenleaf & Kremen 2006a <sup>†</sup>	<i>Solanum lycopersicum</i>	<i>Anthophora urbana</i> , <i>Bombus vosnesenskii</i>	Yes, yes	0%	shrubland Chaparral scrub, oak savannah, riparian woodland	30 – 3,939	USA, California	interior) 13, 4 transects	16, 3
Watermelon (A)	Kremen <i>et al.</i> 2002; Kremen <i>et al.</i> 2004 <sup>†</sup>	<i>Citrus lanatus</i>	<i>A. mellifera</i> , <i>Bombus</i> spp., <i>Halictus</i> spp.	Yes, yes	68%	Chaparral scrub, oak savannah, riparian woodland	49 – 4,800	USA, California	46, 3-4 transects	15, 2
Watermelon (B)	Mandelik_unp_B <sup>†</sup>	<i>Citrus lanatus</i>	<i>A. mellifera</i> , <i>Lasioglossum</i> spp., <i>Ceratina</i> spp.	Yes, no	85%	Shrubland, dwarf shrubland	20 - 290	Central Israel	8, 2 positions (edge vs. interior)	10, 2
<b>Other temperate biomes<sup>¶</sup></b>										
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 <sup>†</sup>	<i>Fagopyrum esculentum</i>	<i>A. mellifera</i>	Yes, yes	92%	Deciduous forest	5 – 1,500	Poland, Lubelszczyzna	10, 10 transects	9, 4
Canola (A)	Arthur <i>et al.</i> 2010 <sup>*</sup>	<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 <sup>*</sup>	<i>Brassica napus</i>	Many wild bees, including species of <i>Andrena</i> ,	No, no	<2%	Aspen woodland, grassland, shrubland, wetland	35 - 210	Canada, Alberta	18, 12 plant pairs	No data
Canola (C)		<i>Brassica rapa</i>	<i>Halictus</i> , and <i>Bombus</i>				24 - 65		8, 12 plant pairs	No data



Cherry	Holzschuh_un p <sup>†</sup>	<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 – 1,875	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 x ananassa</i>	<i>A. mellifera</i>	Yes, no	80%	Calcareous grassland, orchard meadows, fallow	147 - 719	Germany, Lower Saxony	8, 6 transects	8, 4
Watermelon (C)	Winfree <i>et al.</i> 2007; Winfree <i>et al.</i> 2008 <sup>‡</sup>	<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.

<sup>†</sup> Studies used to model the distance ~ proportional area relationship, as they measured both variables.

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

<sup>§</sup> 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.

<sup>¶</sup> 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).