REVIEW AND SYNTHESIS

Landscape effects on crop pollination services: are there general patterns?

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Abstract

Pollination by bees and other animals increases the size, quality, or stability of harvests for 70% of leading global crops. Because native species pollinate many of these crops effectively, conserving habitats for wild pollinators within agricultural landscapes can help maintain pollination services. Using hierarchical Bayesian techniques, we synthesize the results of 23 studies – representing 16 crops on five continents – to estimate the general relationship between pollination services and distance from natural or semi-natural habitats. We find strong exponential declines in both pollinator richness and native visitation rate. Visitation rate declines more steeply, dropping to half of its maximum at 0.6 km from natural habitat, compared to 1.5 km for richness. Evidence of general decline in fruit and seed set – variables that directly affect yields – is less clear. Visitation rate drops more steeply in tropical compared with temperate regions, and slightly more steeply for social compared with solitary bees. Tropical crops pollinated primarily by social bees may therefore be most susceptible to pollination failure from habitat loss. Quantifying these general relationships can help predict consequences of land use change on pollinator communities and crop productivity, and can inform landscape conservation efforts that balance the needs of native species and people.

Keywords

Agriculture, bees, ecosystem services, habitat fragmentation, hierarchical Bayesian model, land use, pollinators.

INTRODUCTION

Crop pollination is a clear example of an ecosystem service – an economic benefit that nature provides to people (Millennium Ecosystem Assessment 2005). Bees and other pollinating animals supply a valuable input to agricultural production that can increase both the size and quality of harvests (Allen-Wardell *et al.* 1998). Crops as diverse as tomatoes, coffee, canola, watermelons and cacao show improved production with animal pollination (NRC 2007).

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Indeed, Klein *et al.* (2007) found that 87 of 115 leading global crops benefit significantly from pollinators, representing 35% of the food supply. Pollinator visits not only move outcross pollen among individuals but also increase the total amount of pollen deposited on flower stigmas, both of which are known to increase quantity and quality of crops (NRC 2007).

Agricultural intensification and land conversion pose one of the largest threats to the earth's ecosystems (Tilman 1999; Green *et al.* 2005). These changes within agricultural landscapes endanger biodiversity directly, but they may also threaten the productivity, diversity and stability of our food production systems by disrupting pollinator communities. Indeed, population reductions in native bees have already been reported in several regions of the world (Biesmeijer *et al.* 2006; NRC 2007). Understanding the magnitude, patterns and mechanisms of pollination services – as well as other benefits ecosystems provide to agriculture – is therefore crucial to the future of food production (Allen-Wardell *et al.* 1998; Kremen *et al.* 2007; Zhang *et al.* 2007).

While crop pollinators include a range of insects (e.g. beetles, flies, butterflies), as well as birds and bats, the majority of crops are most effectively pollinated by bees (Klein *et al.* 2007). Honeybees (*Apis mellifera*) and other managed species are often used to ensure adequate pollination, but many crops are also effectively pollinated by wild bees (both native species and feral honeybees; Kevan *et al.* 1990; Free 1993; Freitas & Paxton 1998; Ricketts 2004). Watermelon, for example, receives pollination services from > 30 species of native bees in addition to *A. mellifera* (Kremen *et al.* 2002), and native bumblebees are much more effective pollinators of blueberry crops than honeybees (Cane & Payne 1988). Furthermore, several diseases have reduced both feral and managed populations of honey bees (Watanabe 1994; Cook *et al.* 2007). The most serious of these is the *Varroa* mite, but the recent and mysterious Colony Collapse Disorder has also caused precipitous honeybee declines in the USA in recent years (Johnson 2007). Given these alarming trends, it is increasingly important to understand the services provided by native pollinators.

Maintaining these pollination services requires the conservation and management of sufficient resources for wild pollinators within agricultural landscapes. These resources include suitable nesting habitats (e.g. tree cavities, suitable soil substrates) as well as sufficient floral resources (i.e. pollen and nectar; Kremen *et al.* 2007). Furthermore, bees are central-place foragers (i.e. returning to fixed nest sites after foraging), so proximity of nesting habitats relative to agricultural fields is critical for bee-pollinated crops (Ricketts *et al.* 2006). Farms within typical foraging distance of suitable habitat may therefore receive enhanced pollination services, while those further away may not.

Several recent studies have examined whether crop pollination services decline with increasing isolation from natural habitats. For example, Ricketts and colleagues (Ricketts 2004; Ricketts *et al.* 2004) found that bee diversity, visitation rate, pollen deposition rate and fruit set are all significantly greater in coffee fields near tropical forest than in fields further away. However, other studies have found little effect of landscape pattern on pollinator visitation. For example, Winfree *et al.* (2007b) found little effect of landscape pattern on pollination services to vegetable crops in the northeastern USA. This observed variance in results is likely due to differences among studies in pollinator communities, plant breeding systems, land use practices within farms and study methods.

Despite differences among studies, distilling general patterns from recent research is important and informative for both ecology and conservation. From an ecological perspective, such a synthesis can provide a predictive understanding of pollinator foraging ranges, effects of land use on pollinator communities and related ecosystem functions, and the landscape ecology of pollinator interactions (Steffan-Dewenter 2003; Kremen 2005; Tscharntke *et al.* 2005; Brosi *et al.* 2007; Greenleaf *et al.* 2007; Steffan-Dewenter *et al.* 2007). For conservation, this information could make clear the benefits derived by farmers from areas of natural or semi-natural habitats, resulting in more complete cost-benefit analyses regarding land use change (Morandin & Winston 2006). Furthermore, it can inform land use planners who seek to balance the needs of both biodiversity and farmers by ensuring adequate habitat protection and sustainable ecosystem service production (Chan *et al.* 2006; Naidoo & Ricketts 2006; Priess *et al.* 2007). Because resources do not exist to conduct separate studies in every landscape, syntheses of current work that allows rigorous predictive 'rules of thumb' are essential.

Here, we synthesize the findings of studies on the spatial relationship between natural habitats and crop pollination services. We found 23 studies, representing 16 crops on five continents, that measured pollinator activity or resulting crop yields along isolation gradients from natural habitat. Using a common exponential decay model and hierarchical Bayesian techniques, we estimate the general relationship between isolation and pollination services. In particular, we ask three major questions. First, do pollinator richness, pollinator visitation rate and fruit or seed set decline significantly with increasing distance from natural habitat? Second, if so, over what scales do these declines occur? And third, how do observed patterns differ between tropical and temperate crops, and between social and solitary bees?

MATERIALS AND METHODS

Studies

Starting in June 2005 with updates through October 2007, we used literature searches and knowledge of the authors to gather studies that relate some measure of crop pollination services with isolation from natural habitat. Our goal was to be comprehensive, knowing that we may have failed to detect studies that were yet to be published, or that had been published in journals not abstracted by the ISI. We found 23 relevant studies (Table 1), representing 16 different crops grown in nine countries. Thirteen studies took place in temperate biomes, while 10 were tropical. In all but three studies, pollinators were bees. The exceptions are studies named 'Blanche 2005', in which flower visitors were beetles in the family Nitidulidae, 'Mayfield 2005', in which visitors included flies, bees, beetles, ants and an introduced weevil, and 'Kremen unpub (a)', in which visitors included bees and flies. One additional study (De Marco & Coelho 2004) addresses similar questions but was not explicit about degrees of isolation from natural habitat, so we were unable to include it.

Eighteen studies are published in peer-reviewed journals, while five are unpublished manuscripts or theses. We do not further describe the published studies here. Below we provide descriptions of unpublished studies to supply context for our synthesis. We corresponded directly with authors of all studies to ensure that data were appropriate for our purposes and to collect necessary data formatted for our purposes; the only exception was for Heard & Exley (1994), where we used data from published tables.

In the study coded 'Bogdanski 2005' (Table 1; Bogdanski 2005), the pollination of yellow passion fruit (*Passiflora edulis* Sims) was investigated in Juazeiro, Brasil. The passion fruit variety studied was self-incompatible and pollinated largely by carpenter bees (*Xylocopa*; Klein *et al.* 2007). Bogdanski (2005) measured pollinator visitation rates and fruit set in 16 sites that varied from 274 m to 1678 m in distance from natural 'Caatinga', a dry shrubland forest habitat. In each site, visitation rates of social bees *(Apis mellifera, Trigona spinipes)* and solitary bees *(Xylocopa griesencis, X. frontalis)* were estimated from three 15-min observation periods on three different days, each with good weather. All observations were made between 12:00 (flower opening) and 16:00. Fruit set was measured as the proportion of flowers that produced marketable fruits, taken over a sample of 30 unmanipulated (i.e. without experimental hand pollination or pollinator exclusion) flowers in each site.

For 'Gemmill-Herren in press', Gemmill-Herren & Ochieng (in press) investigated the pollination of eggplant (*Solanum melongena*) in Nguruman, Kenya. Eggplant flowers are hermaphroditic and self-compatible, but benefit from visitation of bees that can effectively extract pollen from its poricidal anthers through buzz pollination (Buchmann 1983). Gemmill-Herren & Ochieng (in press) measured pollinator visitation rates in 15 sites that varied from < 20 to > 100 m in distance from the riverine *Acacia* forests from which the crop fields had originally been cleared. Visitation rates of all visitors were estimated by observing all flowers in a meter-square plot for 10 min, and *c.* 240 such samples were taken at each site.

For 'Greenleaf unpub', methods are described adequately in Greenleaf & Kremen (2006b). For 'Kremen unpub (a)' (Table 1), Kremen (unpublished data) investigated bee and fly visitation to almond (*Prunus dulcis*) in Yolo County, California in 2004. The almond varieties studied were hermaphroditic but self-incompatible and were visited by a variety of wild bees (10 field-identified species-groups) and flies (10 species-groups). Managed honey bees had been placed by farmers at most sites and were abundant at all sites. Pollinator visitation rates were sampled in 16 sites that varied in distance from 14 to 989 m from natural habitat including riparian, oak-woodland and chaparral shrub vegetation. In each site, visitation rates of social and solitary bees and flies were estimated from 10 whole tree scans per site (*c.* 1 min per tree) on a single day between 10:00 and 15:00 during good weather.

For 'Kremen unpub (b)' (Table 1), Kremen (unpublished data) investigated bee visitation to muskmelon (*Cucumis melo*) in Yolo County, California. Muskmelon is monoecious and is visited by a variety of wild bee species (14 species from vouchered specimens). Managed honey bees had been placed by farmers at many sites, and were abundant at all sites. Kremen measured pollinator visitation rates in 12 sites that varied in distance from 48 to 3017 m from natural habitat including riparian, oak-woodland and chaparral shrub vegetation. In each site, visitation rates of social and solitary bees were estimated from four 10-min observation periods conducted on four separate 50 m transects within the field during one morning (9:00–12:00) and one afternoon (12:00–16:00) period per farm on two separate days during good weather. Rates were averaged per site across all transects and periods. [See (Kremen *et al.* 2002) for a detailed description of transect walk methodology].

Finally, for 'Potts unpub', Potts *et al.* (unpublished data) studied field bean (*Vicia faba*) pollination in the UK. Field beans are partially self-compatible and for the variety investigated (Clipper), seed set benefits from cross-pollination. Ten fields were studied and these were nested in an isolation gradient; distances to fragments (> 5 ha) of semi-natural vegetation ranged between 100 and 1875 m. Each field was surveyed four times during peak blooming and bee abundance in the crop was assessed using standardized water-filled pan traps. In parallel, seed and fruit set per

Table 1 Studies included in this synthesis. Study names match those used in figures

Study name (reference)	Crop name - common	Crop name - latin	Family	Breeding system	Key pollinators	location	Biome	Isolation*	Fruit set†	Analyses‡
Blanche 2005 (Blanche & Cunningham 2005)	Atemoya	*Annona squamosa* x *A. cherimola*	Annonaceae	Hermaphrodite, dichogamous, little self-pollination	Small beetles, especially Nitidulidae	Queensland, Australia	Tropical	Measured		r v
Blanche 2006a (Blanche *et al.* 2006)	Longan	*Dimocarpus longan*	Sapindaceae	Hermaphrodite	*A. mellifera*, stingless bees (Meliponini)	Queensland, Australia	Tropical	Measured	O-E	r v p
Blanche 2006b (Blanche *et al.* 2006)	Macadamia	*Macadamia integrifolia*	Proteaceae	Hermaphrodite, largely self-incompatible	*Apis mellifera*	Queensland, Australia	Tropical	Measured	O-E	r v p
Bogdanski 2005 (Bogdanski 2005)	Passion fruit	*Passiflora edulis*	Passifloraceae	Hermaphrodite, self-incompatible	*Xylocopa frontalis*, *X. griescens*	Brasil	Tropical	Secondary	O	v p s
Chacoff 2006 (Chacoff & Aizen 2006)	Grapefruit	*Citrus paradise*	Rutaceae	Hermaphrodite; variable self-compatibility	*A. mellifera*, stingless bees (Meliponini)	Argentina	Temperate	Measured	O	v p
Gemmill-Herren in press (Gemmill-Herren & Ochieng' in press)	Eggplant	*Solanum melongena*	Solanaceae	Hemaphrodite; self compatible; buzz pollinated	*Xylocopa caffra*, *Macronomia rufipes*	Kenya	Tropical	Measured		r v s
Greenleaf 2006a (Greenleaf & Kremen 2006a)	Cherry tomato	*Solanum lycopersicum*	Solanaceae	Hermaphrodite, self-compatible, buzz-pollination	*Anthophora urbana*, *Bombus vosnesenskii*	California, USA	Temperate	Secondary	O	r v p s
Greenleaf 2006b (Greenleaf & Kremen 2006b)	Sunflower	*Helianthus annuus*	Asteraceae	Dichogamous, self-compatible for hybrid seed	*Svastra* spp., *Diadasia* spp., *Melissodes* spp., *Bombus* spp., *Dialictus* spp., *Halictus* spp., *Megachile* spp., *Apis mellifera*	California, USA	Temperate	Secondary	O (seed)	p
Greenleaf unpub (S. Greenleaf, unpublished data)	Sunflower	*Helianthus annuus*	Asteraceae	Dichogamous, self-compatible for hybrid seed	*Svastra* spp., *Diadasia* spp., *Melissodes* spp., *Bombus* spp., *Dialictus* spp., *Halictus* spp., *Megachile* spp., *Apis mellifera*	California, USA	Temperate	Secondary		r v s

Table 1 (*Continued*)

Study names (reference)	Crop name – common	Crop name – latin	Family	Breeding system	Key pollinators	Location	Biome	Isolation*	Fruit set†	Analyses‡
Heard 1994 (Heard & Exley 1994)	Macadamia	*Macadamia integrifolia*	Proteaceae	Largely self incompatible	*A. mellifera, Trigona carbonaria*	QLD and NSW, Australia	Tropical	Modeled		r v
Klein 2003a (Klein et al. 2003a)	Coffee	*Coffea arabica*	Rubiaceae	Hermaphrodite, variable self-compatibility	*Apis* spp., *Trigona* spp., Halictidae	Sulawesi, Indonesia	Tropical	Measured	O	r v p s
Klein 2003b (Klein et al. 2003b)	Coffee	*Coffea canephora*	Rubiaceae	Hermaphrodite, variable self compatibility	*Apis* spp., *Trigona* spp., Halictidae	Sulawesi, Indonesia	Tropical	Measured	O	r v p s
Kremen 2002 (Kremen et al. 2002)	Watermelon	*Citrullus lanatus*	Cucurbitaceae	Monoecious, self-compatible	*A. mellifera, Bombus* spp., *Halictus* spp	California, USA	Temperate	Secondary		r v
Kremen 2004 (Kremen et al. 2004)	Watermelon	*Citrullus lanatus*	Cucurbitaceae	Monoecious, self-compatible	*A. mellifera, Bombus* spp., *Halictus* spp.	California, USA	Temperate	Secondary		r v
Kremen unpub (a) (C. Kremen, unpublished data)	Almond	*Prunus dulcis*	Prunaceae	Hermaphrodite, self-incompatible	*Andrena* spp., *Bombus* spp., *Halictus* spp., *Lasioglossum (Evylaeus)* spp., *Lasioglossum (Dialictus)* spp.	California, USA	Temperate	Secondary		r v
Kremen unpub (b) (C. Kremen, unpublished data)	Muskmelon	*Cucumis melo*	Cucurbitaceae	Monoecious or andro-monoecious, self-compatible	*Peponapis* spp., *Melisodes* spp., *Halictus* spp., *Agapostemon* spp., *Lasioglossum (Evylaeus)* spp., *Lasioglossum (Dialictus)* spp.	California, USA	Temperate	Secondary		r v
Mayfield 2005 (Mayfield 2005)	Oil Palm	*Elaeis guineensis*	Arecaceae	Monoecious	*Elaeidobius kamerunicus*	Costa Rica	Tropical	Measured		v
Morandin 2005 (Morandin & Winston 2005)	Canola	*Brassica napus, B. rapa*	Cruciferaceae	Hermaphrodite, largely self-incompatible	*Bombus* spp., *Megachile* spp., *Hylaeus* spp., *Anthophora* spp.	Alberta, Canada	Temperate	Modeled	H-O (seed)	r v p s
Morandin 2007 (Morandin et al. 2007)	Canola	*Brassica napus, B. rapa*	Cruciferaceae	Hermaphrodite, largely self-incompatible	*Lasioglossum* spp., *Andrena* spp., *Bombus* spp.	Alberta, Canada	Temperate	Modeled		r v s

Table 1 (*Continued*)

Study names (reference)	Crop name – common	Crop name – latin	Family	Breeding system	Key pollinators	Location	Biome	Isolation*	Fruit set†	Analyses‡
Potts unpub (S. Potts, unpublished data)	Field bean	*Vicia faba*	Fabaceae	Hermaphrodite, partially self-compatible	*Bombus* spp., *A. mellifera*	UK	Temperate	Measured	O (seed)	r v p s
Ricketts 2004 (Ricketts 2004; Ricketts *et al.* 2004)	Coffee	*Coffea arabica*	Rubiaceae	Hermaphrodite, variable self-compatibility	*A. mellifera*, stingless bees (Meliponini)	Costa Rica	Tropical	Measured	H-O	r v p
Ricketts 2006 (Ricketts *et al.* 2006)	Kiwifruit	*Actinidia deliciosa*	Actinidiaceae	Dioecious	*A. mellifera*	New Zealand	Temperate	Measured	O	r v p
Winfree 2007 (Winfree *et al.* 2007b)	Watermelon	*Citrulus lanatus*	Cucurbitaceae	Monoecious, self-compatible	*Bombus impatiens, Melissodes bimaculata, Peponapis pruinosa, Augochlora pura, Lasioglossum (Dialictus)* spp.	NJ and PA, USA	Temperate	Secondary	O	r v s

*'measured': linear measurements of distance were used in the original study; 'secondary': proportional area used in original study, but linear distance measurements supplied by authors; "modeled": only proportional area was used in original study, so linear distances modeled (see Methods).

†Measures of fruit or seed set used in original studies. See Methods for codes. "(seed)" denotes seed number as observed variable; all others used fruit set as observed variable.

‡Analyses in which each study was included. r, richness; v, native visitation rate; p, production (i.e., fruit or seed set); s, social vs. solitary bee comparison.

plant were measured in 20 plants per field under open pollination conditions.

Variables

From each study we extracted data, if available, on four variables: isolation from natural habitat, pollinator richness, pollinator visitation rates and fruit or seed set. Not all studies measured all variables (Table 1), so different analyses have different sample sizes. Furthermore, not all studies measured the same variable in the same manner; therefore, some standardization among studies was necessary and is described in the following paragraphs. Importantly, our modelling technique estimates relative, not absolute, changes in response variables (see below), such that no conversions were necessary among data ranges and units (e.g. number of minutes or flowers over which pollinator visitation is sampled).

For isolation, the original studies measured either linear distance (i.e. the distance from a study site to the nearest patch of natural habitat), or proportional area (i.e. the proportion of a circle of given radius that is covered by natural habitat). We followed each author's decisions regarding what constituted habitat for pollinators, which included a variety of natural and semi-natural habitats known to support bee populations. For simplicity, we refer to these as 'natural habitat'. To standardize among studies, we expressed isolation in all studies in terms of linear distance. Of the 23 studies, 11 already used linear distance as the primary measure of isolation (Table 1: 'measured' in Isolation column). In nine additional studies, authors preferred proportional area as the primary measure of isolation but also measured linear distances, which they provided us ('secondary'). Studies differed in the radius of circles used to estimate proportional area, and in the minimum habitat patch sizes considered in calculating linear distances. In all cases, we followed the decisions made by original authors (available in published papers or in paragraphs above), because they were best able to determine the relevant dynamics and scales for their studies.

Three studies measured isolation only in terms of proportional area. For these, we developed a simple predictive model of linear distance as a function of proportional area, based on data from the 10 studies that measured both variables (i.e. the nine studies marked 'secondary' in Table 1, plus 'Ricketts 2004'). We determined that log(distance/radius) is an approximately linear function of arcsine square-root (proportional area), where radius is the study-specific radius of circles used to estimate proportional area. We parameterized this relationship as a linear mixed-effects model (Pinheiro 2004), yielding fixed effect estimates of the slope and intercept while also allowing for study-level random variation in both coeffi-

cients. Restricted maximum-likelihood estimates of the fixed effects were then used to predict linear distance for each site in the three studies lacking distance data ('modelled' in Table 1).

For pollinator richness, we found suitable data in 19 of the 23 studies (Table 1). In each study, pollinators were identified to the most precise taxonomic level possible. In some cases, identifications were made to species, while in others, morphospecies or 'identifiable taxonomic units' were used to identify pollinators on the wing without disturbing their behaviour. Such estimates of morphospecies richness can underestimate or (less likely) overestimate richness, but when consistently applied allow rigorous comparisons of relative richness among sites (Oliver & Beattie 1996; Oliveira *et al.* 1997). Some studies exclude introduced *Apis mellifera* from richness estimates, while most studies include them. However, *A. mellifera* is typically found in every site if found in any, so their inclusion or exclusion has little effect on relative richness. For all but four studies, richness data are based on observed flower visitors, recorded over some interval of time and for some number of flowers or area (these were constant within studies but varied among them, but again our modelling approach is robust to these differences in sample effort; see below). For 'Morandin 2005' 'Morandin 2007' and 'Potts unpub', richness estimates were instead derived from pan traps and field netting in each site, and for 'Winfree 2007' from field netting. These methods do not directly capture flower visitors and therefore may introduce some bias (e.g. they may underestimate non-bee visitors). However, the crops included in these studies are independently known to be pollinated by bees (Table 1; Free 1993; Klein *et al.* 2007). Furthermore, some studies (e.g. 'Winfree 2007') performed visual flower surveys to confirm important visitors, and 'Morandin 2005' shows a strong relationship between seed set and pollinators sampled in this way (Morandin & Winston 2005; Winfree *et al.* 2007b).

For visitation rate, we limited our analysis to native species because our focus was wild bees and it is often difficult to determine whether honeybee visitors to flowers are from wild or managed colonies. We found suitable data for 22 of the 23 studies. Again, sampling effort (e.g. number of flowers observed, number of minutes and sample number) varied among studies, but was constant within each study. In most studies, visitation rate was calculated as the number of times a potential pollinator was observed landing on, foraging from, or touching a flower, and thus includes multiple visits by the same individual. In three studies, visitation rate data were not available, but pollinator abundance (collected by sweep netting, pan trapping, or both) was deemed as an appropriate proxy, because the data were collected within crop fields themselves, and because these two variables are often highly correlated (Ricketts

2004). These studies are 'Morandin 2005', 'Morandin 2007' and 'Potts unpub'.

For 10 studies, authors were able to provide visitation rates separately for social and solitary bees (Table 1). For these analyses, we generally defined 'social' bees as eusocial species (Michener 2000). For most studies, these species included *Apis* spp. (when native), *Bombus* spp., and stingless bees in the tribe Meliponini. For 'Greenleaf unpub' and 'Winfree 2007', *Halictus* and *Dialictus* species were also included when known to be social; species with unknown sociality were treated as solitary.

For fruit and seed set, we found suitable data in 12 of the 23 studies (Table 1). Nine of these studies measured fruit set, defined as the proportion of flowers that sets fruit. Three studies (Table 1) measured seed set, defined as the number of ovules that develop into marketable seeds. We combined both measures for this meta-analysis, because both indicate the effect of pollination services on crop productivity. Furthermore, units and sample effort varied among studies [e.g. some measured fruit set over a constant number of flowers (Ricketts *et al.* 2004), others did so over a constant length of raceme (Blanche *et al.* 2006), and one measured whole plant fruit set ('Potts unpub')], but again our modelling techniques focus on relative changes within each study, allowing combination of disparate measures of yield.

The 12 studies included both observational and experimental approaches to estimating fruit set, requiring us to standardize the results before meta-analysis. Eight of the 12 studies observed fruit or seed set of unmanipulated plants in each site (Table 1, denoted 'O' in 'Fruit set' column). This approach measures changes in fruit or seed set along an isolation gradient, but does not experimentally establish pollination services as the cause of these changes. Other variables such as soil quality or moisture, which may also be correlated with isolation, could explain this variation. Four studies also manipulated plants in each site to provide experimental control and thereby separate the effect of pollination services. Two of these studies hand-pollinated flowers, to compare production under ambient pollination to that with sufficient pollen supplied by hand. They report the difference between the hand-pollinated ('H') and open ('O') treatments (i.e. the degree of pollination limitation (Kearns & Inouye 1993; Burd 1994); Table 1, 'H–O'). Two additional studies excluded pollinators from flowers in each site, to compare ambient production to that without any pollinator service. They report the difference between the open ('O') and excluded ('E') treatments (Table 1, 'O–E').

Standardization is necessary because the observational studies measured changes in absolute fruit set along isolation gradients, while the experimental studies measure changes in the difference between ambient fruit set and a control. The same amount of relative change (say, 10%) in these different response variables imply different magnitudes of change in overall crop yield. Therefore, to put all response variables on equivalent terms, we calculated for each experimental study the study-wide mean of the control treatment (i.e. '$\bar{\text{H}}$' or '$\bar{\text{E}}$'; values available from the authors). Then, for each site in the study, we either added (for 'O–E' studies) the estimate of fruit/seed set to this mean, or subtracted (for 'H–O' studies) it from the mean. This process returns all fruit/seed set values to approximately absolute terms, allowing synthesis to proceed. More formally, for 'O–E' studies, the calculated absolute fruit set, O′, is:

$$O' = \bar{E} + (O - E)$$

and for 'H–O' studies, O′ is:

$$O' = \bar{H} - (H - O)$$

Modelling the exponential decay of fruit and seed set with increasing distance (see below), the intercept values derived using O′ differed less than 10% from those derived using O in each of the four studies. This indicates that $\bar{\text{H}}$ and $\bar{\text{E}}$ are approximately correct values for returning these difference values to their appropriate absolute terms.

Model

We examined separately the relationship between isolation and each of three different measures of wild pollination services: richness, visitation and fruit or seed set. In the methodological description below, we use the general term 'pollination' to refer to all of these variables, specifying the variable only when needed for clarity.

We used a basic model of exponential decline in pollination as a function of distance from nearest natural habitat. Although it is just one of several simple models that can be used to describe foraging patterns (Aronson & Givnish 1983), the exponential model is intuitively appealing for several reasons. First, it conforms to a simple mechanistic model of pollinators foraging out from natural habitat with constant stopping probability (Turchin 1998). Second, because this model is multiplicative rather than additive, there is no need to rescale pollinator data to account for differences in sampling units across studies. Finally, the model allows straightforward interpretation of the exponential decay parameter as a measure of how strongly isolation affects pollination. Results from this exponential model were indistinguishable from, or superior to, a power-law model (another common choice) in all but one study (see Appendix S1).

Although a unique site-specific relationship between isolation and pollination can be modelled for each individual study, our objective here is to quantify the general nature of

this relationship across all studies. We therefore constructed our analyses in the form of a Bayesian hierarchical model (Gelman *et al.* 1995; Carlin *et al.* 2006). Hierarchical models provide an efficient and natural way to handle grouped data, especially when the goal is to make inferences across groups (i.e. across studies). In typical modelling approaches one must choose between pooling the data into a single analysis or fitting models to each group separately; hierarchical models strike a compromise between these extremes, achieving a 'partial pooling' that reflects the relative magnitudes of within-group vs. among-group variance terms (Gelman & Hill 2007). An advantage of a Bayesian approach is that it explicitly models the uncertainty in among-group variance, rather than proceeding with a point estimate of this term (as is performed in mixed effects models).

At the first level of the model, we use the equation

$$Y_{ij} = \exp(\alpha_i + \beta_i D_{ij}) + \varepsilon_{ij}$$

where Y_{ij} is an observed pollination datum j in the ith study, D_{ij} is the associated distance (in meters) from nearest natural habitat, α_i is a study-specific intercept term, β_i is rate of change in pollination service with increasing distance from natural habitat and ε_{ij} is a fitted error term. Analogous to a generalized linear model, this can be rewritten to give $\ln(Y)$ as a linear function of distance, with an appropriate error distribution on Y (see Appendix S1).

The model is hierarchical in that we do not fit the β_i terms separately for each study, but instead assume that they are themselves normally distributed across studies:

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta^2).$$

To complete the Bayesian specification, we assigned the following non-informative priors to model parameters in all cases:

$$\alpha_i \sim \text{Normal}(0, 10\,000)$$

$$\mu_\beta \sim \text{Normal}(0, 10\,000)$$

$$\sigma_\beta \sim \text{Uniform}(0, 100)$$

$$a_i \ \text{Uniform}(0, 100)$$

The posterior distribution of each model parameter was simulated using Markov chain Monte Carlo (MCMC; Gilks *et al.* 1996). Bayesian computation was carried out in WINBUGS 1.4 (Spiegelhalter *et al.* 2003), with all other data processing and computation performed using the R statistical environment (R Development Core Team 2006) and the R2WinBUGS package (Sturtz *et al.* 2005). For each model, we simulated two MCMC chains for 20 000 iterations after a burn-in of 10 000 iterations, thinning the results by a factor of 20 to reduce autocorrelation in the sample. To check for convergence of the MCMC chain, we confirmed that $\bar{R}$ is approximately equal to 1.0 for the estimands (Gelman *et al.* 1995; Gelman 1996).

We focus our interpretations on the resulting posterior distributions of β_i and μ_β. The means of each β_i give estimates of the study-specific decay rates, taking into account information from all studies. Because we use a hierarchical model, these values will differ from those obtained by fitting each study-specific dataset separately; notably, β estimates for studies with smaller sample sizes and/or greater residual variation will be more strongly pulled toward the overall mean (μ_β; see Fig. S1–S3). In turn, the mean of μ_β represents the average decay rate across studies, where the relative influence of each study depends on its sample size and the precision of its local model fit. This quantity can be regarded as our best estimate of the overall effect of isolation on pollination. Throughout, we refer to β_i and μ_β as 'decay rate' and 'overall decay rate' respectively.

For all relevant parameters, we report the 90% credible interval (CI), a range containing the middle 90% of simulated posterior values. Similar to a confidence interval in more traditional statistics, a Bayesian CI expresses the level of uncertainty in a parameter. For μ_β, note that the CI does *not* describe the variability in decay rates among studies (this is captured by σ_β), but indicates the range of likely values of the overall decay rate itself. Finally, for the overall decay rates we report the proportion of simulated posterior values that are less than zero. This can be directly interpreted as the probability, given our data and model formulation, that greater isolation is associated with reduced pollination on average.

Comparative analyses

To assess differences in the effect of isolation in temperate vs. tropical settings, we repeated the above analyses using separate Gaussian distributions for the two sets of decay parameters:

$$\beta_{i,b} \sim \text{Normal}(\mu_{\beta,b}, \sigma_{\beta,b}^2)$$

where biome b is either temperate or tropical. All other aspects of the model are as described above. Note that this is equivalent to analyzing tropical and temperate subsets of the data separately, insofar as no parameters depend jointly on data from both biomes. To quantify whether mean decay parameter differed between biomes, we calculated $\mu_{\beta,trop} - \mu_{\beta,temp}$ across all MCMC draws of the posterior distribution, and determined the proportion that exceed zero.

We implemented a final version of the model to allow for different responses of social vs. solitary bees. Unlike the

biome model, this model includes sociality as a nested factor within study:

$$Y_{ij} = \exp(\alpha_i + (\beta_i + I\Delta_i)D_{ij}) + \varepsilon_{ij}$$

where I is an indicator variable for visitation by solitary ($I = 0$) vs. social ($I = 1$) bees. As in previous models, we assume the β_i terms are normally distributed across studies. However, in this case, we further assume that the study-specific differences in decay rate between solitary and social bees, represented by Δ_i, also vary across studies as

$$\Delta_i \sim \text{Normal}(\mu_\Delta, \sigma_\Delta^2).$$

Using the MCMC draws of μ_Δ directly, we calculated the expected difference between the decay rates of social and solitary bee visitation, and the probability that the decay in social bee visitation is steeper than the decay in solitary bee visitation.

RESULTS

For pollinator richness, we find that decay rate estimates vary widely among studies but that means are negative in 16 of 19 cases, indicating a decline of pollinator richness with increasing isolation from natural habitat (Fig. 1a). The 90% credible intervals also vary widely among studies, indicating differences in certainty around these estimates. Based on all studies, we find strong evidence of decline in pollinator richness with increasing isolation (Fig. 1a, bottom; entire credible interval < 0). We use this overall decay rate estimate to plot expected pollinator richness against isolation, and find a relatively steep decline (Fig. 1b). The distance at which pollinator richness drops to half of its maximum value (i.e. at distance = 0) is 1507 m (Table 2).

For visitation rate by native pollinators, we again find wide variation among studies, both in terms of decay rate estimates and 90% credible intervals around them (Fig. 2a). Nevertheless, in 20 of the 22 studies decay rate estimates are negative. Overall, we find strong evidence of a decline in native visitation rate with increasing isolation from natural habitat (Fig. 2a, bottom). Using this overall estimate to plot expected native visitation rate against isolation, we find an even steeper decline than that for pollinator richness (Fig. 2b). The distance at which native visitation rate drops to half of its maximum value is less than half that for richness: 668 m (Table 2). Twenty studies also recorded visitation rates of introduced bees, mostly *A. mellifera*. Including these visits, overall visitation rates still decline with distance for natural habitat, but less steeply ($\mu_\beta = -0.00032$; point of 50% decline = 2170 m).

For fruit and seed set of crops, studies again vary widely both in terms of decay rate estimates and credible intervals (Fig. 3a), but decay rates are negative in eight of 12 studies. Overall, we find less clear evidence of decline in fruit and
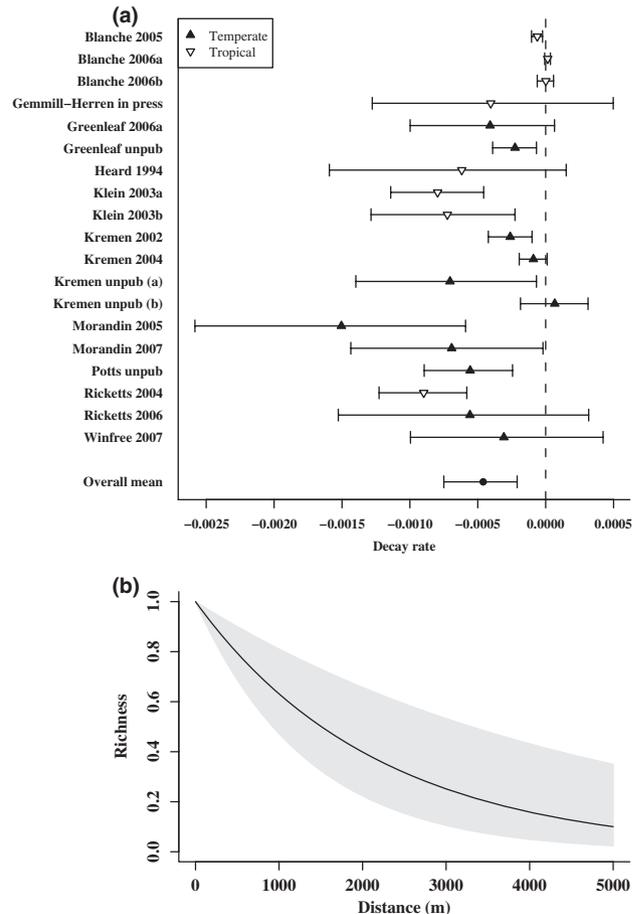
Figure 1 Relationship between pollinator richness and isolation from natural habitat. (a) Decay rate (β_i) and 90% credible interval for each study in which pollinator richness was measured ($n = 19$). Overall decay rate (μ_β) for all studies is shown at bottom. (b) Richness decay curve, based on overall decay rate and 90% credible interval from panel a. The distance at which richness drops to 50% of the maximum is 1507 m (Table 2).

seed set with increasing isolation, with the 90% credible interval around our overall estimate overlapping zero (Fig. 3a, bottom). Using this overall decay rate to plot fruit and seed set as a function of isolation, we find a shallower decline than found in either richness or visitation rate. Indeed, the calculated distance at which fruit and seed set drops to half of its maximum value is 26 826 m (Table 2). Repeating these analyses with open fruit set for all studies (instead of calculating O′ for the four experimental studies; see Materials and methods) does not qualitatively change these results (data not shown).

We used our models to compare patterns of native visitation rates between temperate and tropical studies, and found strong evidence of decline with isolation in both biomes. Our overall decay rate estimate is steeper (i.e. more negative) for tropical studies than for temperate (Fig. 2a,

Table 2 Estimates of overall decay rate (μ_β) for pollinator richness, native pollinator visitation rate, and crop fruit or seed set, based on hierarchical Bayesian models

Variable	N	μ_β	Pr ($\mu_\beta < 0$)*	Point of 50% decay (m)†
Richness	19	−0.00046	> 0.999	1507 (921–3332)
Visitation rate	22	−0.00104	0.996	668 (395–1727)
Temperate	11	−0.00053	0.971	1308 (437–13849)
Tropical	11	−0.00118	0.959	589 (296–8186)
Social	10	−0.00158	0.985	439 (240–1791)
Solitary	10	−0.00117	0.946	591 (274–ND)
Fruit/seed set	12	−0.00003	0.698	26 826 (5038–ND)

*Posterior probability that overall decay rate (μ_β) is less than zero.
†Distance at which variable is 50% of the maximum value at distance = 0, along with 90% credible interval. ND signifies an undefined upperbound, occurring for studies in which the credible interval contains zero.

bottom); with points of 50% decline at 589 m and 1308 m, respectively (Fig. 4; Table 2). Credible intervals overlap substantially (Figs 2a, 4), but in Monte Carlo sampling the overall decay rate for tropical studies was more negative than the overall temperate decay rate in 80.1% of samples (see Materials and methods; data not shown). This indicates an 80.1% probability that the overall visitation decay rate is steeper in tropical studies.

Using the 10 studies that sampled social and solitary bees separately, we found evidence (albeit somewhat weak) that visitation rates of social bees decline more steeply than those of solitary bees (Fig. 5). The overall decay rate is more negative for social than solitary bees in all 10 studies, and the point of 50% decline is lower (439 m vs. 591 m; Table 2). While credible intervals around decay estimates overlap substantially (Fig. 5b), the interval for social bees does not overlap 0, while that for solitary does. Finally, in Monte Carlo sampling, overall decay rates for social bees were more negative than for solitary bees in 95.1% of samples.

Several studies reported significant declines of one or more variables in the original publications, but show less strong evidence of decline here (i.e. 90% credible intervals overlap zero in Figs 2 or 3). This seeming contradiction is largely because we report results from the full Bayesian hierarchical analysis, rather than individual model fits to each study. Because each study influences the fits of the others, the results of all studies are 'pulled' toward the overall mean, more so for studies with smaller sample sizes or larger residual variances (see Materials and methods). In addition, original studies often used different analytical approaches (e.g. different models, or categorical rather than continuous distance measures). Our work is intended not to re-analyze previous studies, but to synthesize them to illuminate general patterns.
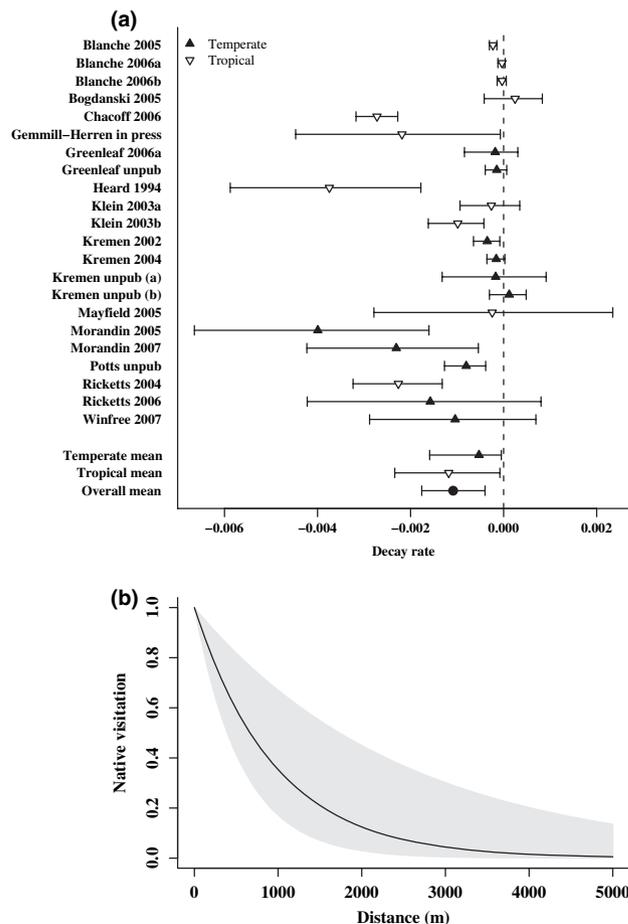
Figure 2 Relationship between native pollinator visitation rate and isolation from natural habitat. (a) Decay rate (β_i) and 90% credible interval for each study in which pollinator visitation was measured ($n = 22$). Overall decay rate (μ_β) for all studies, as well as that for tropical and for temperate studies, are shown at bottom. (b) Native visitation decay curve, based on overall decay rate and 90% credible interval from panel a. The distance at which native visitation rate drops to 50% of the maximum is 668 m (Table 2).
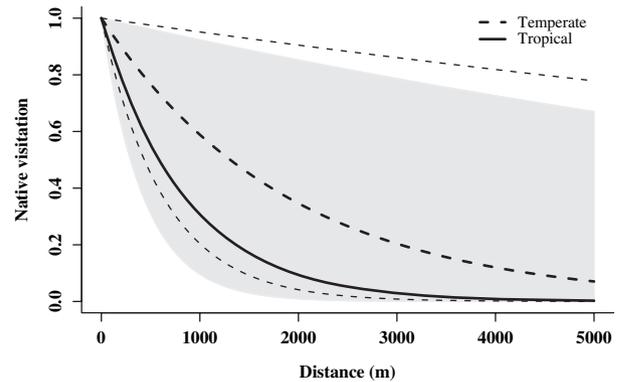
DISCUSSION

Our syntheses reveal that pollinator richness and visitation rate on crops show general and significant exponential declines with increasing distance from natural habitat. We found weaker evidence for overall decline in fruit and seed set, although in some studies distance effects were substantial. Tropical studies displayed steeper decays in visitation rates than did temperate studies, and visits by social bees decayed more steeply than those by solitary bees. These findings represent the 'consensus' of existing studies, but individual studies vary widely. Nevertheless, the emerging general relationships we find can be used to predict consequences of past or future land use change on pollinators and crop productivity, and can inform landscape
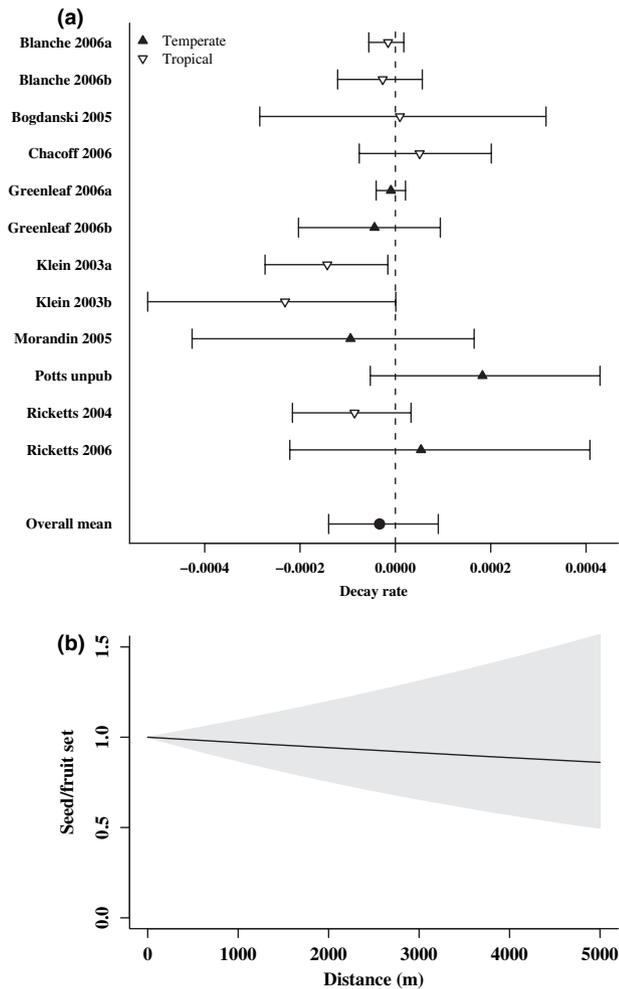
Figure 3 Relationship between fruit or seed set and isolation from natural habitat. (a) Decay rate (β*ᵢ*) and 90% credible interval for each study in which fruit or seed set was measured (*n* = 12). Overall decay rate (μ_β) for all studies is shown at bottom. (b) Fruit/seed set decay curve, based on overall decay rate and 90% credible interval from panel a. The calculated distance at which fruit or seed set drops to 50% of the maximum is 26 826 m (Table 2).

Figure 4 Decay curves for native visitation rates in tropical and temperate studies, based on overall decay rates (μ_β) and 90% credible intervals in Fig. 2a. Solid line and shading: tropical studies (*n* = 11); dashed line and lighter dashed lines: temperate studies (*n* = 11). Distances at which native visitation drops to 50% of the maximum is 589 m (tropical) and 1308 m (temperate; Table 2).

conservation efforts that aimed at balancing the needs of native species and people.

We found strong support for a general decay of pollinator richness as distance from natural habitat increased (Fig. 1). This decay suggests that, on average, fields 1.5 km away from natural habitat patches can be expected to contain 50% of the pollinator diversity of fields closest to these patches (Table 2). As distances from natural habitat increase, fewer pollinator species are able to either forage to that distance or nest in fields so isolated from native resources. Indeed, evidence from one study (Larsen *et al.* 2005) suggests that in California watermelon fields, the

species most often absent from isolated fields also tend to be the most efficient pollinators, exacerbating the effect of declining richness on pollination services. However, some pollinators appear able to use resources within managed areas themselves and persist at any distance from natural habitat (Klein *et al.* 2003a; Kremen *et al.* 2004; Morandin *et al.* 2007), and one reason for variation among studies may be the degree to which managed areas provide resources supporting wild bees. In general, the overall scale of the effect we find corresponds to estimates of foraging distance for specific bees (Greenleaf *et al.* 2007); for example, Greenleaf & Kremen (2006b) estimated that the largest common sunflower pollinator has a maximum foraging distance of 3000 m and a typical foraging distance of 1500 m.

Visitation rates of native pollinators also declined with increasing distance from natural habitat (Fig. 2). Visitation rate is probably a more direct indicator of pollination services than richness, because it measures the frequency of actual pollinator visits to flowers (Vazquez *et al.* 2005). We found that overall decay in native visitation rate was steeper than that estimated for richness, falling to 50% of its maximum value at < 1 km (668 m) from natural habitat (Table 2). These results indicate that native pollinators, although present at distant farms, often occur at low abundances and therefore provide fewer visits in more isolated fields (Ricketts 2004). These relatively infrequent visitors may represent individuals foraging to uncommon distances from nests in natural habitat, or small (perhaps sink) populations persisting within agricultural fields (Pulliam 1988; Ricketts *et al.* 2006). Including *A. mellifera* and other introduced pollinators in these analyses, we still found that visitation rates declined, but much less steeply
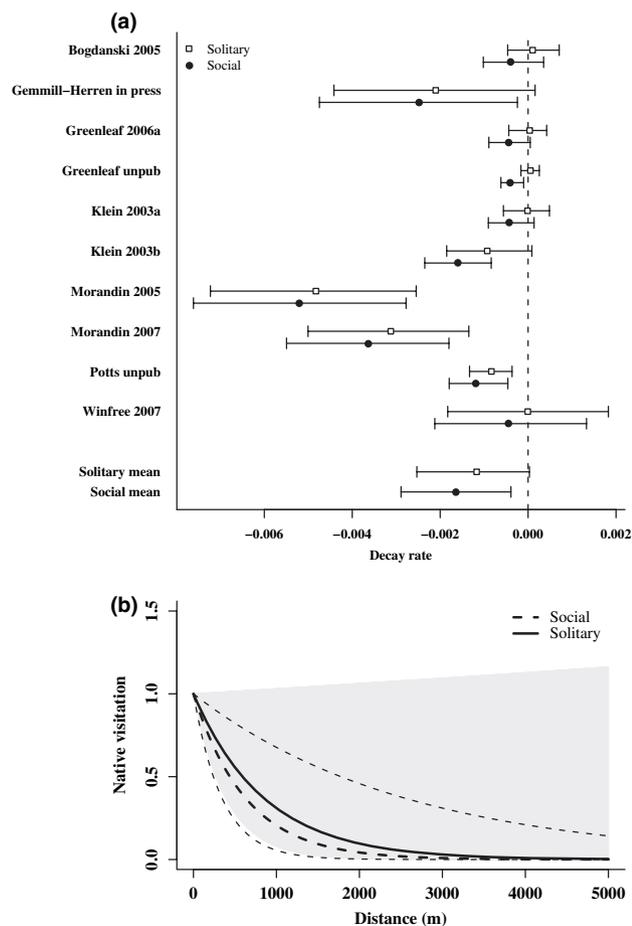
Figure 5 Differences between social and solitary bees in the relationship between native visitation rate and isolation from natural habitat. (a) Decay rate (β_i) and 90% credible interval for social and solitary bees for each study in which visitation rates of both were measured ($n = 10$). Overall decay rates (μ_β) for social and solitary bees are shown at bottom. (b) Visitation decay curves for social and solitary bees, based on overall decay rates and 90% credible intervals from panel A. Solid line and shading: solitary bees; dashed line and lighter dashed lines: social bees. Distances at which visitation rate drops to 50% of the maximum is 439 m (social) and 591 m (solitary; Table 2).

(data not shown). This supports several reports that *A. mellifera*, with relatively large foraging ranges and the ability to nest within farms, are less sensitive to the amount of nearby habitat than many native species (Steffan-Dewenter & Kuhn 2003; Ricketts 2004).

Pollinator richness and visitation rate indicate levels of pollinator activity, but the most meaningful measures of actual pollination services relate to crop productivity itself. Only 12 of the 23 studies included fruit or seed set as direct measures of crop productivity. While some studies showed substantial declines in fruit or seed set with increasing

distance from natural habitat (Fig. 3a), evidence of overall decline was less clear (Fig. 3b).

Why did we not find stronger decline in fruit and seed set, despite steep declines in native pollinator visitation? Introduced *A. mellifera* (either managed or feral populations, which were both excluded from our visitation analyses, see Results) may provide sufficient pollination throughout agricultural landscapes, even though abundance of native pollinators is low in farms distant from natural habitat. Even in studies without managed honeybees, relatively low richness and abundance of wild pollinators may be sufficient to pollinate distant fields, making crops less reliant on abundant native pollinators than is often thought. Diverse pollinator communities, however, may nevertheless provide more stable pollination services over time, buffering crops against population fluctuations in, or extinction of, any given pollinator species (Kremen *et al.* 2002; Ricketts 2004; Fontaine *et al.* 2006). Indeed, the current precipitous declines in *A. mellifera* in the United States due to Colony Collapse Disorder are making clear the dangers of relying on a single pollinator species (Johnson 2007; NRC 2007). In addition, many crops are pollinated by a range of taxa in addition to bees (e.g. beetles, flies, bats; Free 1993; NRC 2007). These taxa likely respond differently to landscape isolation and other factors, so a diversity of pollinator taxa may help reduce the effects of land use change on pollination services.

Several additional reasons for the difference in our visitation and fruit/seed set results relate to data availability and analysis. First, simple exponential decay may not be an appropriate model for fruit and seed set, because it assumes an eventual decay to 0. Many of the crops studied are partially self-compatible (Table 1) and thus would be expected to decline instead to some non-zero asymptote. Fitting a simple exponential model to such data forces an artificially low decay estimate. We investigated more complex models that included a parameter for a non-zero asymptote, but these demand a higher sample size of studies that we had available. Second, perhaps the subset of studies that investigated fruit or seed set have weaker declines in visitation rate, such that visitation and fruit/seed set results in fact match for these studies. However, overall decay rate in native visitation is slightly steeper among this subset of studies ($\mu_\beta = -0.00120$) than among all studies (Table 2; $\mu_\beta = -0.00104$). Finally, there are fewer studies included in this analysis, reducing its power relative to the richness and visitation rate analyses. Despite these factors potentially reducing the decay signal, our posterior probabilities show the most likely consensus among all studies to be a slight decline in fruit and seed set with increasing isolation.

Comparing native visitation between temperate and tropical studies, we found clear declines in both but a steeper decay rate in the tropics (Figs 2b, 4). Indeed, our

models predict tropical visitation rate to drop to 50% of its maximum at less than half the distance as the temperate visitation rate (Table 2). Understanding the reasons for this difference will require further study, but these results suggest some intriguing possibilities that relate to nesting substrates, floral resources, and foraging behaviour. First, social bees are important pollinators in both the temperate and tropical zones. In the tropical studies included here, however, social bees were often Meliponines (i.e. 'stingless bees'), which largely rely on natural habitat, because they prefer to nest in tree cavities and have relatively short foraging radii (Roubik & Aluja 1983; Heard 1999; Eltz *et al.* 2003). In the temperate zones, native social bees were often dominated by *Bombus* (i.e. bumblebees), which are able to nest in ground cavities and other substrates more available in modified habitats, and which often display relatively large foraging radii (Westphal *et al.* 2006). Second, floral resources may be more plentiful in tropical agricultural landscapes, which are typically more vegetatively complex, less intensively managed, and more species-rich. Potential crop pollinators nesting in natural habitat may therefore have less incentive to fly longer distances into crop fields than those in the temperate zone. Finally, environmental differences (e.g. temperature, humidity) between farms and adjacent natural habitat may be stronger in tropical than temperate zones. These differences may discourage tropical pollinator species, adapted to moist tropical forests, from nesting or foraging in relatively hot and dry modified areas, while temperate species may experience fewer such barriers (Fagan *et al.* 1999). Whatever the reason, our findings indicate that tropical farmers may lose crop pollinators more quickly from land use change and the resulting isolation of their farms from natural habitat.

Social bees are dominant pollinators of many crops in both temperate and tropical areas (Free 1993; Roubik 1995). We found that visitation rates of native social bees consistently decline more steeply with increasing distance than those of solitary bees (Fig. 5). The difference in decay rate is slight overall, but pronounced in some studies; for example, in 'Klein 2003a' the point of 50% decline for social bees occurred at < 1/20 the distance as that for solitary bees (data not shown, Klein *et al.* 2003a). Indeed, for five of the 10 studies, no decay was detected at all for solitary bees (Fig. 5). In the tropics this pattern is consistent with nesting tendencies of native social bees, which are more likely to nest in cavities within and beneath mature trees and therefore prefer natural habitat (Wille & Michener 1973; Griswold *et al.* 1995; Michener 2000), while solitary bees often nest in the ground or in hollow stems that can occur in disturbed areas such as agricultural fields and borders (Michener 2000; Potts *et al.* 2005; Morandin *et al.* 2007). There are plenty of exceptions, however, including solitary carpenter bees (*Xylocopa*) that nest in

mature or dead wood (Bogdanski 2005) and temperate bumble bees, dominant social pollinators that mainly nest in the soil or in herbaceous vegetation (Michener 2000). Another possibility is that social bees, often with relatively long flight seasons, require the phenological diversity of floral resources provided in natural habitat, while solitary bees, with shorter flight seasons, may be able to complete reproduction within the blooming period of crops and therefore nest within crop fields (Cane 1997). The reasons for the differences we observed likely vary among pollinator faunas, landscapes, crops and biomes, complicating the interpretation of these synthetic results. Nevertheless, our findings indicate that tropical crops pollinated primarily by social bees may be most susceptible to pollination failure due to surrounding land use change.

In pursuing this synthesis, we identified important research needs to further illuminate general landscape effects on pollinator activity and pollination services. First, more studies are needed that directly measure the effects of pollinators on crop productivity, ideally through controlled experiments. Pollinator richness and visitation clearly decline sharply with increasing isolation from natural habitat (Figs 1, 2), but we found only weak evidence that this affected crop productivity (Fig. 3). In part, this is because only 12 of the 23 studies measured fruit or seed set, and only four of these were experimental (i.e. comparing productivity under ambient pollination to controls where pollen is either added or excluded). Such studies are labour intensive, but they are critical to understanding the ultimate ecosystem service of crop pollination. Additional work in this area will provide more power to future syntheses to quantify the effects of pollinator losses on crop productivity. Second, establishing consistent methods for pollination studies would simplify syntheses substantially (Kearns & Inouye 1993). Differences among studies in sample sizes, measurement units, experimental approaches and types of controls impede effective synthesis and progress toward predictive, general understanding of this important ecological and conservation issue. Third, these studies (and therefore our synthesis) focused on isolation of crops from natural habitat, but more information is needed on the effects of habitat size and quality (Tscharntke *et al.* 2005). Patches in most agricultural landscapes vary in both their size and the resources they offer pollinator populations (Kremen *et al.* 2004). Disturbed areas, and agricultural fields themselves, can offer nesting and floral resources (Cane 1997; Westphal *et al.* 2003; Brosi *et al.* 2007; Williams & Kremen 2007), but the quality of these resources will depend on farming practices (e.g. pesticide applications, tillage; Holzschuh *et al.* 2007). Evaluating the contributions of all these landscape elements to pollinator populations and crop pollination would allow more informed management of agricultural landscapes for both biodiversity and pollination services.

The syntheses we report here represent the consensus findings of the literature to date, but landscape effects on pollination services can vary substantially and in ways still poorly understood. For example, Kremen *et al.* (2002) found a strong positive relationship between nearby natural habitat and pollinator activity in California, while Winfree *et al.* (2007a), using similar methods on the same crop in the northeastern USA, found no such effect. Individual results that differ from the consensus or from expectation can also indicate important additional factors. For example, passion fruit is self-incompatible and in Bogdanski's (2005) study is pollinated almost entirely by carpenter bees nesting in tree cavities. One would therefore expect a farm's proximity to forest to strongly influence pollinator activity and yields. However, no such relationship was found (Figs 2, 3), in part because high insecticide use in the fields reduced bee populations and blurred any landscape signal. The general findings reported here must therefore be applied to specific situations with care.

Despite these differences among studies, syntheses such as those we conduct here remain valuable. Our findings indicate that we can expect declines, on average, in pollinators and crop pollination if further land use change increases the isolation of farms from natural habitat. These declines can be counteracted by conserving areas of natural or semi-natural habitat near farms, by managing farms themselves to support pollinators, or by adding managed pollinators to the landscape. Our consensus decay rates can also serve as parameters for general models of ecosystem service delivery across changing landscapes (Naidoo & Ricketts 2006; Priess *et al.* 2007). They can inform conservation plans that seek to balance the needs of biodiversity and people, identifying win–win areas where conservation can benefit both, as well as areas of trade off where difficult choices must be made (Chan *et al.* 2006; Steffan-Dewenter *et al.* 2007). They can help predict the positive and negative impacts of conservation actions on nearby farmers. And they can inform the design of further experiments and point out research priorities, as we continue to learn about the ecosystem services provided by native pollinators and the habitats that support them.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

A pdf file containing the following:
- **Figure S1** Relationship between pollinator richness and isolation for each study.
- **Figure S2** Relationship between native pollinator visitation and isolation for each study.
- **Figure S3** Relationship between fruit/seed set and isolation for each study.

Appendix S1 Captions for figures S1, S2 and S3, and decay model comparison.

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